The Peruvian Upwelling Ecosystem: Dynamics and Interactions

Edited by

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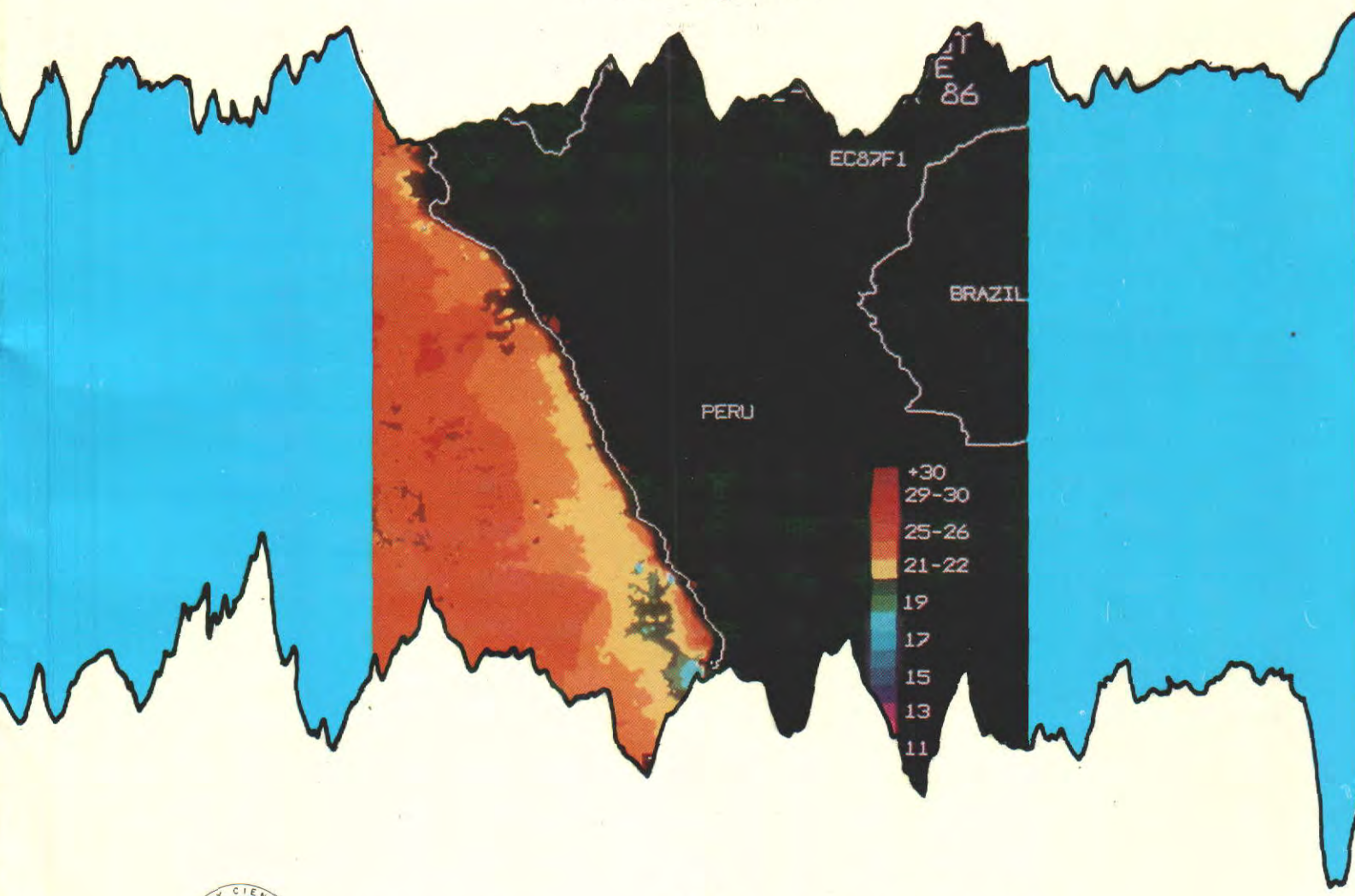

Instituto del Mar del Peru

Deutsche Gesellschaft für Technische Zusammenarbeit GmbH

International Center for Living Aquatic Resources Management

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1989

INSTITUTO DEL MAR DEL PERÚ (IMARPE)
CALLAO, PERÚ

DEUTSCHE GESELLSCHAFT FÜR TECHNISCHE ZUSAMMENARBEIT (GTZ), GmbH
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INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT
MANILA, PHILIPPINES

Reproduction of the Peruvian Anchoveta

Other Studies on the Peruvian Anchoveta

Ecology, Dynamics and Anchoveta Consumption of Peruvian Hake

Ecology and Exploitation of Large Vertebrates off Peru

Syntheses: Towards Management of the Peruvian Upwelling Ecosystem

Appendices

*Prepared by V.C. Sambilay, Jr., ICLARM, MC P.O. Box 1501, Makati, Metro Manila, Philippines.

Prologo del IMARPE

Entre las múltiples tareas de IMARPE, una de la más importantes es aquella de proveer asesoramiento cientifíco concerniente a la pesqueria industrial, basada esencialmente en el recurso anchoveta, una de las fuentes más importantes de ingreso de divisas para el Perú.

El personal cientifico del IMARPE y el de su predecesor, el Instituto de Investigación de los Recursos Marinos (IREMAR), han estudiado la biología, dinámica y habitat de la anchoveta, desde los inicios de los años 50. Los conocimientos obtenidos a través de estas investigaciones y los informes emitidos, han ayudado a nuestro gobierno en la formulación de regulaciones para el manejo de la pesquería pelágica durante esta turbulenta historia.

A lo largo de su historia, IMARPE ha albergado proyectos cooperativos de investigación con instituciones extranjeras y ha acogido con beneplacito a científicos del exterior. Ello ha robustecido nuestra productividad y ha coadyuvado a afianzar los contactos internacionales, sin lo cual hoy en día, no podrian conducirse investigaciones sólidas y profundas.

En los años 80, nuestro principal colaborador del exterior ha sido el personal de la Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), con sede en IMARPE a través del Proyecto Cooperativo Peruano-Alemán de Investigación Pesquera (PROCOPA). Ellos, y sus contrapartes peruanas, han producido desde 1982 a la fecha, alrededor de 90 contribuciones sobre diversos aspectos de los recursos del sistema peruano de afloramiento (ver Apéndice II de este libro). Estamos muy complacidos con esta alta producción.

Este magnífico libro, que es el 4° volumen publicado por PROCOPA y que contiene 11 contribuciones de PROCOPA, representa un adecuado broche final del proyecto más productivo que IMARPE ha llevado a cabo en los ultimos anos.

Este libro, al mismo tiempo, inicia una nueva fase para nuestras investigaciones. Sobre la base de los datos y análisis que este contiene, asi como aquellos incluidos en su volumen compañero publicado en 1987, harán posible finalmente, desarrollar el modelo de simulación orientado al manejo de los recursos pesqueros del sistema peruano de afloramiento.

El International Center for Living Aquatic Resources Management (ICLARM), con ayuda de GTZ, nos apoyarán en esta tarea.

A juzgar por el alto nivel alcanzado en la producción de este libro y el de su predecesor, y por la oportunidad en que se presentan, confiamos que este plan que producirá un modelo de simulación para el manejo de nuestra pesquería pelágica será exitosamente implementado y esperamos con gran interés su culminación.

Deseo tomar esta oportunidad para expresar a nombre de IMARPE, nuestro agradecimiento a GTZ e ICLARM por el esfuerzo puesto de manifiesto en este libro; particularmente al Dr. Salzwedel, penúltimo jefe de PROCOPA, por su apoyo al taller de trabajo que condujo a la publicación de este libro; al Dr. P. Muck, último jefe de PROCOPA, por nuestra fructífera cooperación; a Jaime Mendo e Isabel Tsukayama, por su aporte científico y editorial; a los participantes y observadores del taller de trabajo antes mencionado y habilmente presidido por J. Csirke de FAO. Deseo agradecer también a los Drs. M. Bilio y W. Schmidt de la sede central de GTZ por su incesante apoyo a PROCOPA, al US National Marine Fisheries Service por las contribuciones de varios de sus científicos, y por último en orden pero no en importancia, nuestro profundo agradecimiento al Dr. D. Pauly, por concebir el taller de trabajo que generó este libro y por el impulso brindado a todo el equipo comprometido hasta finalizar con las más de 400 páginas de esta obra.

Jaime Sobero Taira

GTZ Foreword

The pace of progress towards a comprehensive understanding of the Peruvian upwelling ecosystem is astounding: after only a decade of intensive research efforts, a fourth book on the subject can be published in the context of Peruvian-German cooperation in fisheries research. The former books were:

i. "El Niño, Su Impacto en la Fauna Marina", edited by W. Arntz, A. Landa and J. Tarazona (Bol. Inst. Mar Perú - Callao, Vol. extraord. 1985);

ii. "The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change", edited by D. Pauly and I. Tsukayama (ICLARM Studies and Reviews 15, 1987);

iii. "Recursos y Dinámica del Ecosistema de Afloramiento Peruano", edited by H. Salzwedel and A. Landa (Bol. Inst. Mar Perú - Callao, Vol. extraord. 1988).

The present volume is another example of the catalyzing effect of ICLARM on international research cooperation, proving the effectiveness of a determined and methodologically well-organized approach to a clearly defined goal.

The four volumes, as the more bulky parts of a total of over 90 scientific contributions, are the most conspicuous evidence of the large written output produced by the Programa Cooperativo Peruano-Aleman de Investigación Pesquera (PROCOPA), funded by the German Ministry for Economic Cooperation (BMZ) and executed jointly by the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH and the Instituto del Mar del Perú (IMARPE). It is hoped that the wealth of information contained in these publications will be recognized and used by the competent authorities for the purpose for which it was produced: to serve as an indispensable management basis for a rational and sustained exploitation of the unique fishery resources of the sea off Peru.

Scientific progress of today is pushed ahead by an ever increasing potential of information analysis and interpretation through electronic data elaboration. Contrary to a former tendency to publish only secondary (or elaborated) data, it appears now more useful to make the entire sets of original data available to the scientific public in order to allow for future possibilities of even more sophisticated or otherwise differently-oriented analysis. Many tables of the present volume attest to the application of this principle, as was already the case in the second book of the above list.

The compilation of the present volume is considered the last step before the development of a simulation model for the management of the fishery resources of the Peruvian upwelling system. To develop such a model, all relevant biological, ecological, fishery and economic information will be integrated into one model, which will be parameterized using data sets now available as well as data that will emerge in the near future. With the help of this system, it should be possible to appraise at any time the advantages and disadvantages of different management options, taking into consideration the current size and fishery potential of the stocks, the ecological situation (and expected changes) in the distribution area, the requirements of economical fishing-fleet management, the fish prices on domestic and international markets and other relevant parameters. The task of making this concluding step has been entrusted to IMARPE and ICLARM staff.

In the Peruvian-German cooperation in fisheries research, a considerable number of internationally renowned scientists from countries other than Peru and the Federal Republic of Germany have been involved. Substantial amounts of original data have been contributed by researchers of the USA (see Pauly and Tsukayama 1987). In view of the extensive activities of Soviet research vessels off the Peruvian coast, it would be of great importance to have public access to pertinent data collected in research efforts made by the Soviet Union. This could probably contribute to an even broader and more complete view of the ecosystem, in particular by inclusion of additional information on the straddling stocks of mackerel and horse mackerel living within and outside of the Exclusive Economic Zone (EEZ) and affecting the anchoveta stocks as well.

I conclude by thanking those at IMARPE, PROCOPA and ICLARM who organized and ran the August 1987 workshop on "Models for Yield Prediction in the Peruvian Ecosystem" which led to this book, as well as the editors of this magnificent volume.

Martin Bilio

ICLARM Foreword

This book is the second volume produced by ICLARM dealing exclusively with Latin American resources. Like its predecessor, ("The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change", edited by D. Pauly and I. Tsukayama, ICLARM Studies and Reviews 15, 1987), this book presents studies based on long time series which are fully documented in the form of tables included in each contribution. This volume goes beyond its predecessor, however, in that all of its figures and tables have English and Spanish legends. Also, the report of the workshop upon which this book is based, is presented in Spanish (see Csirke et al., this vol.). We hope this will make this book more accessible than its predecessor to our colleagues in Latin America and, in particular, Peru.

In addition, the editors have included as Appendix I of this book a brief documentation of twelve 5-1/4" diskettes for MSDOS (i.e., IBM PC compatible) microcomputers, available to outside researchers for a modest fee from ICLARM, and which contain all data used by the authors of contributions included in this volume and its predecessor. The editors hope, as do we at ICLARM, that this will encourage researchers in Peru and elsewhere to perform further and deeper analyses of these data; such analyses will benefit them as much as it will benefit, in the long term, the management of the Peruvian fisheries.

ICLARM is extremely pleased to have been able to contribute to the considerable efforts which went into the production of this volume. Particularly, I would like to express our thanks to Mr. Jaime Sobero Taira, Executive Director of IMARPE, and his predecessor, Mr. Rogelio Villanueva, for their support of the August 1987 workshop which led to this volume, and of the subsequent activities of this project; to Mr. Jaime Mendo and Ms. Isabel Tsukayama for their scientific and editorial inputs; to the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), particularly Drs. H. Salzwedel, P. Muck, M. Bilio and W. Schmidt; as well as to Drs. A. Bakun, R. Mendelssohn and R. Parrish of the US National Marine Fisheries Service for their willingness to contribute to this effort.

We at ICLARM look forward very much to our future cooperation with IMARPE and GTZ and hope that readers will find the present volume to be a useful contribution to the literature on Latin American resources.

Ian R. Smith

Informe del Taller de Trabajo Sobre Modelos Para la Predicción del Rendimiento en el Sistema de Afloramiento Peruano IMARPE, Callao, 24-28 Agosto 1987*

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CSIRKE, J., J. MENDO, J. ZUZUNAGA, G. CARDENAS, P. MUCK and F. CHAVEZ. 1989. Informe del taller de trabajo sobre modelos para la predicción del rendimiento en el sistema de afloramiento Peruano, IMARPE, Callao, 24-28 Agosto 1987, p. 1-13. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

A summary and the conclusions of a workshop on "Models for Yield Prediction in the Peruvian Ecosystem", held on 24-28 August 1987 at the Instituto del Mar del Perú are presented. Emphasis is given to those presentations and discussions which pertained to long time series and to consistent data collection and to the key elements of a future model of the Peruvian upwelling ecosystem for use in fishery management.

Resumen

Se presenta un resumen y las conclusiones del "Taller de trabajo sobre modelos para la predicción del rendimiento en el sistema de afloramiento peruano", realizado el 24-28 de Agosto de 1987 en el Instituto del Mar del Perú. Se pone énfasis en aquellas presentaciones y discusiones referentes a series de tiempo de largo plazo, recolección de datos y a los elementos claves para un modelo futuro del ecosistema de afloramiento peruano para ser usado en el manejo pesquero.

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*PROCOPA Contribution No. 86.

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Introducción

La reciente publicación del libro "The Peruvian anchoveta and its upwelling ecosystem: three decades of change" (Pauly y Tsukayama 1987) pone a disposición de la comunidad científica internacional un gran volúmen de información a nivel mensual desde 1953 hasta 1982 sobre la población y pesquería de la anchoveta peruana y de las condiciones del ambiente marino frente al Perú. Se incluyen además, algunos análisis preliminares y otros más detallados de los datos presentados en el libro.

Como una primera acción de seguimiento del valioso esfuerzo que significó reunir en un solo volumen datos de 30 años de investigaciones, PROCOPA, ICLARM e IMARPE decidieron convocar este taller de trabajo sobre "Modelos para la predicción del rendimiento en el sistema de afloramiento peruano" para lo cual se invitó tanto a los autores que habían contribuido con el libro, así como a otros expertos internacionales con el fin de discutir, ampliar y analizar la base de datos disponibles a la fecha.

Los objetivos del taller de trabajo fueron:

i) revisar la base de datos disponsible sobre el sistema de afloramiento peruano y discutir su utilidad para los fines de investigación y ordenamiento pesquero;

ii) identificar modelos predictivos y métodos de ordenación que, teniendo en cuenta las características especiales del ecosistema del afloramiento peruano, puedan ser más adecuados que aquellos modelos de rendimiento en uso, donde por lo general se asume que el sistema está compuesto por stocks o unidades poblacionales aisladas que podrían ser mantenidos en un estado de equilibrio;

iii) sugerir líneas de investigación de mayor interés, tanto para el personal del IMARPE, como el personal de PROCOPA y otros grupos o agencias de asistencia bilateral o internacional vinculadas al sector pesquero peruano, así como a la comunidad científica internacional.

El taller de trabajo se llevó a cabo en el Instituto del Mar, Chucuito, Callao, Perú, del 24 al 28 de Agosto de 1987 y contó con la participación de científicos de IMARPE, PROCOPA e ICLARM como organismos auspiciadores, así como de otros organismos nacionales e internacionales. La lista de participantes se presenta en Tabla 1. El taller se inició el día lunes 24 de Agosto de 1987 con las palabras del Blgo. R. Villanueva, Director Ejecutivo del IMARPE, a cuya sugerencia se rindió homenaje a la fallecida Dra. H. Santander, guardando un minuto de silencio. Sigueron las palabras del Dr. H. Salzwedel, en representación de PROCOPA y del Dr. D. Pauly, en representación de ICLARM. El Almirante AP (R) R. Zevallos Newton, Presidente del Directorio del IMARPE, dió por inaugurado el taller de trabajo.

Por aclamación se eligió al Blgo. J. Csirke, de la FAO, como Presidente del Taller de Trabajo y al Blgo. J. Mendo, del IMARPE como Relator, luego de lo cual se procedió con las sesiones del Taller según la agenda aprobada.

Las sesiones consistieron de dos fases. Los dos primeros días se efectuaron las presentaciones y discusiones de trabajos de investigación y datos originales que amplían, complementan o analizan los datos y resultados ya publicados en el libro, luego de lo cual se procedió a formar dos grupos de trabajo con la finalidad de puntualizar dos de los aspectos generales de mayor importancia para el Taller:

a) El muestreo, colección y análisis de datos, que fue asignado al grupo que se reunió bajo la coordinación del Ing. J. Zuzunaga de IMARPE, actuando como relatora la Blga. G. Cárdenas, y

b) Desarrollo de modelos, asignado al grupo que se reunió bajo la coordinación del Dr. P. Muck de PROCOPA y donde actuó como Relator el Dr. F. Chávez, del Duke University.

Luego de haber sido discutidas en plenario, las contribuciones de estos dos grupos de trabajo fueron incorporadas como partes principales del presente Informe.

Trabajos Presentados

Dentro de las primeras actividades del Taller de Trabajo se programó la presentación y discusión de resultados preliminares y avances de trabajo donde se hubieran utilizado los datos

Tabla 1. Lista de participantes del Taller de Trabajo sobre Modelos para la Predicción del Rendimiento en el Sistema de Afloramiento Peruano, IMARPE, Callao, 24-28 Agosto 1987.

Table 1. List of participants of the Workshop on Models for Yield Prediction in the Peruvian Upwelling Ecosystem, IMARPE, Callao, 24-28 August 1987.

Participantes	Observadores	Personal de Apoyo
Agüero, Max[1]	Chirichigno, Norma[3]	Aranda, Carlos[2]
Alamo, Alejandro[3]	Chirinos de Vildoso, Aurora[3]	Bravo, Ricardo[3]
Antonietti, Emira[3]	Izaguirre, Luis[10]	Calisto, Rosela[2]
Bohle-Carbonell, Martin[4]	Martinez, Carlos[11]	Carbajal, Roger[2]
Cárdenas, Gladys[3]	Munaylla, Ulises[10]	Castillo, Janett[3]
Calienes, Ruth[3]	Rivera, Torcuato[3]	Chaparro, Cecilia[2]
Carrasco, Sulma[3]	Robles, Ulises[3]	Diez-Quiñonez, Aida[3]
Csirke, Jorge[5]	Sánchez,Enrique[10]	Huerta, Michael[3]
Chávez, Francisco[6]	Soldi, Héctor[8]	Orué, Carmen[3]
Dioses, Teobaldo[3]	Véliz, María[3]	Silva, Omar[3]
Espinal, Javier[12]	Villanueva, Rogelio[3]	
Espino, Marco[3]	Wosnitza-Mendo, Claudia[2]	
Fuentes, Humberto[3]	Zuta, Salvador[3]	
Gómez, Olga[3]		
Lagos, Pablo[7]		
Majluf, Patricia[9]		
Mendieta, Armando[3]		
Mendo, Jaime[3]		
Muck, Peter[2]		
Ochoa, Noemi[3]		
Palomares, Maria Lourdes[1]		
Pauly, Daniel[1]		
Peña, Nora[3]		
Salzwedel, Horst[2]		
Tovar, Humberto[3]		
Zuzunaga, Jorge[3]		

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[2]PROCOPA (Programa Cooperativo Peruano-Alemán de Investigación Pesquera), Instituto del Mar del Perú, P.O. Box 22, Callao, Perú.
[3]IMARPE (Instituto del Mar del Perú), Esq. Gamarra y Gral. Valle s/n, La Punta-Callao, Perú.
[4]Institut für Meeresksunde, Troplowitzstr. 7, 2000 Hamburg 54, República Federal de Alemania.
[5]Organización de las Naciones Unidas para la Agricultura y la Alimentación (FAO), via delle Terme di Caracalla, 00100 Roma, Italia.
[6]Duke University, Marine Laboratory, Rivers Island, Beaufort, North Carolina 28516-9721, USA.
[7]IGP (Instituto Geofísico del Perú), Los Alamos 241, San Isidro, Lima, Perú.
[8]DHNM (Dirección de Hidrografía y Navegación de la Marina), Gamarra 500, Chucuito, Callao, Perú.
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[10]MIPE (Ministerio de Pesquería), Paseo de la República 3103, San Isidro, Lima, Perú.
[11]IFOP (Instituto de Fomento Pesquero), Casilla 1287, Santiago, Chile.
[12]PESCA PERU, Av. Petit Thouars 115, Casilla 4682, Lima 100, Perú.

publicados en el libro editado por Pauly y Tsukayama (1987), así como la presentación de nuevos datos que podrían ser considerados en las series de tiempo disponible.

La primera presentación estuvo a cargo del Dr. Max Agüero (ICLARM), quien sustentó su trabajo anterior (Agüero 1987) y en el que se trata de integrar en un modelo de programación matemática, los diferentes componentes del sector pesquero con el objeto de determinar el rendimiento económico óptimo en la explotación de un recurso (por ejemplo la anchoveta).

Dicha presentación hace una revisión de la evolución de la pesquería de la anchoveta desde el punto de vista económico, basado en los datos del libro antes mencionado.

La versatilidad del modelo está dada por la inclusión de diferentes curvas de rendimiento, datos ambientales, variación de precios, esfuerzo de pesca, etc.

En base a lo presentado por el Dr. Agüero, se llegó a la conclusión de que si se tiene como objetivo maximizar el rendimiento económico neto de la pesquería, será necesario ajustar modelos como el propuesto donde se integra la parte biológica y los aspectos económicos. Esto daría lugar a un trabajo conjunto entre las entidades que se dedican a la investigación (i.e., IMARPE) y a las que planifican la economía en el sector pesquero (Instituto Nacional de Planificacion, Ministerio de Economiá y Finanzas, etc.).

La experiencia del colapso de la anchoveta en los años setenta y la necesidad de evitar que se repitan, nos obliga a ésta integración, ya que por un lado se estará preservando el recurso y por otro, se obtendrá un rendimiento económico superior.

La presentación del Dr. M. Bohle-Carbonell sobre cambios temporales del sistema de afloramiento peruano, analizando los datos de series de tiempo disponible, llega a la conclusión que muchos rangos de variables independientes están describiendo un camino fraccional al azar (Bohle-Carbonell, este vol.).

Los análisis espectrales de las series de tiempo muestran una variabilidad temporal de mucho ruido ("noisy temporal changes") con una señal estacional débil ("weak seasonal signal").

Así mismo, para rangos cubiertos por la variable independiente no se ha encontrado un ajuste, por lo que los cambios de las variables dependientes son más complicados que lo asumido por un modelo estadístico simple.

La interpretación geométrica indica que dentro de los datos observados existen rangos de combinaciones de parámetros improbables. Ciertos valores o combinaciones de valores de la variable dependiente no son posibles de obtener. Desde el punto de vista biológico esto puede significar que el sistema se encuentra en múltiples estados de equilibrio.

Esta presentación sugiere que el modelaje y el análisis de datos debe tratarse con un sentido estadístico.

El Dr. F. Chávez (Duke University, Marine Lab.) contribuyó con la presentación de un modelo para estimar el potencial de la nueva producción primaria, usando series de tiempo mensuales de 1953 a 1984. El se basó en datos de afloramiento y profundidad de la termoclina publicados por Bakun (1987) y Brainard y McLain (1987), respectivamente. La profundidad de la termoclina fue convertida a concentración de nitrógeno a los 60 m usando una relación entre la profundidad de la termoclina y la concentración de nitrato a 60 m.

Durante los años de "El Niño" aumenta el transporte vertical (afloramiento), pero la concentración de nutrientes en las aguas afloradas son bajas. Este incremento en el transporte vertical hace que la producción primaria estimada por el modelo durante los años "El Niño" sea más alta de la esperada (Chávez et al., este vol.).

Este modelo simple puede ser muy útil para el cálculo de los nutrientes en base a parámetros físicos, sin embargo la parametrización de las variables debe mejorarse con el objeto de que el modelo adquiera una mayor robustez (ver Mendo et al., este vol.).

Un resumen del estado actual de la investigación cuantitativa del macrobentos en el Perú fue presentado por el Dr. Horst Salzwedel (PROCOPA). La mayoría de los trabajos cuantitativos se publicaron después de 1980, siendo las áreas de mayor interés la Bahía de Ancón (40 km al norte de Lima) y la plataforma continental entre 12°S (Callao) y 3°30'S (Ecuador). Para la Bahía de Ancón, existen series de tiempo de datos desde 1981 hasta la fecha, cubriendo así años normales y años "Niño". Para el sublitoral, más allá de los 25 m de profundidad hay sólo tres cruceros efectuados por el IMARPE (1981, 1983 y 1984) de los cuales el material ha sido evaluado hasta el nivel de especies.

Una recopilación de los datos existentes revela los siguientes resultados: Niños moderados (1976, 1987) suben la concentración promedio del oxígeno y la temperatura de las aguas cercanas al fondo sólo hasta los 9°S apróximadamente. Se encuentran con altas biomasas y densidades y bajo número de especies, siendo ellas bien adaptadas a las bajas concentraciones de oxígeno durante años normales. Uniendo los datos del sublitoral de 3 m hasta 4,000 m de profundidad resaltan desfases en las biomasas y las densidades en apróximadamente 80 m de profundidad que por ahora no se han podido explicar por la cantidad limitada de datos evaluados.

Se concluye que los conocimientos cuantitativos del macrozoobentos son muy escasos para poderlos relacionar en forma adecuada con las largas series de tiempo que existen para otros

datos abióticos y bióticos contenidos en el libro. Se recomienda continuar con las investigaciones regulares en la Bahía de Ancón y ampliarlas a aguas más profundas.

La Dra. P. Majluf (Cambridge University), presentó algunos aspectos de la ecología y producción del lobo fino (*Arctocephalus australis*) de Punta San Juan, Perú (15°22'S) durante 1983 y 1987, así como de la dieta, comportamiento alimenticio, reproducción, crecimiento y mortalidad de crías. Los resultados indican que los lobos consumen predominantemente anchoveta adulta y que las variaciones en la disponibilidad local para la flota pesquera se reflejan en la composición y diversidad de la dieta.

Con referencia a otras especies de lobos del mismo género, las mortalidades encontradas fueron altas, especialmente durante el fenómeno de "El Niño" 1982-83 y en 1984-85. Las mayores mortalidades de las crías (de 0-30 días de edad) durante la temporada de reproducción (40%), se debió principalmente a la alta densidad de hembras en la playa donde se reproducen. La mortalidad entre los 30 días y un año de edad parece estar relacionada con cambios en la disponibilidad de anchoveta adulta para los lobos (Majluf, este vol.).

El incremento de la población de lobos coincide con un incremento en su protección; sin embargo no se descarta el efecto de la disponibilidad local del recurso de anchoveta principalmente para las madres.

El análisis presentado por la Srta. Majluf, sugiere que se podría tomar a los lobos como un indicador de la disponibilidad local de anchoveta y por lo tanto, como una medida de la captura por unidad de esfuerzo.

Por otro lado, dado el daño que provoca la población de lobos a los pescadores locales, es importante plantear la alternativa de utilizar a los lobos como un atractivo turístico. Esto permitiría el ingreso de divisas que compensarían las pérdidas de los pescadores en cuanto a redes se refiere.

El Blgo. A. Alamo (IMARPE), expuso un análisis preliminar del contenido estomacal de la anchoveta. En su presentación hizo la comparación de la dieta de la anchoveta bajo los efectos de "El Niño" y bajo condiciones normales. Durante "El Niño" se incrementó la proporción de copépodos consumidos por anchoveta. Para la interpretación de estos cambios, se sugirió que se realice un análisis multivariado tomando en cuenta variables tales como temperatura, hora, día, estacionalidad, variaciones interanuales, latitud, etc. Este estudio se podrá llevar a cabo en el futuro utilizando la base de datos disponibles sobre contenido estomacal (ver Rojas de Mendiola, este vol., Alamo, este vol., Pauly et al, este vol.).

El Blgo. H. Tovar (IMARPE) presentó los resultados de un estudio sobre la predación del piquero (*Sula variegata*, Tschudi) sobre algunos recursos ícticos del litoral peruano, sosteniendo que en febrero de 1986, el piquero se alimentó principalmente de anchoveta (*Engraulis ringens* J.) y en menor proporción de otras especies como sardina (*Sardinops sagax*), jurel (*Trachurus murphyi*), pejerrey (*Odonthestes regia*), cojinova (*Seriolella violacea*), anchoveta blanca (*Anchoa nasus*) y de agujilla (*Scomber saurus*). Dentro de la discusión de éste tópico se consideró de interés el uso de los bolos alimenticios como un indicador local de la población de anchoveta y de su disponibilidad como alimento. Por otro lado, se enfatizó la necesidad de continuar con la obtención de información mensual de las poblaciones de aves guaneras, así como la realización de censos poblacionales para lo cual es necesario la coordinación con la Dirección de Fertilizantes de Pesca-Perú.

El Dr. P. Muck (PROCOPA), presentó una revisión general de las tendencias mostradas por las poblaciones incluidas en el libro de Pauly y Tsukayama (1987). En su análisis, mostró que las poblaciones de anchoveta, bonito y aves guaneras disminuyeron entre los años 1960 y 1980, y la flota bolichera a partir de 1970. Sin embargo la disminución de la flota no fue suficiente para evitar la drástica disminución de dichas poblaciones. La merluza (*Merluccius gayi*), jurel y caballa se mantuvieron estables y la sardina y los lobos marinos aumentaron su población durante el período cubierto por el estudio.

Se señaló que la sobrepesca fue la principal responsable del descenso de las poblaciones mencionadas en primer término. Por otro lado el jurel, merluza y caballa incrementaron sus poblaciones ya que sufrieron capturas limitadas y no son dependientes de la disponibilidad de anchoveta. El incremento del stock de sardina en cambio está asociado a la disminución del stock de anchoveta, la que preda los huevos de sardina y además compite con ella por el

alimento. Por otro lado, el incremento de la población de lobos marinos se debió principalmente al incremento de la protección legal.

En general, los cambios biológicos observados en el ecosistema peruano en los 20 años, se deben principalmente a los efectos directos e indirectos de la sobrepesca y al fenómeno de "El Niño" que actuó solo como un factor agravante (Muck, este vol.).

La Blga. S. Carrasco (IMARPE), presentó las variaciones de la biomasa del zooplancton en el mar peruano en base a muestreos realizados por IMARPE durante el período 1964-1987. Los resultados indicaron una disminución notable de los valores de biomasa a través de los años (ver Carrasco y Lozano, este vol.). Se observa una similitud entre las variaciones en la biomasa de zooplancton y la variación en la biomasa de anchoveta, sugiriendo que en la década de los años 60 existía un ecosistema (no sólo en lo que se refiere a peces pelágicos) diferente al que existe actualmente. Igualmente durante los años "El Niño" existen cambios en la distribución de zooplancton, en los que se observa que los máximos en la abundancia se encuentran más alejados de la costa que en condiciones normales y así mismo, una disminución en la abundancia de zooplancton. Se concluye al respecto la necesidad de estudiar las causas de ese decrecimiento en relación con el fitoplancton, el consumo de peces planctívoros, etc. Se hizo hincapié que aún existen muchos datos históricos que necesitan trabajarse. Se recomienda que esta información sea extraída, estandarizada y publicada.

El Blgo. J. Csirke (FAO), presentó un análisis de las fluctuaciones del coeficiente de capturabilidad mensual para el período comprendido entre el año 1961 y el año 1972, el cual será ampliado con nuevos datos disponibles en IMARPE para los años más recientes (ver Csirke, este vol.). Los resultados presentados muestran una clara estacionalidad en la fluctuación del coeficiente de capturabilidad, el que alcanza valores máximos en los meses de verano y disminuye considerablemente en invierno. El resultado más interesante es que los datos muestran una relación inversa entre el coeficiente de capturabilidad y la biomasa de anchoveta, donde el coeficiente de capturabilidad aumenta en forma exponencial a medida que la biomasa total disminuye. Este tipo de relación es semejante al encontrado en algunas poblaciones de peces pelágicos pequeños en otras partes del mundo, y constituye una primera prueba de que en la anchoveta peruana también se da este tipo de relación depensatoria que implica un aumento de la mortalidad por pesca a menor abundancia del recurso. Este hallazgo también refuerza la observación hecha a inicios de los años setenta de que la capturabilidad de la anchoveta no era constante, en base a lo cual se abandonó la colección y uso de datos de captura por unidad de esfuerzo para estimar fluctuaciones del recurso y para la aplicación de modelos de producción. Los resultados presentados demuestran sin embargo que, al ser posible determinar la posible relación entre el coeficiente de capturabilidad y la biomasa total, es posible usar esta información para corregir los valores de captura y esfuerzo. Se recomendó por tanto que se reinicie e intensifique la colección de datos de esfuerzo usando en lo posible medidas alternativas del poder de pesca, los cuales constituyen un medio útil para monitorear las fluctuaciones de la abundancia a bajo costo, los cuales sin embargo, se deberán validar y complementar con estimaciones hechas por otros métodos.

El Dr. P. Lagos (IGP) presentó un trabajo sobre la variabilidad estacional de la temperatura superficial a lo largo de la costa del Perú. Usando las series de tiempo mensuales de calor neto local, transporte Ekman y profundidad de la isoterma de 14°C, se ha llegado a pronosticar la estacionalidad media de la temperatura superficial del mar.

El concluye que la estacionalidad media consiste de una variabilidad anual debida al calor local, probablemente con un cambio pequeño de la amplitud y fase de año a año y de una variabilidad semi-anual debido a la dinámica interna del océano.

Los resultados del estudio de balance del calor pueden ser usados en el desarrollo de los modelos físico-biológicos que requieren las tendencias de las condiciones ambientales.

Modelaje del Ecosistema Peruano

Necesidad de un Modelo

En la actualidad los administradores de la pesca no disponen de un instrumento para predecir las fluctuaciones anuales de la biomasa de recursos pesqueros. La pesquería pelágica

frente a Perú está compuesta de múltiples especies, cuya abundancia relativa es una función de la pesquería y de los cambios bióticos y abióticos. Para tratar con un gran número de propiedades que varían con el tiempo y que afectan en forma diferenciada la abundancia de cada especie, es necesario algún tipo de modelo computarizado capaz de simular el ecosistema pelágico. Este modelo ayudará a estimar el esfuerzo con que deberá explotarse cada una de las especies que componen el ecosistema. Por ejemplo, el modelo podrá mostrar como la biomasa de la especie A podría afectar la biomasa de la especie B (para la costa peruana las especies A y B podrían ser anchoveta y sardina). El modelo podría tener no sólo valor predictivo sino también de diagnóstico, por lo que podría utilizarse también para explorar posibles interacciones. En este nivel, el modelo identificaría los componentes críticos del ecosistema (y sus funciones que la deciden) lo cual requiere estudios más detallados. En el futuro, éste modelo también proveería los datos requeridos en un modelo económico.

Tipo de Modelo Necesario

Este tópico requiere de un amplio estudio. Se sugiere varios niveles o tipos de modelo que pueden intentarse:

a) Un modelo de "anchoveta" que utilice la serie de tiempo disponible para predecir el reclutamiento en base a las relaciones con los factores bióticos y abióticos para el manejo de los recursos.
b) Un modelo de evaluación de stock de peces que incluya sólo aquellos elementos de magnitud suficiente como para alterar los stocks de peces. Por ejemplo, los mamíferos que no predan peces a altos niveles deberán ser excluídos.
c) Un modelo del ecosistema que adicione al modelo de evaluación del stock de peces aquellos elementos del sistema pelágico que no fueron incluídos en el ejercicio previo. Estos elementos (por ej. aves y mamíferos) no afectan la variabilidad de los stocks de peces, sin embargo, son afectados por la variabilidad en los stocks de peces. Estos elementos tienen valor socio-económico y requieren ser tomados en consideración.

El desarrollo del modelo deberá considerar siempre el gran objetivo, cual es definir el nivel de explotación de un stock y la especie preferida.

Validez del Modelo

El modelo contemplará, en base a la serie de tiempo disponible, (1) la entrada de datos para el modelo, y (2) la verificación de la validez del modelo. Un modelo predictivo y realístico deberá captar la estructura esencial de la serie de tiempo existente.

A continuación se presenta el concepto iterativo simple del desarrollo del modelo:

a) empezar con el modelo conceptual más simple,
b) desarrollar funciones de transferencia,
c) correr el modelo utilizando datos mensuales y comparar los datos observados, y
d) mantener o cambiar las funciones de transferencia para obtener un "mejor" dato simulado.

Forma Conceptual del Modelo

El modelo conceptual deberá incluir: 1) producción primaria y secundaria, los peces (anchoveta, sardina, jurel, caballa y merluza) y la pesquería como parte del componente biótico; y 2) temperatura superficial del mar, fuerzas metereológicas locales y remotas y temperatura subsuperficial como parte del componente abiótico. El modelo de ecosistema incluirá aves y mamíferos (ver Fig. 1).

Las dos dimensiones predictivas importantes del modelo son el espacio y el tiempo, requiriéndose también la componente geográfica. La resolución espacial deberá incluir el área

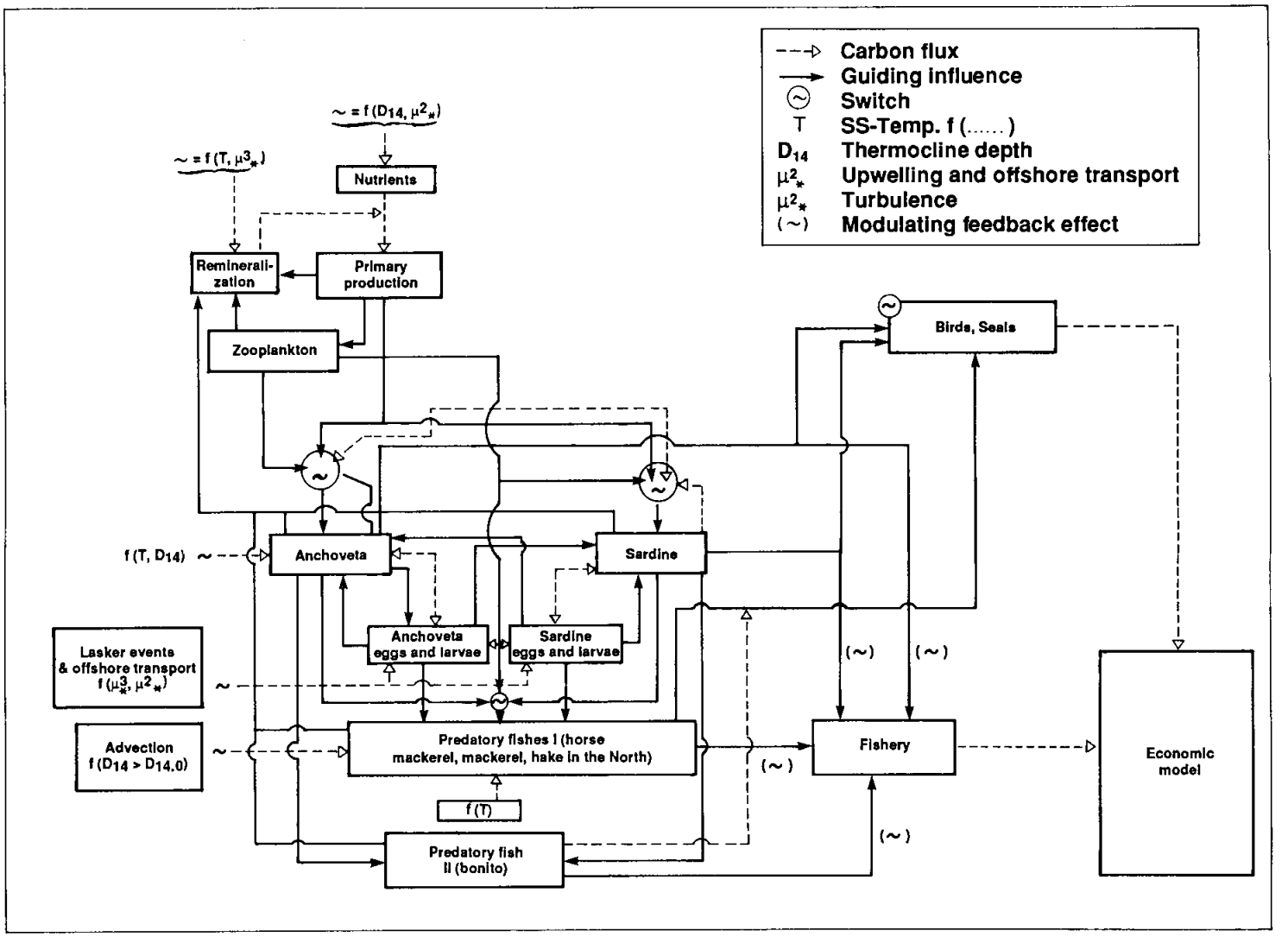

Fig. 1. Elementos a ser considerados en un modelo de simulación del ecosistema de afloramiento peruano. Notar el papel importante de la temperatura superficial del mar (TSM) y los parámetros derivados del viento.

Fig. 1. Elements to be considered in a simulation model of the Peruvian upwelling ecosystem. Note strong role of SST- and wind-derived parameters.

principal de distribución de la anchoveta, esto es 4-14oS y 60 millas mar afuera, que de ser necesario podría ser dividida.

Los Datos y sus Características

La serie de tiempo existente, gran parte de la cual ha sido compilada y publicada en Pauly y Tsukayama (1987) provee una base de datos suficiente para iniciar el modelaje de multiespecies. Las series de tiempo de datos que aún faltan (por ej. zooplancton) deberán reconstruirse utilizando la literatura y datos no publicados de IMARPE y/o por funciones de transferencia a partir de por ej., la producción primaria.

El modelo deberá simular los cambios de los peces en cada paso. Ello significa que el modelo deberá incluir efectos no lineales. Existen modelos que ya simulan pasos como cambios en las poblaciones de peces, pudiendo incorporarse dichas ecuaciones en el presente modelo.

Los diferentes compartimentos del modelo deberán mantener un grado similar de complejidad de forma que sean compatibles. Por ejemplo, el compartimento de producción primaria deberá ser compatible con el de producción de peces.

La gran cantidad de características oceanográficas deberá ser investigada, poniendo particular atención en los cambios que pudieran no haber sido observados en las estaciones costeras. Un ejemplo es la distribución de las aguas sub-tropicales superficiales (ASS) que podrían definir el tamaño del habitat de la anchoveta. Existen evidencias de cambios sistemáticos en la distribución de estas masas de aguas con anterioridad a la generación de perturbaciones que se propagan hacia el Este (ondas Kelvin) en el Pacifico Oriental (Bohle-Carbonell, este vol.). La fuerza remota es responsable de los dramáticos efectos de "El Niño"; sin embargo, los cambios que ocurren antes del fenómeno de "El Niño" también pueden tener efectos dramáticos sobre las poblaciones de peces. Se recomienda mantener comunicación con modeladores que trabajan a mayor escala (por ejemplo con aquellos que trabajan con la zona del Pacifico Tropical de Australia a América del Sur).

Acciones Futuras

Deberá continuarse con el muestreo que provee los datos para la serie de tiempo existente. Estos incluirán datos de biomasa temporal y espacial, elementos biológicos del modelo, comportamiento de alimentación, tasas de explotación (captura), así como factores abióticos tales como viento y datos hidrográficos. Los datos deberán estandarizarse y analizarse en tiempo real a fin de proveer las entradas de datos requeridas en el modelo. Se pondrá especial atención a la colección de datos de composición, biomasa y producción del fitoplancton y zooplancton.

Para lograr el gran objetivo del modelaje, cual es el de crear un instrumento para el manejo pesquero, IMARPE y PROCOPA deberán formalizar un compromiso para este modelaje mediante la conformación de un grupo de trabajo.

Los esfuerzos para el modelaje deberán iniciarse lo antes posible. La información compilada y publicada en Pauly y Tsukayama (1987), en este volumen, así como los datos de IMARPE aún no procesados, son suficientes para iniciar el modelaje del ecosistema del mar peruano.

Análisis y Colección de Datos

Las diferentes actividades que deben desarrollarse en el análisis y colección de datos han sido divididas de acuerdo a la necesidad de implementar nuevos datos de series de tiempo, al procesamiento de éstos y a las prioridades que se deberán tener en cuenta para el modelaje del ecosistema. Estas se resumen de la siguiente forma:

A. Colección de Datos

Dentro de la gama de información factible de ser colectada se ha priorizado aquellas indicadas en la Tabla 2 adjunta.

Tabla 2. Colección de datos generales para los estudios de investigación de IMARPE.

TIPO	FUENTE	INFORMACION ESPECIFICA	FRECUENCIA ESPACIO	FRECUENCIA TIEMPO
BIOLOGICO	PESQUERIA	Composición por especies	Ptos/Areas	Mensual
		Longitud	Puerto	Mensual
		Peso	Puerto	Estacional
		Edades	Región	Estacional
		Alimentación	Región	Estacional
		Madurez	Región	Estacional
		Grasa	Puerto	Estacional
	PROSPECCION PESQUERA	Biomasa	Región	Semestral
		CPUE	Región	Semestral
		Longitudes	Región	Semestral
		Producción Primaria	Región	Estacional
		Producción Secundaria	Puerto	
	OTROS	Población aves	Islas/Puntas	Mes
		Alimentación aves	Islas/Puntas	Estacional
		Población mamíferos		Estacional
ESTADISTICO	PESQUERIA	Captura	Pto/Región	Mensual
		Esfuerzo	Flota	Mensual
		CPUE	Flota	Mensual
AMBIENTAL OCEANOGRAFICO	Estac. fijas	Temp.	Puerto	Diaria
		Salinidad	Puerto	Diaria
		Nivel del Mar	Puerto	Diaria
	Exploración	Temp., O_2 S ‰	Región	Mensual
		Nutrientes	Región	Mensual
	Satélite	TSM, Corrientes	Global	Mensual
METEOROLOGICO	CORPAC y Estac. fijas	Vientos, temp. del aire	Local	Diario
		Presión atmosférica		
	Satélite	Vientos, radiación y nubes		
ECONOMICO	Playa, Mayorista Consumidor MERCADO	Precios	Según muestra	diario/ semanal

B. Evaluación de las prioridades y problemática

Los datos colectados por IMARPE deben estar orientados al logro de dos aspectos fundamentales:

- Optimizar el asesoramiento al gobierno, particularmente al sector pesquero en la toma de decisiones para un mejor manejo de los recursos.
- Desarrollar modelos propios del ecosistema aplicando metodologías que tengan capacidad predictiva.

Para el logro de estos objetivos se señala la necesidad de resolver problemas referentes a:

- Alto costo que requiere la toma de información a través de las exploraciones en el mar, muestreo de pesquerías, adquisición y mantenimiento de equipos de laboratorio, transporte, etc.
- Insuficiencia de recursos humanos y necesidad de capacitación permanente del personal existente que se encarga de la colección de datos.
- Deficiencia de coordinación y apoyo de entidades estatales y privadas del sector pesquero e instituciones afines.

C. Análisis de la Información

La información colectada deberá ser procesada y analizada utilizando los métodos disponibles, enfatizándose la necesidad de estandarización de los mismos y el uso máximo de las computadoras disponibles en el IMARPE. El objetivo final deberá ser la publicación de los resultados.

D. Política de intercambio de datos

El intercambio de datos se plantea en dos niveles:

- Difusión inmediata de datos, sujeto simplemente a la culminación de su recopilación, consistencia y procesamiento básico.
- Difusión mediata, con la elaboración de informes científicos e informes varios.

La oportuna difusión de la información en ambos niveles estará condicionada por las facilidades de edición y publicación de informes.

Conclusiones y Recomendaciones

En base a las presentaciones que se hicieron durante los dos primeros días del taller y las discusiones sostenidas en Plenario y en los Grupos de trabajo, se llegó a las conclusiones y recomendaciones siguientes:

a) El conocimiento científico acumulado hasta la fecha debe volcarse en un modelo que permita predecir las fluctuaciones anuales de la biomasa de recursos pesqueros, además de poder ser utilizado para explorar los resultados de distintas alternativas de administración o manejo pesquero.

b) Además del modelo del ecosistema del mar peruano se requiere un modelo que integre tanto la parte biológica, como los aspectos económicos. Este tipo de modelo será particularmente útil si se tiene como objetivo maximizar el rendimiento económico neto de las pesquerías peruanas y requerirá un trabajo y colaboración más estrecha entre las entidades nacionales que se dedican a la investigación (IMARPE) y los que planifican la economía en el sector pesquero (Ministerio de Pesquería, Instituto Nacional de Planificación, Ministerio de Economía y Finanzas).

c) Los esfuerzos para concretar la formulación de estos modelos deben iniciarse lo antes posible, considerándose que la información publicada en el libro editado por D. Pauly e I. Tsukayama recientemente, la información incluida en éste volumen y los datos aún no procesados que posee IMARPE son suficientes para inciar el modelaje del ecosistema del mar peruano.

d) Para permitir que este modelo pueda ser empleado en forma efectiva en el futuro, se recomienda que se continúen los muestreos que proveen de datos para actualizar las series de tiempo disponibles. Esto incluye datos sobre cambios de la biomasa y las capturas, así como otros elementos biológicos (alimentación, plancton, etc.) y factores abióticos (vientos, datos hidrográficos, etc.).

e) Para lograr este gran objetivo de modelar el ecosistema del mar peruano, el IMARPE deberá propiciar la formación de grupos de trabajo conformados por científicos altamente especializados del país y del extranjero, cuya participación en este ejercicio podrá ser canalizada en base a la cooperación técnica bilateral e internacional ya existentes u otros que podrían instituirse en el futuro. Dentro de este contexto, PROCOPA ha jugado un rol catalizador muy importante que, en opinión del Taller de trabajo, debería ser continuado y reforzado para apoyar al IMARPE en la puesta en práctica e implementación de las otras recomendaciones que se hacen en este Informe. Se consideró que también se debería estimular la participación de otras agencias y organismos de asistencia técnica internacional,

resaltándose el apoyo recibido de ICLARM, así como la participación de la FAO en este taller.

f) Con respecto al colapso de importantes pesquerías y la disminución de algunos recursos del ecosistema del mar peruano tales como la anchoveta, el bonito y las aves guaneras, el taller concluyó que aún cuando los cambios del ambiente han jugado un rol importante, fue la sobrepesca la causa principal del colapso y disminución de estas poblaciones. Otras poblaciones como jurel, merluza y caballa han aumentado en los últimos años ya que han sido explotadas en forma limitada y no dependen de la disponibilidad de anchoveta. En cambio el aumento de la población de sardina sí parece estar asociado con la disminución de las poblaciones de anchoveta, a nivel de predación de huevos y competencia por alimento.

g) En el taller se mostró que es posible encontrar una estrecha relación entre el coeficiente de capturabilidad y la biomasa total, lo cual permitiría corregir los datos de captura por unidad de esfuerzo cuyo uso para fines de evaluación de la pesca se abandonó a inicios de los años 70 al constatar que la capturabilidad no era constante. Dado que sería posible corregir y usar los valores de captura y esfuerzo, se recomienda que se reinicie y se refuerce la colección y procesamiento de este tipo de datos, los cuales constituyen un medio útil y de bajo costo para monitorear las fluctuaciones de la abundancia del recurso, complementando así las estimaciones que se hacen con otros métodos. Esta información de captura y esfuerzo podrá también ser empleada en análisis económicos de la pesca.

h) El taller también acordó resaltar que hay información sobre la abundancia y comportamiento de aves y mamíferos marinos que pueden ser empleados como indicadores de posibles cambios en el ecosistema y en las poblaciones de peces. Se acordó por lo tanto recomendar que se continúe con la colección y el análisis de la información mensual de la población de las aves guaneras y que se prosiga con los censos poblacionales en coordinación con la Dirección de Fertilizantes de Pesca-Perú. Se recomienda así mismo que se considere también la posibilidad de emplear los bolos alimenticios de aves guaneras para obtener información sobre estructuras por tamaños y disponibilidad de anchoveta. Se señaló también que los lobos marinos podrían ser empleados como indicadores de la disponibilidad local de anchoveta.

i) En cuanto a otros datos biológicos, se recomienda que se intensifiquen los estudios de alimentación de peces en sus diferentes estadíos y, como parte del sistema de colección de información en el mar, se recomienda que se establezcan estaciones fijas para la colección de muestras y datos biológicos en forma similar a como viene haciéndolo el grupo de oceanografía del IMARPE para obtener datos abióticos.

j) Para mejorar la colección y análisis de datos se recomendó que se realicen conversatorios periódicos para evaluar los sistemas de colección y procesamiento de datos.

k) Se resaltó que uno de los objetivos finales y principales de todo trabajo científico es publicar los resultados de las investigaciones y se recomendó que los científicos del IMARPE tengan esto como meta final. Para ello se requerirá que al preparar proyectos de investigación se asegure la asignación de fondos necesarios para publicar los hallazgos del proyecto.

Referencias

Agüero, M. 1987. A bioeconomic model of the Peruvian pelagic fishery, p. 307-324. *In* D. Pauly and and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly and and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984, p. 14-45. *In* D. Pauly and and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

On the Variability of the Peruvian Upwelling System

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BOHLE-CARBONELL, M. 1989. On the variability of the Peruvian upwelling system, p. 14-32. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

The behavior of the Peruvian upwelling ecosystem is shown to be determined to a large degree by random events which make it oscillate between multiple disjoint states. The mean characteristics of these nonstationary random processes were identified partly as resulting from a correlated fractal noise process. Thus, any prediction of future changes of the Peruvian upwelling ecosystem must consider its stochastic nature. Predictions relevant for management decisions for periods longer than some months ahead may be beyond reach. However, physical parameters were identified which are most closely related to changes of anchoveta biomasses than those commonly observed to characterize El Niño events. This allows the development of new monitoring schemes and will lead to a better understanding of the dynamics of the interface between physics and biology in the Peruvian upwelling system.

Resumen

Se demuestra que el comportamiento del ecosistema peruano de afloramiento está determinado, en un alto grado, por eventos aleatorios que lo hacen oscilar entre múltiples estados disjuntos. La media característica de estos procesos aleatorios no estacionarios fué identificado parcialmente como un resultado de procesos correlacionados de ruido fractal. Es decir, una predicción de futuros cambios del ecosistema peruano de afloramiento debe considerar su naturaleza estocástica. Predicciones relevantes, para decisiones administrativas, de períodos mas allá de algunos meses estan probablamente fuera de alcance. Sin embargo, fueron identificados parámetros físicos, los cuales estan mas cercanamente relacionados a cambios de la biomasa de anchoveta que aquellos comunmente observados para caracterizar los eventos de El Niño. Esto permite el desarrollo de nuevos esquemas de monitoreo y conducirá a un mejor entendimiento de las dinámicas de la interfase entre física y biología en el sistema peruano de afloramiento.

Introduction

The Peruvian upwelling system is one of the most productive fishing grounds of the world. Its fishery yields depend in a complex manner, as recently illustrated in a monograph edited by Pauly and Tsukayama (1987), on physical and nonphysical conditions. However, a clear understanding of many of the underlying mechanisms is still lacking.

The question to be tackled here concerns the predictability of the Peruvian upwelling system. However, no prognostic will be given; rather, the past will be investigated to determine how much of the observed changes were due to random events. Thus, it is the degree of stochasticity of the Peruvian upwelling system which is dealt with here. Less stochasticity will be assumed to imply a high degree of predictability.

It may seem strange to attribute the label "stochastic" to an ecosystem, especially if, as generally, each individual interaction in this ecosystem can be described in a deterministic way. However a deterministic description of any system is no assurance against probabilistic properties of that same system (Lasota and Mackey 1985). The prerequisite of stochastic properties, or apparently chaotic behavior, is a nonlinear and dissipative dynamic system (Bohr

and Cvitanovic 1987). This prerequisite is fulfilled with regard to the nonlinearity of the physical laws of hydrodynamics and to most biological processes. The nondissipative character of the system will depend on a special choice of the dynamic constants.

The physics of the Peruvian upwelling system are locally and remotely forced by meteorological events. The local winds drive the upwelling and the remote winds over the central Pacific trigger perturbations which may reach the Peruvian coast. The fluctuations of the winds around the seasonal and diurnal average conditions are random. When the forcing is stochastic, e.g., a white noise, the response of the forced system may quite well be deterministic, if it is a well-tuned oscillator. But, does the Peruvian upwelling system function like a well-tuned oscillator?

The Peruvian upwelling system is sensitive to El Niño - Southern Oscillation (ENSO) events. These events are understood as produced by the feedback of the ocean atmosphere dynamics (Philander and Seigel 1985) leading first to a slow build-up of potential energy and second to its quick release. How the release is triggered is not well understood (Käse 1985) and even low-latitude volcanic eruptions cannot be disregarded as a triggering mechanism (Hofmann 1987). However, independently of the trigger, this auto-oscillation (D. Seidov, Acad. Sc., Moscow, USSR, pers. comm.) is only quasi-periodic and randomly forced sea surface temperature anomalies may be the crucial trigger mechanism (Ponte 1986). Thus, the timing and strength of El Niño events are probably random occurrences.

Going up the hierarchy, the biology of the Peruvian upwelling system is, as anywhere, a complex web of interactions between different species and the nonbiological environment. The interactions may be known or hypothesized to exist, but are generally not evaluated with regard to their relative importance. Thus, no theoretical estimate is available to evaluate if an ensemble of external perturbations of the ecosystem will propagate deterministically or diffuse randomly through it. Furthermore, no theoretical estimate can be derived to evaluate the influence of the stochasticity inherent to the physical environment on the biology.

Some interactions of the species in and with the Peruvian upwelling system are known, e.g., the cannibalization of anchoveta eggs by anchoveta (*Engraulis ringens*) (see Pauly and Soriano, this vol.). Historically, up to some months before the occurrence of the surface signal of the 1971-1972 El Niño, a large stock of anchoveta had been supported by the Peruvian upwelling system and this stock formed the base of the largest fishery in the world. After the collapse, the stock never recovered to former levels. Evidently, it is a worthwhile task to identify "the cause(s)" for the collapse and the nonrecovery of anchoveta, although this may imply a knowledge of the degree to which the observed fluctuations were determined ... "deterministically."

Thus, to summarize the previous considerations: the Peruvian upwelling system may exhibit a variability - at least partly - which is stochastic in character. Furthermore, little is known on the response characteristics of the biological components of the system to external perturbations or to internal instabilities. Thus, it seems appropriate to investigate to which degree the observed changes of the Peruvian upwelling system may be understood as random events. The degree of randomness inherent to the Peruvian upwelling ecosystem will determine the predictability of future changes.

In order to do so, several of the time series of 30 years monthly means, recently made available by Pauly and Tsukayama (1987), will be used. First, some known features of the time series will be interpreted with respect to the stochasticity of the underlying mechanisms. Then, the theoretical background of the hypotheses adopted for further data analysis is given. This is followed by methodological considerations concerning the technique for data analysis.

Preliminary Data Analysis

The following section refers mainly to results of time series analysis on physical parameters as published by Brainard and McLain (1987), Bakun (1987) and Pauly et al. (1987). Most of these time series cover about 30 years by monthly means, with some temporal interpolations.

Seasonality and Anomalies

The parameters to be considered first are the temperature data and the related quantities, such as heat content, isotherm depths and radiation flux. A well-defined seasonal signal is found at the surface and at depths down to about 75 m. At greater depths, e.g., at the depth of the 14° isotherm, the seasonal signal is not visible any longer.

These features are well described by the autocorrelation functions calculated by Brainard and McLain (1987). Fluctuations of the spatially averaged sea surface temperature (SST) are explained to 60% (autocorrelation extreme of about +/- 0.8) by the seasonal cycle. Fluctuations of the local SST, e.g., La Punta and Talara, are explained to about 10% by the seasonal cycle. At depth, e.g., at the depth of the 14° isotherm, 5% of the annual temperature extrema are explained by seasonal fluctuations. This behavior shows that the seasonal signal is generally of limited importance in these depths.

This lesson seems to contradict the impression gained by visual inspection, e.g., of the local SST. However, visual inspection overemphasizes organized structures in terms of variance. Thus, a relatively strong periodic signal superimposed by noise would clearly be seen by eye.

Autocorrelation functions calculated from the time series after subtracting the mean seasonal signal decrease rapidly. The autocoherence drops to values below 0.2 for lags greater than 4 to 12 months, depending on the parameter, and does not increase significantly for longer lags (up to 48 months). The time series of anomalies displays events of the same sign of longer and shorter duration. The amplitudes of these anomalies are, on the average, about one standard deviation. Thus, aside from the seasonal cycle, no other quasi-periodic structure appears to be present in the temperature time series.

The next group of parameters to be discussed concerns wind forcing and sea surface level. Local sea level, Southern Oscillation Index (SOI) and locally and spatially averaged winds show a noticeable seasonal pattern which does not dominate the variance of the time series. Time series of these parameters show, after suppression of the seasonal signal, no well-defined periodic structure. In general, no qualitative differences between these time series and those of the temperature-related parameters are found.

It is common to both groups of parameters that the autocorrelation drops to about 0.7, or less, at a time lag of 2 months. Thus less than 50% of the variance in any month can be explained by the observations 2 months before.

To date, the time series on biological parameters have not been subjected to any analysis similar to those performed with the physical parameters. Visual inspection shows some biannual variability for the anchoveta biomasses and several pulses starting from different background levels. The overall impression is that of a more regular behavior than for the physical parameters, combined with larger amplitudes of the fluctuations.

These observations suggest that most of the variability in the time series is caused by relatively short, not-correlated events. Periodic, mainly seasonal signals, are present but are submerged by a strong background noise. In order to test this, a statistically robust form of spectral analysis has been applied (see below).

Data Preprocessing

Spectral and other analyses have been applied to the SST-related time series (spatial mean temperature and local measurements at La Punta, Callao) as well as to other series: depth of the 14° isotherm, upwelling and turbulence indexes (calculated from spatially averaged winds), offshore Ekman transport, SOI, absorbed solar radiation and VPA-biomass estimates of the anchoveta length classes centered about 4.25 cm (recruits) and 16.25 cm (mature adult fish). It is assumed that the two biological time series contain most physical and nonphysical influences affecting anchoveta. Thus, they are taken as a measure of the integrated response of the ecosystem to natural and anthropogenic (fishery-induced) perturbations.

Table 1 gives the sources of all time series discussed here; these sources provide detailed descriptions of the time series and their derivation from raw data. The period considered, January 1953 to December 1977, excludes the extreme 1982-1983 El Niño and its possible preludes from

Table 1. Monthly time series on the Peruvian upwelling ecosystem analyzed in this contribution.[a]
Tabla 1. Series de tiempo mensuales del ecosistema peruano de afloramiento analizado en esta contribución.

No.[b]	Code	Definition (units)	Source
1	SST_M	Spatially averaged sea surface temperature (°C)	Pauly and Tsukayama (1987, Table 2)
2	SST_L	Local sea surface temperature (°C)	Brainard and McLain (1987, Table 3)
3	TUI	Turbulence index (m^3s^{-3})	Bakun (1987, Table 7)
4	UPI	Upwelling index ($m^3s^{-1}m^{-1}$)	Bakun (1987, Table 5)
5	D_{14}	Depth of 14° isotherm (m^{-1})	Brainard and McLain (1987, Table 7)
6	EKV	Offshore Ekman transport ($m^3s^{-1}m^{-1}$)	UPI/D_{14}
7	SOI	Southern Oscillation Index (millibars)	Brainard and McLain (1987, Table 1)
8	Q	Absorbed solar radiation (watts m^{-2})	Bakun (1987, Table 8)
9	$A_{4.25}$	Biomass of 4.25 cm anchoveta recruits (tonnes)	Pauly et al. (1987)
10	$A_{16.25}$	Biomass of 16.25 cm adult anchoveta (tonnes)	Pauly et al. (1987)

[a]All time series on a monthly basis, from 1953 to 1977.
[b]The rate of change of any series is coded n'. Thus, e.g., rate of change of D_{14} is coded 5'.

the analysis. Furthermore, at least some of the time series on physical parameters seem to have changed their behavior in the late 1970s, compared to the preceding period. Thus limiting the analysis to the period 1953 to 1977 favors stationarity of the derived statistics.

Each time series has been analyzed in four different forms: (i) in its original form but with interpolated missing values, (ii) after transformation as described below, (iii) after differentiating in time by central differences, (iv) after differentiating and transformation.

Differentiating eliminates linear trends. The transformation eliminates the seasonal signal of the time series and normalizes the deviations from the seasonal signal. For transformation, the median-seasonal cycles of the time series have been calculated. In order to get reliable and independent estimates of the medians, three consecutive months were grouped into one season (January, February, March = summer, etc.). Then each data point has been replaced by an index (1,2, ... 12) indicating the twelfth-quantile (quantile width: 8.33%) to which it belongs. The use of medians and quantiles instead of means and standard deviations is due to the need to calculate robust statistical estimates from non-normally distributed data (Huber 1981). Twelfth-quantiles are used because these describe directly some common statistics data sets. The 95% confidence limits of the medians correspond to the 5/12 and 7/12 quantiles; also, two-thirds of the data are between the 2/12 quantile and the 10/12 quantile.

Fig. 1 shows seasonal cycles of four parameters. The mean seasonal cycle is generally not sinusoidal. Seasonal means of the spatial averaged SST are the same for the periods July to September and October to December. The mean depth of the 14° isotherm is the same from January to September. Upwelling has different strengths in all seasons and mean biomass of mature adult anchoveta shows no seasonal cycle. Deviations from mean conditions dominate the seasonal signal for all parameters. The amplitudes of the deviations from the medians are asymmetric. Thus, means estimated by arithmetic averaging will lead to different estimates of the seasonal cycle. The difference is due to the tendency of the arithmetic mean to minimize the variance.

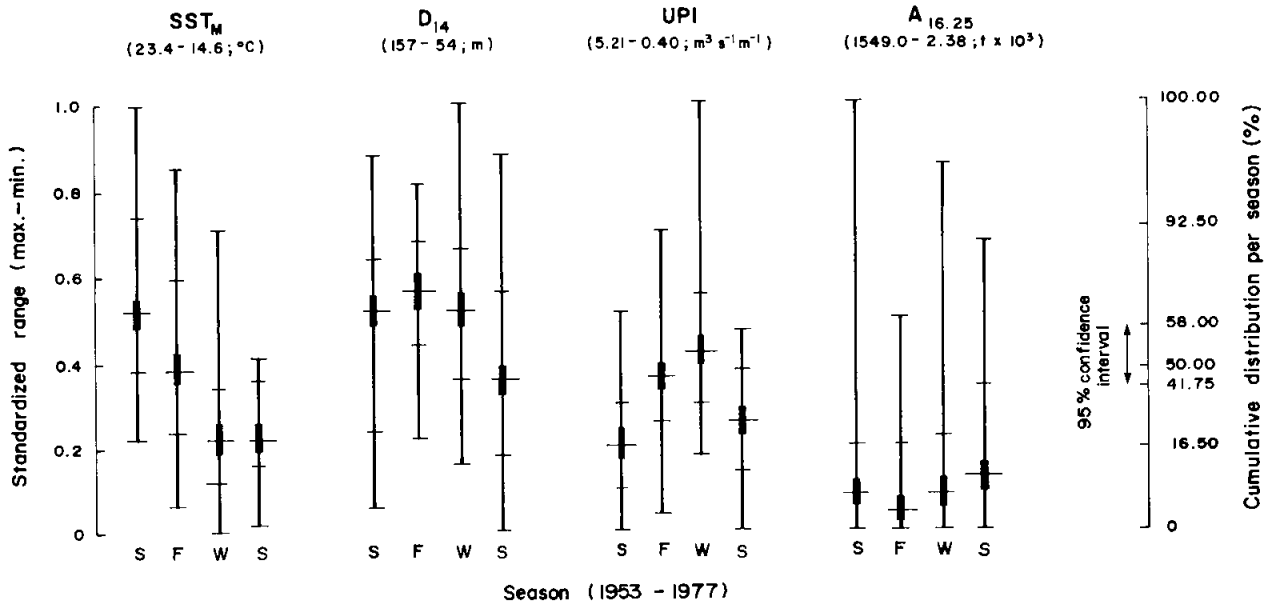

Fig. 1. Examples of the mean seasonal signal shown by the normalized form of four parameters (see Table 1 for definition). The total ranges are shown (top and left scale). The standard errors (bold) refer to the 95% confidence intervals of the medians (see right scale). The seasons (SFWS) refer (from left to right) to months: January-March, April-June, July-September, October-December.

Fig. 1. Ejemplos de la señal estacional media mostrados por la forma normalizada de cuatro parametros (ver Tabla 1 para la definición). Los rangos totales son mostrados (ver arriba y escala izquierda). Los errores estándares (linea gruesa) se refieren al 95% intervalo de confianza de las medias (ver escala derecha). Las estaciones (SFWS) se refieren (de izquierda a derecha) a los meses: Enero-Marzo, Abril-Junio, Julio-Septiembre, Octubre-Deciembre.

Spectral Analyses

The technique used for spectral analysis, a modification of Nuttals' (1971) procedure of short averaged periodograms was used to estimate Fourier transforms of 9 five-year long, prewhited - recolored and 50% overlapping lags of the time series. Median power spectra and their 95% confidence intervals were calculated, and the slopes of the median spectra were estimated for periods ranging from 60 to 6 months.

The results obtained by the spectral analysis are summarized in Fig. 2 and Table 3. Bands of high variance are identified as "peaks" if the confidence limits do not overlap. The widths of the confidence limits show the variability on the time scales longer than 5 years. The spectra are generally less structured. The variance is distributed continuously over a broad range of periods, a feature typical for time series of random sequences of individual events. No important changes in the main features of the spectra were found when the spectra of the time series themselves were compared to their rates of change. Thus, the time series of the observed variables and their rate of change are similar sequences of random events.

No significant peaks were found, except for absorbed solar radiation "Q" at a period of 12 months. Thus, only this parameter has a clear seasonal signal which covers broadly, including the spectral bandwidths, the period range from 18 to 9 months. All spectra of original time series show bands of high variance centered around a 12-month period. Several spectra show a steplike decrease of variance to shorter periods at periods near to 12 months. Thus, the seasonal cycle is relatively well represented, but cannot be statistically distinguished from the events which form the background signal at neighboring periods. The seasonal fluctuations have high variances but vary so much at longer time scales that they are not statistically different from fluctuations at other periods.

Some spectra of the transformed time series show relatively high, but not statistically different variances for the period range 45 to 25 months. This feature was found for SST,

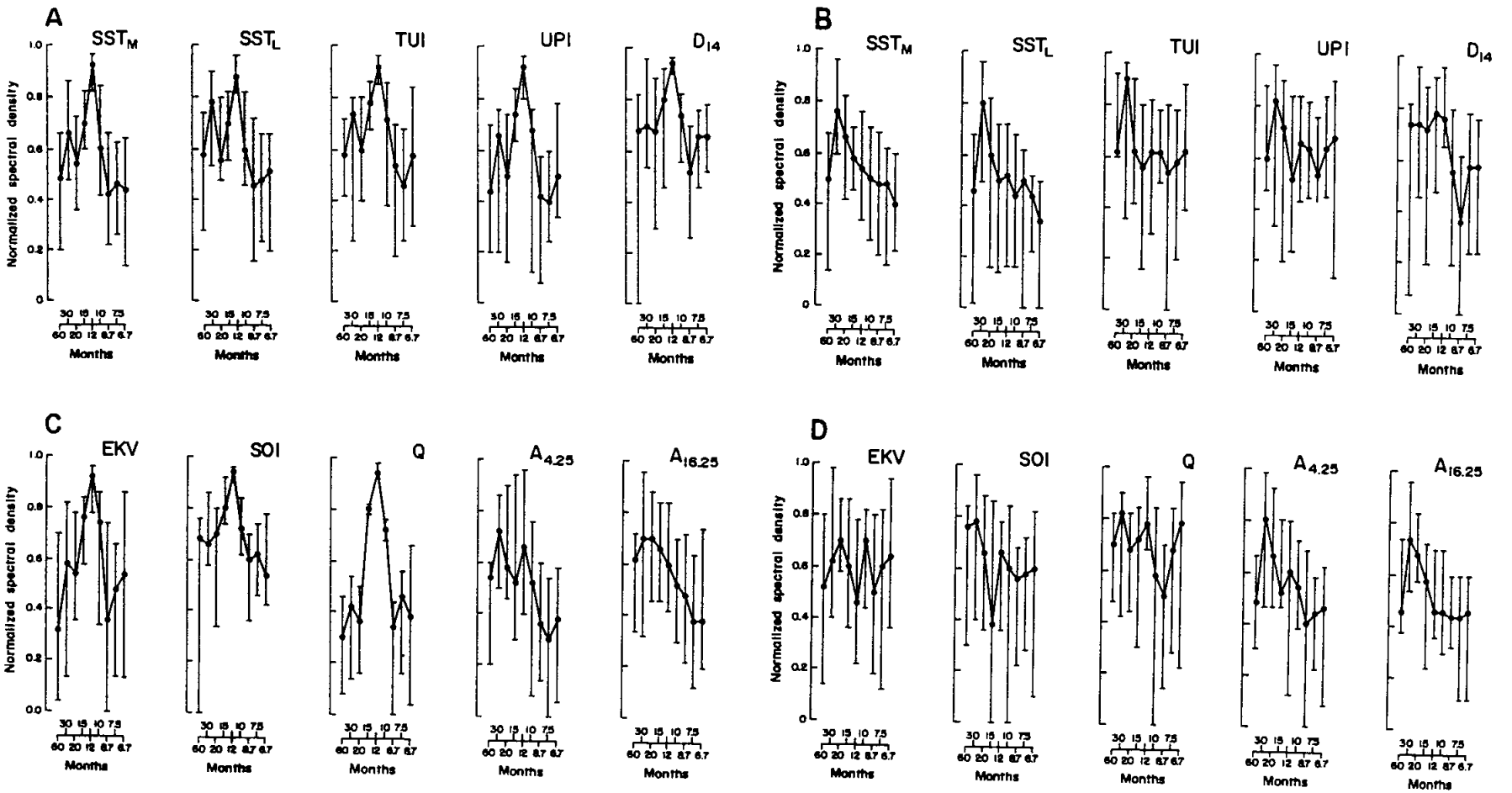

Fig. 2. Mean variance spectra (logarithmic and normalized) showing the 95% confidence interval of the median variance (see Table 3 for further statistics on these spectra). A. Original time series; B. Transformed time series; C. Original time series; D. Transformed time series.

Fig. 2. Espectros de la varianza media (logaritmicos y normalizados) mostrando el 95% intervalo de confianza de la varianza mediana (ver Tabla 3 para otras estadísticas de estos espectros). A. Series de tiempo originales; B. Series de tiempo transformadas; C. Series de tiempo originales; D. Series de tiempo transformadas.

anchoveta biomasses, SOI, the turbulence index and to a lesser degree, for the upwelling index also. This signal is most probably due to the mean time interval between two successive El Niño events. Therefore, it should be noted that the spectra of the transformed time series on the depth of the 14° isotherm is flat for periods longer than 12 months. One result of this is that the temporal changes of the temperature structure of the upper layer are different at depth and near the surface. This corroborates similar results obtained by Brink et al. (1983) for motions on shorter time scales.

To summarize: the spectra have properties which are inconsistent with the hypothesis that the time series are composed of a small number of periodic signals. The spectra obtained corroborate the suggestion that the variability of the Peruvian upwelling system should be described as a sequence of random events. Periodic deterministic patterns are of little importance and are probably restricted to the seasonal cycle.

Theoretical Considerations

The results of the preliminary data analyses suggest that a substantial part of the observed changes in the Peruvian upwelling system are due to sequences of random events. Here a mathematical tool will be developed to handle sequences of random events.

The general model

$$Y(x+t) = Y(x) + V * t^a \qquad ...1)$$

was used (Turcotte 1988). Here, "Y" takes the place of any derived quantity, but could be the observation itself; "x" is the value of the independent variable at the starting point and "t" is its increment; "a" is a constant to be determined, and "V" is a stationary random variable taken from a distribution with unknown moments which, likewise, have to be determined if the process (1) is to be completely described. Thus, equation (1) defines Y by a random process which is nonstationary in t if a is not equal to zero.

If E() is a linear estimator of the expectation, e.g., of the mean, then (1) may be rewritten:

$$E(Y(x+t)) = E(Y(x)) + U * t^a \qquad ...2.1)$$

$$U = E(V) \qquad ...2.2)$$

Averaging is done over an ensemble of Y values at different starting points x and same increments t. Thus, E() is an ensemble average and its expected value varies with t^a.

If E(Y(x)) is equal to zero, then

$$\ln(E(Y(x+t))) = \ln(U) + a * \ln(t) \qquad ...3)$$

holds. Equation (3) holds approximately for nonvanishing E(Y(x)) if $U * t^a$ is sufficiently larger than E(Y(x)).

It can be expected that given values of a and of the statistical moments of V hold only for a limited range of t values. Their lower and upper bounds give the range within which the process (1) is correlated.

Equations (2.1) and (2.2) can now be interpreted on three different levels. First, the equations give only an average power law dependence of Y as a function of t. Second, the equations describe the average geometrical properties of Y as a function of t. Third, they determine the nonstationary mean characteristic of the random process (1).

In order to illustrate the random process characteristics of the model, equation (1) may be rewritten as

$$(Y(t) - Y(O))/(t^a) = V \qquad ...4)$$

(where the x has been dropped for convenience).

Thus, the normalized increment of Y is a random variable. Equation (4) is identified as a definition of a random walk, if a is equal to 1/2 and V is Gaussian. If a is zero and V is Gaussian, then (4) describes a Gaussian white noise process. Thus, (1) is a generalization of a first order stationary noise process.

The geometrical interpretation can be performed by comparing to the particular forms of (1). First, the "new" value of Y is estimated in "one step":

$$Y(T) = Y(O) + V * T^a \qquad ...5.1)$$

and second, the "new" value of Y is estimated in "several steps" (n):

$$Y(n * t) = Y(O) + (V_1 + V_2 + ... V_n)\, t^a \qquad ...5.2)$$

Both forms of estimation of new values of Y lead to the same expected value of new Y, if

$$a = \ln(n)/\ln(T/t) \qquad ...6)$$

holds.

Equation (6) is the definition of the fractal dimension a. Here, a relates the ratio of the scales of increments T and t to the number of repetitive use of the smaller scale to "measure the same object". The object measured is the mean difference between old Y and new Y as a function of the increment of the independent variable.

Using (6) in (5.1) gives the expectation of Y(T) as a function of the small increment t:

$$E(Y(T)) = E(Y(O)) + n * E(V) * t^a \qquad ...7.1)$$

$$\ln(n) = \ln(T/t) * a \qquad ...7.2)$$

Thus, the prognostic of Y(T) done by small steps of length, for example, "t = 0.1 * T" can be done in 10 steps only if a is equal to one.

In consequence, (nearly) any *ad hoc* decomposition of the increment T of a given process (1) into smaller increments will lead to different estimates of its mean characteristics. Commonly used refinements of increments, such as "divide T in two parts of length T/2 each" will have no influence on the estimate E(Y(T)) only if the process is stationary (a=0) or linear (a=1). Thus, estimates, e.g., of the mean values will depend on the sampling frequency, for any quantity varying with (1) if the statistical process is neither stationary nor linear.

Summarizing the properties of the model (1): If a is greater than zero and fixed for a given interval of t, then (1) describes a correlated random process which has a mean fractal geometry and is defined for the given interval of t. Thus the process (1) is a "correlated fractal noise process" (CFNP).

Methodological Considerations

The following section briefly discusses the quantities analyzed using the concept of a CFNP, as developed above. Furthermore, the main lines of interpretation and the questions to be answered by the analysis are presented.

Estimates of the nonstationarity of the time series are considered first. Prognostics can be given only if the degree of nonstationarity is known. Second, mean spectral slopes are relevant because CFNP's (time as independent variable) can be identified by their variance spectra (Turcotte 1988). Thus, the contribution of noise processes to the observed fluctuations must be considered. The last quantity analyzed involves the concept of the phase space and the distribution of observations (the phase points) in this space. Here correlation over distance in the phase space and its geometry is used to draw conclusions regarding the interdependence of different parameters, e.g., SST and SOI.

Direct estimates of the exponent a of the CFNP (2.1) are calculated by means of linear regression (equation 3). The slope of the linear regression is evaluated for the widest (centered) interval of the independent variable for which: (1) the square of the regression coefficient is above 0.33 (i.e., explained variance is above 33%), (2) the regression coefficient is statistically different from zero (95% confidence level) and (3) the interval of the independent variable for which the regression holds can be divided in sub-intervals for which conditions (1) and (2) are fulfilled.

Analyses of Nonstationarity

In order to estimate the degree of nonstationarity of the time series, three quantities have been analyzed using the model (1): (i) the difference of mean values calculated from two lagged fractions of the same time series as a function of the lag; (ii) the covariances of two lagged fractions of the same time series minus the variance found for lag zero as a function of the lag; (iii) the number of extrema (minima or maxima) during an observation period of given length as a function of the observations period. Nonstationarity of the time series will show up either via the difference of mean values and of covariances, which depend on the lag, or via the counts of extrema (which do not increase linearly with the length of the observation period).

The variability of mean values and covariances of the time series for lags between 3 to 97 months was analyzed by a technique based on a procedure in McHardy and Czerny (1987). Two fractions of the time series, each about 8 years long, were taken, which are separated by a given lag. The difference of their means and the difference of their covariances are estimated. This procedure is then repeated for about 100 starting points (see equation 1) along the entire time series. The medians of these differences are analyzed as a function of the lag t.

If the averaging period is sufficiently long and if the process which generated the time series has stationary means and covariances, then the differences should vanish (in the statistical sense). The exponent a in equation (2.1) would thus be estimated as zero and Y(t) would be identified as a stationary random variable. Any drift of the differences would reflect a trend, i.e, a nonstationarity of the underlying process. If no functional dependence of the averaged distances exists, then the process (1) cannot be used validly to describe the observed form of nonstationarity.

The number of extrema above or below a given threshold has been counted for periods of increasing length, from 3 to 97 months, as was the median counts for about 100 starting points. The threshold has been defined by either the seasonal 2/12-quantiles or the 10/12-quantile (Fig. 1). Thus, extrema are counted relative to the mean seasonal signal. If the process generating extreme values is stationary, then the counts should increase proportionally with time and a in equation (2.1) should be estimated as one.

Spectral Slopes

The spectral analyses covers the time interval from 5 months to 5 years. Spectra have been calculated as reported above. Then, the mean increase of the median variance as a function of the period was analyzed. In order to do so, a power function was fitted to the spectra for the range of periods from 60 to 6 months. The exponent (b) of the power function of the dependence of spectral variance was related by Turcotte (1988) to the exponent a of the CFNP process (1) via:

$$b = 2 * a + 1 \qquad ...7)$$

A white noise process is described by a flat variance spectrum, while a random walk process has a variance spectrum that increases in proportion to the period squared. Thus, the spectral slope and the fraction of the explained spectral variance describe, for the interval of periods analyzed, the mean characteristic and relative importance of the process by which the time series has been generated. If no mean slope can be estimated, then CFNP of form (1) do not contribute to the observed time series.

Distribution of Phase Points

This analysis starts from the concept of the phase space. Two variables observed at the same time or one variable and its rate of change can be plotted as a function of each other. The surface defined by this procedure can be understood as a (two-dimensional) phase space. The observations are the discrete representation of the phase line (Fig. 3). A cyclically changing variable and its rate of change or two variables which are out of phase but have a fixed phase lag would define a closed loop (i.e., a phase cycle) in the phase space. Less well correlated variables would define a cloud of points in the phase space. Here, only one case of a phase cycle has been found; it pertained to absorbed solar radiation and its rate of change. All other clouds of phase points scattered without structure over the phase space.

The mean geometrical structure of the clouds of phase points was analyzed using the approach of Lovejoy et al. (1986). If two independent random variables are plotted against each other, then their scatter plot will show no internal structure. Furthermore, the phase points of two parameters related in complex fashion will be scattered over their phase space likewise such that no internal structure is apparent (Fig. 3). However, not all combinations of values of two such parameters are possible. Thus, there are areas in the neighborhood of a given phase point which will never include a phase point. Thus, the phase space is a patchwork of voids, forbidden regions, and of phase lines along which the phase points are distributed. Therefore, subregions of the scatter plot with high and low density of points will be found, and the number of points found in the neighborhood of a given point will increase in proportion to the power of less than two (i.e., the square of the distance). Thus the local dimension of the scatter plot of phase points will differ from two.

The quantity to analyze, in accordance with the CFNP model (1), is the average number of phase points within a circle of a given radius as a function of the radius. The phase space defined by the observed minima and maxima of the parameter has been divided in M cells, M being equal to the number of observations (N) squared. Thus, two parameters depending upon each other in strictly linear fashion will tend to form a phase line along a diagonal of the phase space. In this case, the number of points within a circle of a given radius increases proportionally to the length of the radius. If, on the other hand, the phase points were distributed regularly on a cartesian grid, counting the number of points within circles of increasing radius (large increase compared to the grid spacing) would show that the number of points increases proportionally to the square of the radius. Thus, if the distribution of phase points on the cartesian grid is done

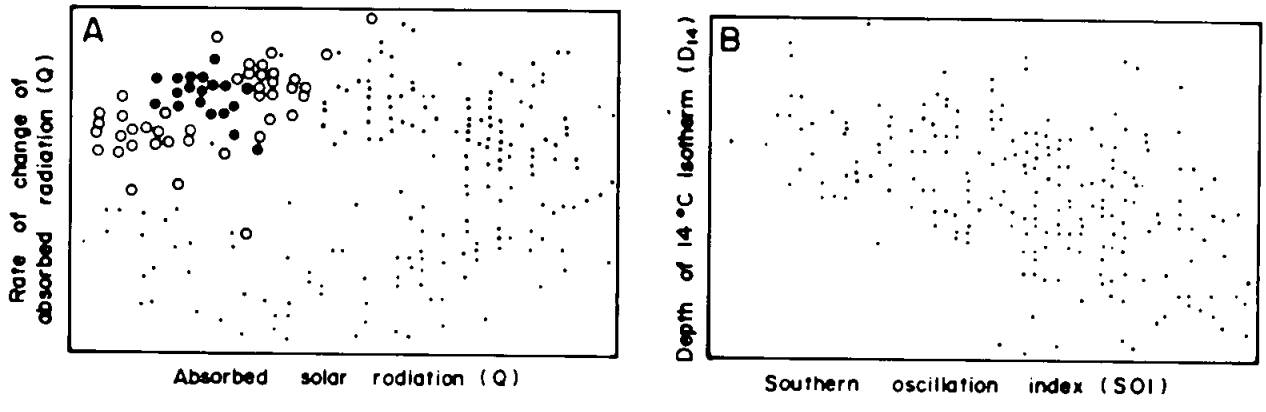

Fig. 3. Two examples of a two-dimensional phase space, as defined by two parameters each. Note the roughly circular structure of the phase points of the phase space for rate of change of absorbed solar radiation *vs.* absorbed solar radiation. (Closed circles represent August observations; open circles represent July and September observations; small dots represent the other observations).

Fig. 3. Dos ejemplos de un espacio de fase bidimensional, definido por dos parámetros. Notar la grosera estructura circular de los puntos del espacio de fase para tasas de cambio de radiación solar absorbida contra radiación solar absorbida (circulos llenos representan observaciones en Agosto; circulos vacios representan observaciones en Julio y Septiembre; los puntos representan otras observaciones).

regularly (in the statistical sense), then the square dependence of the number of points within the circle defined by a given radius will be recovered, on the average.

Two estimates of the mean dimension of the cloud of phase points are given here, one for lengths of radius ranging from 0.1 * N cells to 0.9 * N cells (long radius, $R_{(G)}$, or "global" dimension), and the second for the range 0.015 * N to 0.15 * N cells dimension (short radius, $R_{(L)}$, or "local" dimension). In order to avoid strong border effects, the reference points from which the counting procedure start are those phase points whose coordinates lie within the range given by the seasonal 4/12-quantiles and 9/12-quantiles.

Comparing the (fractal) dimensions of phase spaces defined by different parameters then shows which parameters are more closely related than others. The "global" and the "local" geometry of the cloud of space points is estimated by the dimensions for long ($R_{(G)}$) and short ($R_{(L)}$) radius lengths. Dimensions of about two will be found for space points which are evenly distributed. The interpretation is that the investigated pair of parameters is not related and that any combination of values is possible. Dimensions somewhere between about one and less than two will be found for space points which are distributed along intersecting lines. The interpretation is that many but not all combinations of a pair of parameters are possible. Dimensions below one will be found for space points which cluster in disjoint patches. The interpretation is that only few parameter combinations can occur.

Results and Discussion

Stationarity

Table 2 gives the results of the six different tests of stationarity of the time series and their rate of change which have been performed.

The overall ratio of "failed" to "passed" is 91 to 29. This ratio is biased toward "failed" because some of the observed nonstationarities cause only small effects. Therefore, some "failed" cases might be classified as "practically stationary". However, discussing this further would involve arguments on the range of nonstationary changes which are acceptable. It seems to be reasonable to rely only on those criteria (for accepting a regression) which have been presented above. Therefore, we conclude that temporal changes of the Peruvian upwelling system are mainly nonstationary. Three details should be mentioned, however, which qualify this statement:

(i) 8-year means are nonstationary for all time series and all derived time series, whether they have been transformed or not (by eliminating the seasonal signal and normalizing the fluctuations). Thus, stable mean values characterizing the Peruvian upwelling system need averaging over periods considerably longer than 8 years to eliminate the influence of long-lasting anomalies.

(ii) the covariances of the transformed time series are generally stationary, the single exception being absorbed solar radiation. The covariances of original time series are stationary for all temperature-related series (SST_M, SST_L, D_{14}), for upwelling (UPI) and for the biomass of anchoveta recruits ($A_{4.25}$). Thus, covariances characterizing the variability of the Peruvian upwelling system might be estimated from 8-year-long records - at least after elimination of the seasonal signal and normalization of the anomalies.

(iii) the least stationary parameter seems to be the SOI; only the covariance of its transform is stationary. However, the frequency of "failed" cases varies only slightly between all parameters beside local sea surface temperature (SST_L) and biomass of anchoveta recruits; the latter is the most stationary parameter. The stationarity of the least two parameters is documented, in spite of changing mean values, by the occurrence of extreme values in the original series, in their rate of change and in the covariances.

Table 2. Results of tests of stationarity for six time series (upper rows) and their rate of change (lower rows).[a]
Tabla 2. Resultados de pruebas de estacionalidad para seis series de tiempo (renglones superiores) y su tasa de cambio (renglones inferiores).

No.[b]	Variable[b]	Test statistics[c] E+	E-	M_1	C_1	M_2	C_2	Ratio failed:passed
1	SST_M	0	0	0	1	0	1	9:3
		1	0	0	0	0	0	
2	SST_L	1	1	0	1	0	1	7:5
		0	0	0	0	0	1	
3	TUI	0	1	0	0	0	1	9:3
		0	1	0	0	0	0	
4	UPI	0	0	0	1	0	1	10:2
		0	0	0	0	0	0	
5	D_{14}	0	0	0	1	0	1	10:2
		0	0	0	0	0	0	
6	EKV	1	0	0	0	0	1	10:2
		0	0	0	0	0	1	
7	SOI	0	0	0	0	0	1	11:1
		0	0	0	0	0	0	
8	Q	0	1	0	0	0	0	10:2
		0	1	0	0	0	0	
9	$A_{4.25}$	1	0	0	1	0	1	6:6
		1	0	0	0	1		
10	$A_{6.25}$	1	0	0	0	0	1	9:3
		0	0	0	0	0	1	
	Sum	14:6	14:6	20:0	15:5	20:0	8:12	91:29

[a]0 = test failed; 1 = test passed.
[b]See Table 1 for definitions.
[c]E+, E-: frequency of extrema; mean and covariances of original M_1, C_1 and transformed M_2, C_2 time series (see text for details).

Noise-like Temporal Structure

The spectra shown in Fig. 2(A-D) have previously been discussed in relation to the importance of the seasonal signal and the variability on periods longer than 5 years. Here the mean increase of variance in function of the period is discussed because these "spectral slopes" are related to special forms of CFNP's (Table 3). This type of model was used to qualify the random events which contribute to the temporal structure of the time series. The CFNP is accepted as relevant if it describes more than 1/3 of the variance of the time series.

It was found that no original time series of physical parameters fit the CFNP-concept (Figs. 2A and 2C). However, both VPA-biomass time series do. This is due to the seasonal signal which appears more important in the physical data than in the biomasses. Transformed time series of SST's, depth of the 14° isotherm (D_{14}), SOI and VPA-biomasses may be described by CFNP's (Fig. 2B and 2D). It should be noted that all physical parameters linked to

Table 3. Confidence intervals of slope (b) and coefficient of determination (r^2) of linear regressions analysis of variance spectra in Fig. 2 (A-D), i.e., of linear plots of log (variance) *vs.* log period.[a]
Tabla 3. Intervalo de confianza de la pendiente (b) y el coeficiente de determinacion (r^2) del análisis de regresión lineal de espectros de varianza en la Fig. 2 (A-D), es decir, de gráficas lineales de log (varianza) versus log (período).

No.[b]	Variable[b]	Spectrum in figure	Confidence interval of slope[a]	Coefficient of determination (r^2)
1	SST_M	2B	0.25-1.55	0.52
2	SST_L	2B	0.25-2.00	0.48
5	D_{14}	2B	0.25-1.35	0.53
9	$A_{4.25}$	2C	0.50-2.50	0.56
10	$A_{16.25}$	2C	0.50-2.00	0.66
7	SOI	2D	0.15-1.45	0.42
9'	$A_{4.25}$	2D	0.20-1.90	0.42
10'	$A_{16.25}$	2D	0.40-1.80	0.42

[a]Result in this table refers only to significant correlations ($P < 0.05$).
[b]See Table 1 for definitions.

meteorological forcing, e.g., the upwelling index, show no structure which can be described by CFNP's.

Overall, CFNP's describe about half of the variance (42%-66%) of the time series and all spectral slopes are significantly different from zero. Consequently, the CFNP's are different from white noise processes which are characterized by a vanishing slope of the variance spectra. The slopes of the different spectra are, due to the wide confidence limits (95% level), not significantly different from each other and from a slope of one. Thus, details on the nature of the CFNP's cannot be given beyond stating that it is near-brownian (fractal brownian in the notation of Turcotte (1988)). Therefore, equation (1) may take for SST, 14° isotherm depth, SOI and the VPA-biomasses the form:

$$Y(t+x) = Y(x) + V * t^a;\ a \geq o \qquad ...8)$$

However, there is a tendency towards steeper spectral slopes for the VPA-biomasses compared to the physical parameters; this may lead to slightly different exponents in equation (8).

In summary, the main characteristics of the temporal behavior of the parameters analyzed are: (i) parameters related to meteorological forcing (upwelling index, turbulence index, Ekman transport and absorbed solar radiation) are characterized by seasonal variations and an unspecified noise process; (ii) the parameters describing the thermal structure of the upper layer of the Peruvian upwelling system (SST's and depth of the 14° isotherm) are characterized by seasonal variations and a correlated fractal noise process (CFNP) which is of near-brownian nature; (iii) the biological parameters (VPA-biomasses of recruits and of mature adult fish) are characterized by CFNP of near-brownian nature.

Interrelationships Between Parameters

The interrelationship of parameters can be measured, as discussed above, by the dimension of a cloud of phase points. Two estimates of the dimensions have been calculated, a "local"

estimate ($D(R_L)$) for small regions and a "global" estimate ($D(R_G)$) characterizing the whole phase space. These two dimensions (including confidence limits) characterize the cloud of space points of each pair of parameters. Their values are used to define a "point" in a scatter diagram of "global dimension *vs.* local dimension". Fig. 4 presents the possible pairs of parameters, as ordered in three different groups.

Fig. 4A presents all pairs of parameters which are evidently a function of each other. These pairs are: (i) "parameter against its rate of change"; (ii) "two parameters derived from the same data"; and (iii) "mean SST_M *vs.* local SST_L". In Fig. 4A, the global dimensions scatter between 0.25 and 1.5 and the local dimensions scatter between 1.00 and 2.00. This indicates that the phase spaces are unevenly covered with phase points, voids are present, but subregions of some phase spaces are found which are evenly covered by phase points (local dimension near two).

For example, the phase space defined by the absorbed solar radiation (Q) and its rate of change (see Fig. 3A) has a global dimension of about 1.35 - 1.40 and a local dimension of about 1.75 - 1.80 (see Fig. 4A). The phase points in some small subregions of the phase space are more evenly distributed than all phase points over the entire phase space. The corners and the central

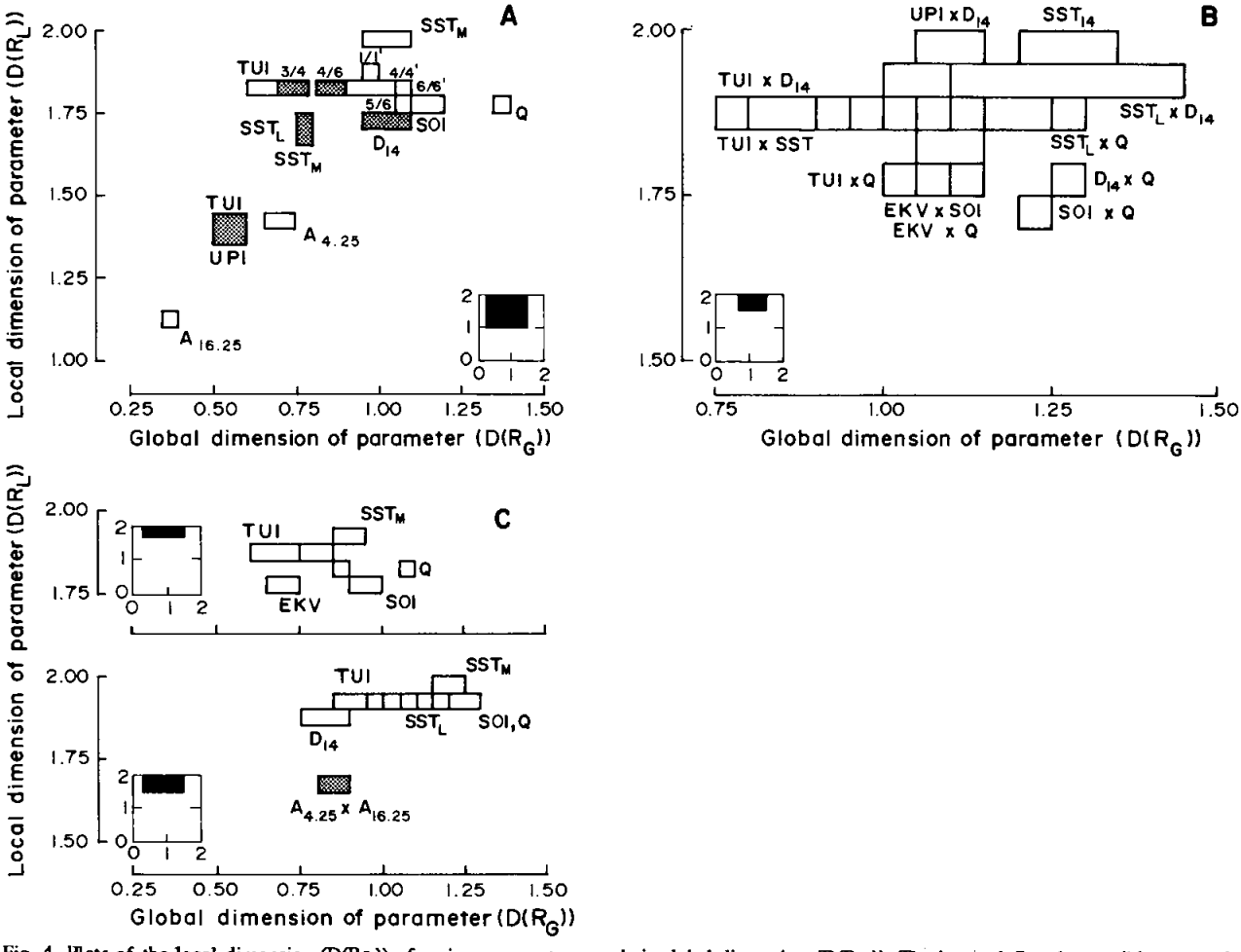

Fig. 4. Plots of the local dimension ($D(R_L)$) of various parameters *vs.* their global dimension ($D(R_G)$). The insets define the possible range of dimension, and the range actually occupied (black rectangles). Some rectangles and/or squares are not labeled, due to space limitation. A. Pairs of parameters were derived from the same databases (shaded rectangles) or one is the rate of change of the other (open rectangles). B. Same as A, but referring to unrelated parameter pairs (different databases, no differentiating). C. Same as A, but for "biological" *vs.* "physical" parameter pairs. Upper graph: physical parameters *vs.* biomass of anchoveta with length of 16.25 cm ("adults"). Lower graph: physical parameters *vs.* biomass of anchoveta with length of 4.25 cm ("recruits").

Fig. 4. Gráficas de la dimensión local ($D(R_L)$) de varios parámetros contra su dimensión global ($D(R_G)$). Los insertos definen los rangos de dimensión posibles, y el rango realmente ocupado (rectángulos negros). Algunos rectángulos y/o cuadrados no estan rotulados, debido a limitaciones de espacio. A. Pares de parámetros fueron derivados de la misma base de datos (rectángulos sombreados) o uno es la tasa de cambio del otro (rectángulos vacios). B. Lo mismo que en A, peró refiriendos a pares de parámetros no relacionados (diferente base de datos, sin diferenciación). C. Lo mismo que en A, pero para pares de parámetros "biológicos" versus "físicos". Gráfica superior; parámetros físicos versus biomasa de anchoveta con longitudes de 16.25 cm ("adultos"). Gráfica inferior: parámetros físicos versus biomasa de anchoveta con longitudes de 4.25 cm ("reclutas").

region of the phase space is nearly empty of phase points (see Fig. 3A). It is concluded that most surface points of the phase space in the neighborhood of a given phase point are possible phase points. The number of voids, or forbidden regions, is relatively small. Thus, future observations of the amount of absorbed solar radiation and its rate of change will be most probably "anywhere near" already observed combinations. However, very different values of one parameter should often go together with different values of the other parameter. These features are expressed by (i) the local geometry of the cloud of phase points - which is roughly a surface and (ii) a global geometry i.e., network of multiple crossing phase lines and voids (forbidden regions).

The ensemble of phase space dimensions of the pairs "physical parameter against its rate of change" in Fig. 4A has a clear main pattern: the global and local dimensions are about 1.0 and 1.8, respectively. These values characterize a phase space which is mainly void on the global scale, but with phase points that are quasi-evenly scattered (local dimension near two) along continuous phase lines (global dimension about one). Different characteristics are found for the phase spaces of the anchoveta biomass, the turbulence index, absorbed solar radiation and spatially averaged SST_M.

The highest local dimension is found for SST_M. This phase space is, on the local scale, evenly covered by phase points (local dimension of two). The local geometry of the cloud of phase points corresponds to a surface. Slightly different values of SST_M are compatible with any slightly different value of its rate of change. The highest and lowest global dimensions for the physical parameters are found for the absorbed solar radiation and the turbulence index, respectively. The phase points of absorbed solar radiation (global dimension well above one) are distributed along multiple crossing phase lines, but for the turbulence index (global dimension less than one) the scatter is around disjunct subregions of the phase space, each indicating a different level of turbulence (strength and rate of change).

The local dimensions of the phase spaces defined by the anchoveta biomasses and their rates of change are relatively small (between 1.10 and 1.45). This suggests that the local geometry of the cloud of phase points does not correspond to a surface, but to a mixture of crossing phase lines and voids, forbidden regions. Thus, the rate of changes of the anchoveta biomasses depend strongly on the biomasses and not all combinations are possible. The global dimensions of the phase spaces defined by the anchoveta biomasses are less than one. This describes the global structure, or geometry, of the cloud of phase points as composed of disjunct sub-clouds, each indicating a different level of the anchoveta stock (biomass and its rate of change).

The combination of local and global features which distinguish the biological parameter from the physical parameter are most pronounced for the biomass of mature adult anchoveta. It might be suspected that the VPA-algorithm is the cause of this different behavior. This argument may be partly correct, but it fails to explain the very different dimensions found for mature anchoveta and anchoveta recruits. Thus, the small dimensions of the phase spaces defined by the biological time series may not be an artifact.

Fig. 4A shows a second ensemble of dimensions, those obtained from parameters which are linked through the data used for their estimation. Most estimates of local and global dimensions scatter for these parameters around 1.75 and 0.90, respectively. These dimensions are smaller than those obtained for parameter pairs which have no common database (in Fig. 4B). What these dimensions measure, however, is the distortion caused either by the mathematical procedure or by the combination of two independent data sources. The individual estimates, as given in Fig. 4A, show: (i) the "blurring" of an unequivocal relation on the local scale (local dimension greater than one) and (ii) a disruption of this relation on the global scale (global dimension less than one). Lower local and global dimensions than those given above are found for turbulence index *vs.* upwelling index. This is not surprising since both are closely related (via the winds used to compute both) and do not depend on a third parameter.

Fig. 4B shows the local *vs.* global dimensions for phase spaces defined by two independently determined physical parameters (of which an example is shown on Fig. 3B). The local and global dimensions scatter around 1.85 and 1.10, respectively, which is not very different from the dimensions of phase spaces defined by dependent physical parameters as discussed above. However, the differences are important when individual pairs are considered.

(i) local dimensions not statistically different from two are found for the parameter pairs upwelling index versus 14° isotherm depth and mean SST *vs.* absorbed

global radiation. Thus, for these parameter combinations, any point of the phase space near a given phase point is a possible phase point, or conversely, there are no voids in the neighborhood of any phase. Global dimensions for these two parameter pairs are about 1.1 and 1.3. Thus, both phase spaces are covered by phase points scattering evenly along multiple crossing phase lines separated by voids. It follows from this that small changes of one parameter, e.g., upwelling index, are consistent with any small change of the other parameter, e.g., 14° isotherm depth (D_{14}).

(ii) small global dimensions (about 0.8), combined with relatively high local dimensions (about 1.85), are found for the parameter pairs "turbulence index" *vs.* "local SST" and "14° isotherm depth", respectively. Therefore, the geometry of the clouds of phase points is determined by disjunct subclouds of nearly evenly scattered phase points. Local geometries have only a small amount of voids, but global geometries consist of disjunct states. Therefore, these two parameter pairs best characterize different physical states (or large changes) of the system as a whole.

(iii) small local dimensions (about 1.75) and relatively high global dimensions (about 1.25) are found for the parameter pairs absorbed solar radiation *vs.* 14° isotherm depth and *vs.* SOI, respectively. Small local dimensions (about 1.75) and relatively small global dimensions (about 1.1) are found for the parameter pairs turbulence index *vs.* absorbed solar radiation and *vs.* SOI, respectively. The geometry of these clouds of phase points is locally and globally a network of multiple crossing phase lines separated by voids. Thus, these pairs of parameters characterize best different physical states (or small changes) on the local scale.

The dimensions of the phase spaces for the parameter pairs anchoveta biomasses *vs.* anchoveta biomass or each other *vs.* physical parameter are shown in Fig. 4C. The main feature of Fig. 4C is that local and global dimensions are mostly above 1.75 or in the range 0.75 to 1.25, respectively, and that the estimates for single pairs of parameters differ considerably.

The local and global dimensions of the phase space defined by the VPA-biomasses of adult, mature anchoveta and of anchoveta recruits are about 1.65 and 0.85, respectively (Fig. 4C). These estimates indicate on the global scale a pattern of different disjunct states. Different combinations of biomasses are possible on the local scale, but forbidden combinations (voids) in the phase space, are important. Indeed, they are more frequent than for all but one pair of physical parameters. However, the combination of the VPA-biomasses on the local scale is not unequivocal and the phase points scatter along multiple crossing phase lines.

The dimensions of the clouds of phase points for the parameter pairs VPA-biomass of anchoveta recruits *vs.* physical parameter show a clear pattern (Fig. 4C). Highest local and global dimensions, 2.0 and 1.2, respectively, are found in conjunction with SST_M. The lowest local and global dimensions, 1.85 and 0.8, respectively, are found in conjunction with the depth of the 14° isotherm. All other combinations have dimensions between these two limits, which cover a considerable range for the global scale (but not for the local scale).

Thus, on both the global and on the local scale, VPA-biomasses of anchoveta recruits are related most closely to the depth of the 14° isotherm than to any other physical parameter. The second best relation is found for the turbulence index. There, the global dimension is below one, indicating that the phase space is composed of different disjunct states. One should remember that both the 14° isotherm depth and the turbulence index are spatial averages. The least pronounced relations between anchoveta recruits and a physical parameter occur in conjunction with SOI, SST_M, absorbed solar radiation, SST_L, in this order..

The dimensions of the clouds of phase points for the parameter pairs "VPA-biomass of mature, adult anchoveta" *vs.* "physical parameter" show a more complex pattern than described above. All local or global dimensions range between 1.75 and 1.95 or 0.6 and 1.1, respectively. The highest or lowest local dimensions are found for SST_M or offshore Ekman transport and SOI, respectively. The highest or lowest global dimensions occurred in conjunction with absorbed solar radiation or turbulence index and offshore Ekman transport, respectively.

Thus, the VPA-biomass of the mature, adult anchoveta is most closely related to offshore Ekman transport if global and local scale are considered. The weakest relation of local and

global scales to physical parameters is found for SST_M. On the global scale, the relation is closest or weakest for the turbulence index or the absorbed solar radiation, respectively. Considering local scales, then the relation with anchoveta VPA-biomass is closest for offshore Ekman transport or SOI.

Overall Summary and Discussion

The results relevant to the problem of predictability of the Peruvian upwelling ecosystem can be summarized as:

(i) The autocorrelations of the physical parameters describing the Peruvian upwelling ecosystem decay rapidly if the seasonal signal is eliminated from the data. On the average, less than 50% of the variance can be explained when the time lag between the observations exceeds two months. This suggests that random events are superimposed on the seasonal cycle.

(ii) The variance attributable, via spectral analysis, to the seasonal signal, is relatively high only for physical parameters, but does not rise significantly above the variance of the noisy background for all but one parameter - absorbed solar radiation. Interannual variability and long periodic modulation of the seasonal signal dominate over the seasonal signal itself.

(iii) The seasonal signal is the only quasi-periodic contribution to the time series. Quasi-regular contributions on longer time scales, i.e., El Niño events, were noticed in some time series as a spectral band of high variances. This feature is shown by the anchoveta biomasses, the SOI, the turbulence index and the SST but not by the time series of the depth of the 14° isotherm. This indicates temporal changes in the vertical structure of the upper oceanic layer which differ between single El Niño events. This is a feature which is corroborated by the observation (J. Mendo, pers. comm.) that the composition of the multispecies fish stock off Peru differs between single El Niño events.

(iv) The characteristics of those noise processes which determine meteorological parameters (upwelling index, turbulence index, Ekman transport and absorbed solar radiation) were not identified, but these processes differ from white noise. Noisy processes describing parameters relevant to the thermal structure of the upper layer of the Peruvian upwelling system (SST's and depth of the 14° isotherm) are identified to be partly (50%) a correlated fractal noise process (CFNP) of near-brownian nature. The biological parameters (biomass of recruits and of mature adults) are also characterized by a CFNP of near-brownian nature.

(v) None of the time series can statistically be described as stationary. This implies that the Peruvian upwelling system is unsteady in its major characteristics, at least on medium time scales. An exception to this is recruitment of anchoveta, which shows stationarity with respect to its mean variability (variance), the occurrence of extreme increases or decreases and the occurrence of high values. This result suggests an adaptation of the anchoveta to a nonstationary, variable environment.

(vi) The basic geometry of phase spaces (parameter and its rate of change) of all physical parameters (except the turbulence index) is about the same. The phase points scatter along multiple crossing phase lines separated mainly by voids on large scales. A different geometry of phase spaces is found for the VPA-biomasses and the turbulence index. There, the phase points scatter around disjunct phase states and voids are found on all scales. That is, the number of possible combinations of, e.g., anchoveta biomasses and its rate of change, is smaller than combinations of, e.g., for SST and its rate of change. This implies that anchoveta biomasses and turbulence index are more frequently "locked" in some distinct phase states than the other parameter.

(vii) Different states of the physical subsystem of the Peruvian upwelling index are best described by the parameter pairs turbulence index *vs.* local SST or depths of the 14° isotherm, respectively, if large changes of the system are to be analyzed.

For small changes, the pairs of parameters to be used should be absorbed solar radiation *vs.* depths of the 14° isotherm or SOI, respectively. If both large and small changes of the Peruvian upwelling system must be described, then parameter pairs such as turbulence index *vs.* absorbed solar radiation, offshore Ekman transport *vs.* absorbed solar radiation, and offshore Ekman transport *vs.* SOI are most suitable.

(viii) The phase spaces defined by the biomasses of mature, adult anchoveta and of anchoveta recruits have a geometry which, on the global scale, reflects disjunct states. Local scale geometry is that of phase points scattering along multiple crossing phase lines, separated by forbidden combinations or voids. The interrelation of the two VPA-biomasses is strong if compared with those of most physical parameters.

(ix) On the global and local scales, the biomasses of anchoveta recruits and of mature adults are related most closely to the turbulence index (for both VPA-biomasses) or to the depth of the 14° isotherm and the offshore Ekman transport, respectively. Both VPA-biomasses are related most weakly with SST_M.

Fluctuations of the Peruvian upwelling system occurring on time scales longer of more than half a year are, in the mean, a mixture of a seasonal signal and of a nonstationary random process with drifting means and variances. The random process has, in part, a fractal geometry (CFNP).

The analyses of the phase spaces defined by the available parameters yield two major features describing the Peruvian upwelling ecosystem: (i) multiple disjunct states are most characteristic of the dynamics of the anchoveta VPA-biomasses and (ii) physical parameters, e.g., the turbulence index, were identified which are most closely related to biological changes. These parameters are not those which are commonly observed to characterize El Niño, e.g., SST and SOI.

These results are consistent with those interpretations which have been developed by only looking at the time series and inferring the basic principles of the underlying dynamics. The theoretical background, mainly the fractal geometry of the noise processes, proved to be helpful to describe the observations and to understand some principles of the relevant dynamics. The detailed data analyses showed that 30 years of data may be a lower limit for the amount of data needed to describe the Peruvian upwelling system. Thus, efforts should be done to extend other existing, but generally shorter time series (e.g., on sardine or zooplankton biomasses) to a period of at least 30 years.

The main lesson learned is that we can answer the question implied by the title of the book edited by Pauly and Tsukayama (1987): "Why three decades of change?" The answer - "random events determine, to an important degree, the changes of the physical properties of the Peruvian upwelling system" - may restrict our ability to predict future changes.

References

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama. (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bohr, T. and Cvitanovic P. 1987. Chaos is good news for physics. Nature 329: 391-392.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984, p. 14-44. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Brink, K.H., D. Halpern, A. Huyer, R.L. Smith. 1983. The physical environment of the Peruvian upwelling system. Progr. Oceanogr. 12: 285-305.

Essex Ch., T. Lookman and M.A.H. Norenberg. 1987. The climate attractor over short timescales. Nature 326: 64-66.

Hofmann, D.J. 1987. Perturbations to the global atmosphere associated with the El Chicon volcanic eruption of 1982. Rev. Geophys. 25(4): 743-759.

Huber, P.J. 1981. Robust statistics. Wiley and Sons, New York.

Käse, R.H. 1985. El Niño. Geowiss. Z. 3(4): 113-119.

Lasota, A. and M.C. Mackey. 1985. Probabilistic properties of deterministic systems. Cambridge University Press, Cambridge, Massachusetts.

Lovejoy, S., D. Schertzer and P. Ladoy. 1986. Fractal characterization of inhomogeneous geophysical measuring networks. Nature 319: 43-44.

McHardy, I. and B. Czerny. 1987. Fractal X-ray time variability and spectral invariance of the Seyfert galaxy NGC5506. Nature 325: 696-698.

Mendo, J., L. Pizarro and S. Castillo. 1987. Monthly turbulence and Ekman transport indexes, 1953 to 1985 based on local wind records from Trujillo and Callao, Perú, p. 77-87. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Nuttal, A.H. 1971. Spectral estimations by means of overlapped FFT processing of windowed data. Naval Underwater Systems Center Report No. 4169. 39 p. Department of the Navy, Washington, USA.

Pauly, D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987. VPA estimates of the monthly population length composition, recruitment, mortality, biomass and related statistics of the Peruvian anchoveta, 1953 to 1981. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Philander, S.G.H. and A.D. Seigel. 1985. Simulation of El Niño of 1982-1983, p. 517-542. *In* J.C.J. Nihoul (ed.) Coupled ocean-atmosphere models. Elsevier, New York.

Ponte, R.M. 1986. The statistics of extremes, with application to El Niño. Rev. of Geophys. 24(2): 285-297.

Turcotte, D.L. 1988. Fractals in fluid mechanics. Ann. Rev. Fluid Mech. 20: 5-16.

The Seasonal Dynamics of Sea Surface Temperature and Its Impact on Anchoveta Distribution off Peru*

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Abstract

Maps of the seasonal distribution of waters ≤17°C and of the 20°C isotherm off Peru were analyzed by planimetry. The resulting values were used to derive a set of relationships linking sea surface temperature and size changes of the habitat of anchoveta (*Engraulis ringens*). These analyses show that anchoveta density and hence availability to the fishery are closely correlated to the offshore and alongshore extent of waters ≤17°C.

Resumen

Los mapas de distribución estacional de las aguas frente al Perú con isotermas ≤17°C y las de 20°C fueron analizados mediante planimetría.

Los valores resultantes fueron utilizados para derivar una serie de relaciones con la temperatura superficial del mar y los cambios en tamaño del habitat de la anchoveta (*Engraulis ringens*). Estos análisis muestran que la densidad de la anchoveta y por ende su disponibilidad a la pesquería estan estrechamente correlacionadas a las extensiones a lo ancho y a lo largo de la costa de las aguas ≤17°C.

Introduction

Sea surface temperature (SST) data have turned out to be rather helpful for modelling biological response (metabolism, feeding, migration) of the principal species of fishes, sea birds and sea mammals in the Peruvian upwelling ecosystem (Villavicencio and Muck 1985; Muck and Vilchez 1986; Muck and Pauly 1987; Muck and Fuentes 1987; Muck and Sánchez 1987; Muck et al. 1987). Moreover, the recently published catalogue of oceanographic data for the

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Peruvian coast (Urquizo et al. 1987) allows detailed, spatially structured analysis of temperature-related parameters, such as area, size and geographical extension of water masses associated with important biological features. One example of such analyses involves the dynamics of the 17°C and 20°C isotherms for describing the distribution area of anchoveta (*Engraulis ringens*) and the inshore offshore migration of its most important predators, mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus murphyi*).

The waters ≤17°C are the cold and nutrient rich waters of the coastal upwelling ecosystem, i.e., the habitat of the anchoveta. The 20°C isotherm is, on the other hand, the boundary of relatively nutrient poor oceanic water masses of the outer part of the continental shelf, where the bulk of the mackerel and horse mackerel biomass generally occurs (Muck et al. 1987).

Thus, seasonal and El Niño-related changes in the location and/or extent of these different habitats will result in changes of (i) anchoveta concentration, (ii) spatial overlapping of anchoveta predators with their prey, and (iii) mixing of cold, nutrient rich with warm, nutrient poor waters, affecting anchoveta vulnerability for predation and fishery, primary production and temperature-related metabolic rates.

Fig. 1 presents false color satellite images showing SST during (a) a period when cold waters stretched all along the Peruvian coast, and (b) during an El Niño event. Such images, although extremely instructive, are usually costly to obtain, analyze and manipulate. As an alternative, the present contribution presents derivations of simple, linear SST-based models for estimating (1) the size of the area ≤ 17°C off Peru, (2) the offshore and alongshore extent of this area and (3) the offshore distance of the 20°C isotherm, our aim being to provide a tool for modelling purposes, e.g., to estimate the vulnerability of anchoveta.

Materials and Methods

The areas and offshore/alongshore distances have been estimated by planimetric analysis of maps published in Urquizo et al. (1987), wherein oceanographic conditions (temperature, salinity, oxygen) off Peru are described on a seasonal basis (i.e., for January-March, April-June, etc.) for the period 1970-1985. Values referring to coastal stretches other than 4-14°S have not been used for the correlation and regression analyses.

The monthly SST values in Pauly and Tsukayama (1987) for the area 4°-14° have been updated (based on IMARPE, unpublished data) and used to compute seasonal means.

Results and Discussion

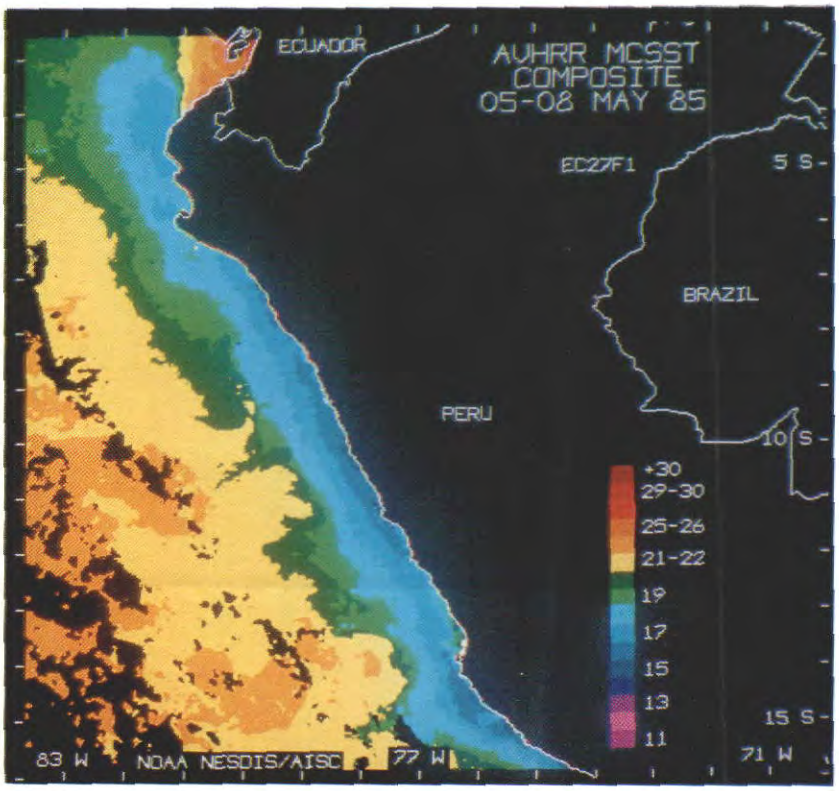
Table 1 gives seasonal means of SST for the entire Peruvian coast and the results of the planimetric analyses of 48 temperature maps (Urquizo et al. 1987). Documented are the size of the area ≤17°C, its offshore and alongshore extent and the offshore distance of the 20°C isotherm.

The results of the correlation and regression analyses (Fig. 2 A-E and Table 2) demonstrate that SST data can be used for estimating the location of the 17°C and 20° isotherms along the Peruvian coast. Fig. 3 presents seasonal means of these parameters for the period 1970-1985.

The dynamics of the area of waters ≤17°C and the offshore/alongshore extent of the 17°C and 20°C isotherms, are as follows: when the overall coastal sea temperature is high (summer, i.e., January-March), the cold area is located at the center and the south of the Peruvian coast, and has a minimum extent and an offshore limit of less than 10 nautical miles. The 20°C isotherm similarly comes close to the coast about 25 nautical miles offshore.

During winter (July-September) most of the Peruvian coastal waters are cold (≤17°C); this zone has a mean offshore extent of 60 nautical miles and a total area ca. 50 times that occurring in summer. The 20°C isotherm is far offshore (over 100 nautical miles). Spring and autumn have characteristics intermediate between those of summer and winter.

During the El Niño of 1982-1983 the normal seasonal pattern was disturbed. There was no cold water area off Peru from spring 1981 to autumn 1983. During this period the 20°C isotherm



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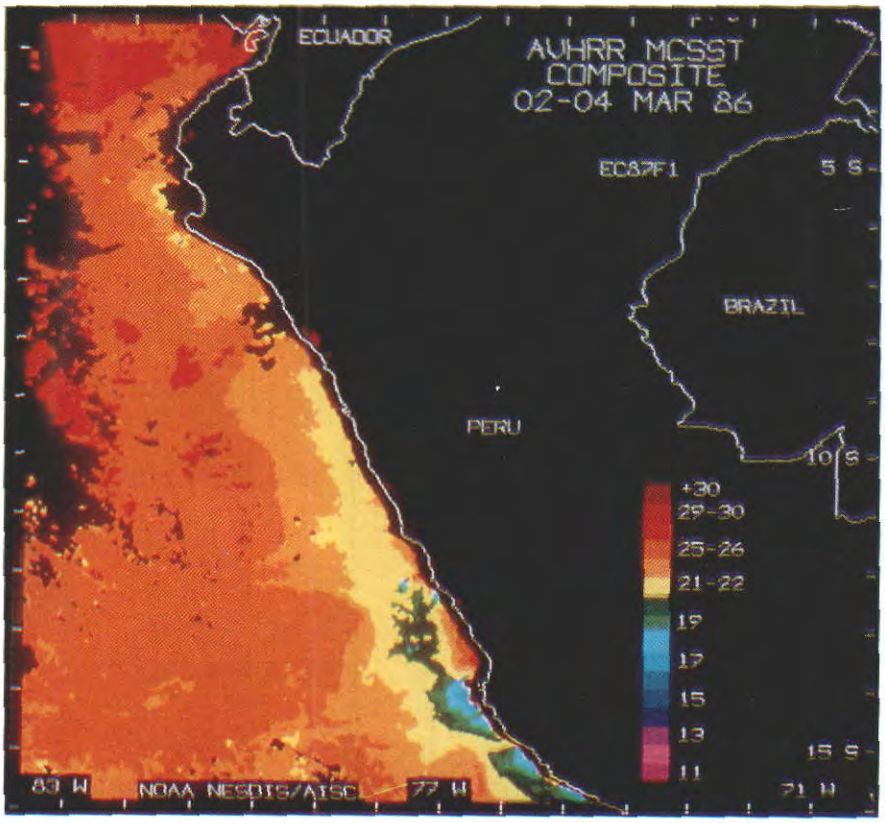

1B

Fig. 1. False color satellite images of the Peruvian upwelling system taken during a 4-day period (5-8 May 1985) with a well developed area of cold waters along the Peruvian coast (A) and during a 3-day period (2-4 March 1986) when warm oceanic waters invaded the nearshore habitat of anchoveta (B). (Images: courtesy of the US National Oceanographic and Atmospheric Administration).

Fig. 1. Color falso de las imágenes de satélite del sistema de afloramiento peruano tomado durante un período de 4 días (5-8 de Mayo 1985) con un área bien desarrolloda de aguas frías a lo largo de la costa peruana (A), y durante un período de 3 dias (2-4 Marzo 1986) cuando aguas oceánicas calientes invadieron la costa cercana al habitat de la anchoveta (B)(Imágenes: cortesía de la US National Oceanic y Atmospheric Administration).

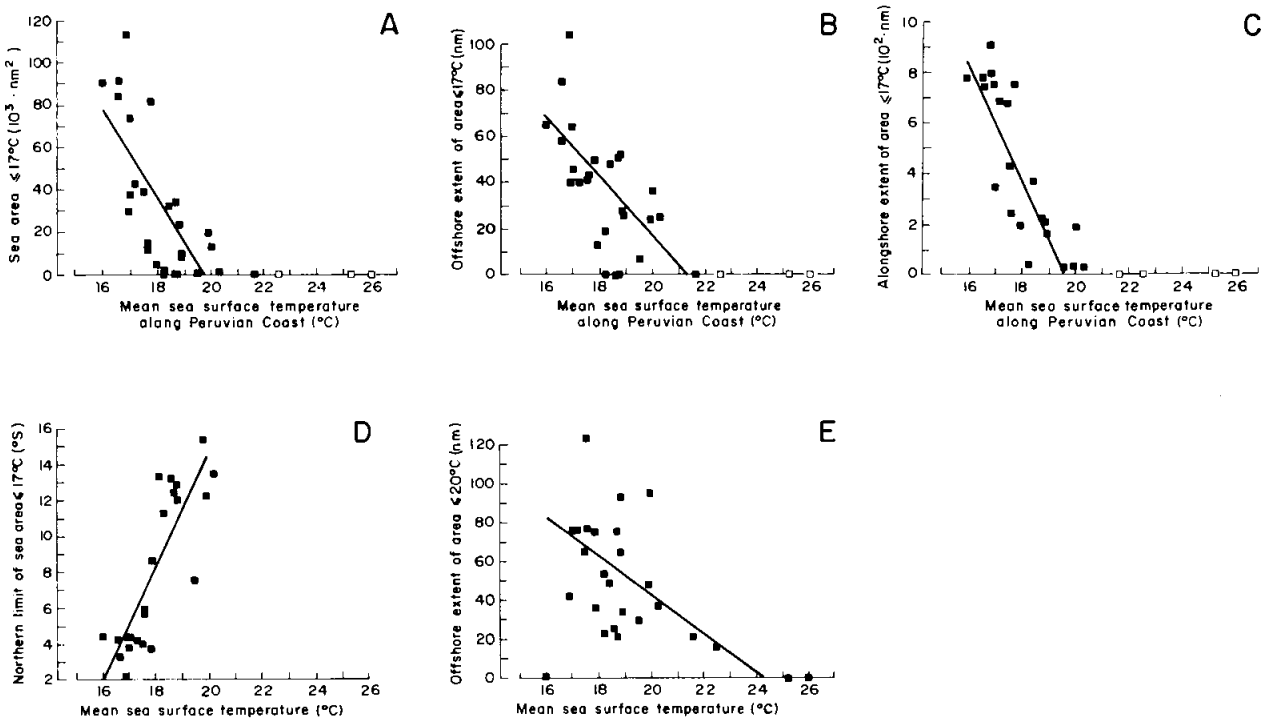

Fig. 2. Plots of various measures of the extent of cold water masses along the Peruvian coast *vs* mean inshore sea surface temperature off Peru (4-14°S).

Fig. 2. Gráficos de varias medidas de las extensiones de las masas de aguas frías a lo largo de la costa peruana contra el promedio de la temperatura superficial del mar cerca a la costa frente al Perú (4-14°S).

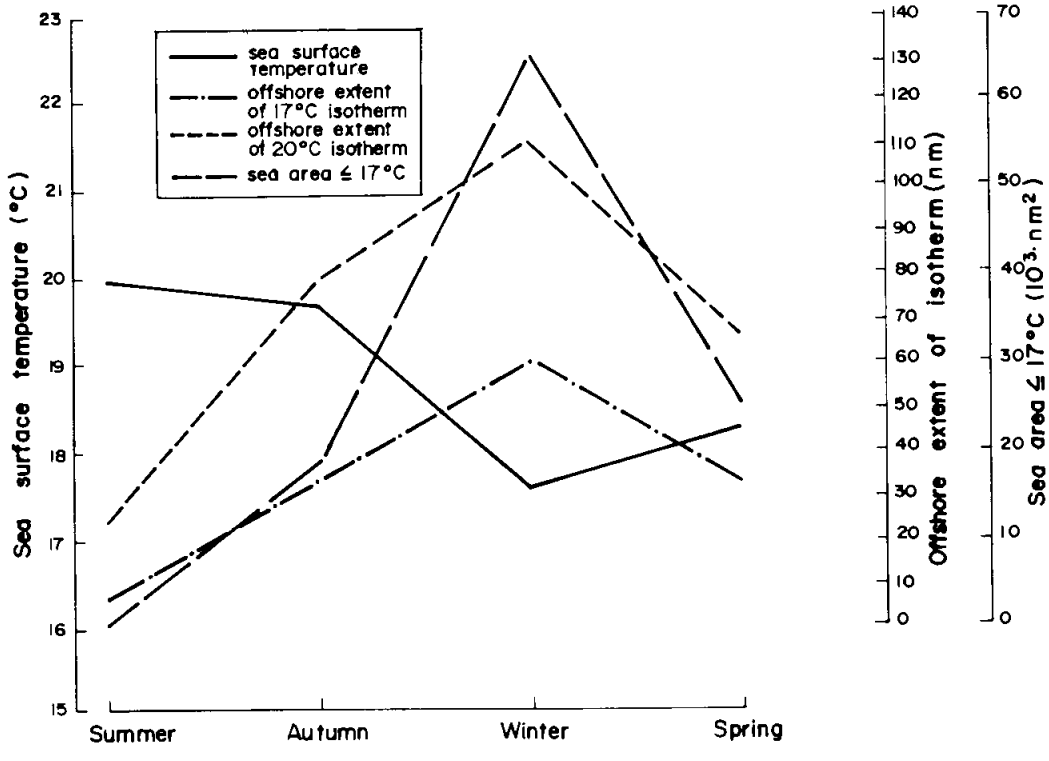

Fig. 3. Seasonal means of some SST-related descriptors of the extent of cold water masses along the Peruvian coast.

Fig. 3. Promedios estacionales de algunos indicadores de TSM relacionados a las extensiones de las masas de agua fría a lo largo de la costa peruana.

Table 1. Sea surface temperature (SST), areas and offshore distances of the ≤ 17°C and the 20°C isotherms.
Tabla 1. Temperatura superficial del mar (TSM), áreas y distancias hacia afuera de la costa de las isotermas ≤17°C y las de 20°C.

Year	Season	Extent of cruise (°S)	Area ≤17°C (°C)	Area ≤17°C nm2	n	Offshore distance of 17°C isotherms (nm) Min	Max	Mean	(°C)	North-south extent of isotherms ≤17°C (°S)	nm	n	Offshore distance of 20°C isotherms (nm) Min	Max	Mean	Mean SST (°C)
1970	Autumn	3°20'-12°58'	16	7,350	1	10	75	38	16	3°20'-7°40'	260	1	6	60	34	
			17	12,850	2	32	118	50	17	3°10'-4°28'	78					18.5
									17	8°20'-12°58'	278					
	Winter	3°25'-18°30'	14	3,818	1	46	150	72	14	14°50'-15°50'	60	1	16	94	42	
			15	11,781	2	90	168	135	15	5°17'-5°53'	36					
			16	84,980					15	7°00'-8°05'	65					
			17	12,544					15	13°58'-16°20'	150					16.9
									16	5°12'-18°30'	798					
									17	3°10'-5°05'	115					
									17	7°15'-9°30'	135					
	Spring	3°38'-18°38'	16	15480	1	18	82	40	16	7°12'-8°10'	58	1	16	70	34	
			17	27,146					16	11°14'-16°45'	331	2	108	139	118	17.2
									17	5°20'-16°58'	698					
1971	Autumn	3°28'-17°38'	16	3,046	1	16	100	52	16	14°08'-15°15'	67	1	2	95	34	
			17	20,196					17	13°22'-16°50'	208	2	62	172	96	18.8
	Winter	4°32'-17°32'	14.5	8,226	1	21	161	50	14.5	14°21'-15°32'	71					
			15	18,733					14.5	16°38'-16°50'	12					
			16	24,573					15	13°52'-17°09'	197					
			17	29,922					16	5°00'-7°07'	127					
									16	9°11'-9°59'	48					17.8
									16	11°09'-12°45'	96					
									16	17°08'-17°51'	43					
									17	5°00'-12°01'	421					
	Spring	3°25'-17°38'	16	308	1	30	58	35	16	15°30'-15°51'	21	1	11	108	78	
			17	37,233	2	31	66	35	17	5°23'-6°22'	59	2	18	122	71	17.0
					3	22	279	139	17	7°08'-9°50'	162					
									17	13°59'-16°04'	125					
1972	Summer	3°30'-18°35'	17	923	1	19	36	25	17	14°22'-14°46'	24	1	11	70	37	20.3
	Autumn	9°32'-17°34'	-					-	-		-	1	5	12	7	
												2	30	75	45	21.3
	Winter	3°32'-18°36'	16	1,217	1	13	82	36	16	13°10'-13°38'	28	1	20	80	30	
			17	11,858					17	14°29'-17°08'	159	2	27	267	121	20.0
												3	13	296	135	
	Spring	3°26'-18°32'	16	647	1	10	36	24	16	16°20'-16°40'	20	1	23	-	23	
			17	1,294					17	16°14'-16°47'	33	2	15	170	72	19.9

continued

Table 1. Continued

Year	Season	Extent of cruise (°S)	Area ≤17°C (°C)	Area ≤17°C nm2	n	Offshore distance of 17°C isotherms (nm) Min	Max	Mean	(°C)	North-south extent of isotherms ≤17°C (°S)	nm	n	Offshore distance of 20°C isotherm (nm) Min	Max	Mean	Mean SST (°C)
1973	Summer	3°15'-17°37'										1	11	50	25	
												2	5	11	7	22.5
	Autumn	3°16'-18°30'	15	2,434	1	13	95	48	15	7°20'-9°46'	146	1	17	70	31	
			16	10,472	2	21	43	34	16	5°20'-6°01'	41	2	62	201	80	
			17	26,125					16	7°11'-11°23'	252	3	61	184	88	17.5
									16	12°30'-14°14'	104					
									17	5°08'-15°50'	642					
									17	16°26'-16°52'	26					
1974	Summer	4°30'-18°30'	16	787	1	6	17	10	16	10°31'-11°00'	29	1	10	91	40	
			17	3,674	2	16	28	14	16	15°42'-15°52'	10	2	20	56	32	
					3	4	26	14	17	9°33'-11°18'	105					17.9
									17	14°09'-15°00'	51					
									17	15°38'-15°52'	14					
	Autumn	4°26'-18°28'	16	3,217	1	8	52	28	16	14°08'-15°25'	77	1	19	130	59	
			17	5,949					17	13°48'-16°28'	160	2	105	125	121	18.9
												3	38	154	98	
1975	Summer	1°36'-12°38'										1	19	59	40	18.6
	Autumn	1°35'-18°32'	15	475	1	16	78	48	15	14°35'-15°15'	40	1	20	41	22	
			16	7,103					16	12°15'-13°10'	55	2	14	57	48	
			17	24,356					16	14°19'-15°40'	81	3	18	151	75	18.4
									16	16°08'-17°58'	110					
									17	12°16'-18°21'	365					
	Winter	6°35'-12°35'	16	1,693	1	5	58	44	16	10°21'-11°45'	84					
			17	11,571	2	12	48	26	17	6°20'-7°26'	66					16.3
									17	7°58'-12°25'	267					
	Spring	4°30'-17°38'	15	1,118	1	10	180	65	15	7°43'-9°14'	91					
			15.5	6,568					15.5	13°22'-16°44'	202					
			16	23,182					16	6°16'-9°32'	196					16.0
			17	59,733					16	11°58'-17°20'	322					
									17	5°21'-18°20'	779					
1976	Autumn	11°38'-15°39'										1	55	119	64	19.8
	Winter	3°25'-18°32'	16	9,035	1	10	85	51	16	14°45'-16°43'	118	1	17	181	75	
			16.5	15,274					16.5	14°41'-17°04'	143					
			17	9,156					17	14°11'-14°48'	37					18.7
									17	17°10'-18°00'	50					
	Spring	2°30'-15°28'	16	5,228	1	8	55	25	16	14°40'-15°50'	70	1	18	47	28	
			17	2,811					17	13°00'-14°32'	92	2	13	62	33	18.9
												3	20	68	42	

Continued

Table 1. Continued

Year	Season	Extent of cruise (°S)	Area ≤17°C (°C)	Area ≤17°C nm2	n	Offshore distance of 17°C isotherms (nm) Min	Max	Mean	North-south extent of isotherms ≤17°C (°C)	(°S)	nm	n	Offshore distance of 20°C isotherm (nm) Min	Max	Mean	Mean SST (°C)
1977	Summer	11°38'-16°16'										1	29	54	39	20.5
												2	34	56	40	
	Autumn	4°28'-6°28'										1	56	151	66	19.3
1978	Summer	7°29'-8°46'														19.3
1979	Summer	3°24'-18°25'										1	19	34	29	
												2	10	24	17	
												3	7	26	18	18.7
												4	7	47	21	
	Autumn	3°24'-12°30'	17	512	1	9	11	10	17	8°31'-9°16'	45	1	15	143	58	18.2
1980	Summer	4°31'-18°28'										1	10	41	25	18.6
	Autumn	4°29'-12°28'										1	15	50	30	18.5
	Winter	4°28'-17°58'	15	2,485	1	13	137	64	15	14°37'-15°57'	80					
			16	25,970					16	4°18'-6°13'	115					
			17	45,341					16	8°05'-16°51'	526					17.0
									17	4°46'-17°18'	752					
	Spring	3°20'-12°30'	17	827	1	11	21	20	17	7°18'-7°52'	34	1	19	148	65	17.0
1981	Summer	4°34'-19°35'										1	8	33	18	
												2	20	42	28	18.2
	Autumn	12°38'-16°38'	16	3,236	1	11	153	49	16	14°17'-15°52'	95	1	175	279	185	18.1
			17	7,661					17	13°54'-16°29'	155					
	Winter	4°30'-17°38'	15	2,645	1	16	174	58	15	14°13'-14°54'	41	1	298	381	292	
			16	19,018					15	16°20'-16°42'	22					
			17	62,284					16	6°12'-10°24'	252					16.6
									16	13°24'-16°51'	207					
									17	5°12'-17°38'	746					
	Spring	1°40'-10°39'										1	75	90s77	17.0	
1982	Summer	1°38'-13°30'										1	22	42	29	18.5
	Spring	4°47'-17°32'										1	11	35	21	21.6

Continued

Table 1. Continued

Year	Season	Extent of cruise (°S)	Area ≤17°C (°C)	Area ≤17°C nm²	n	Offshore distance of 17°C isotherms (nm) Min	Max	Mean	(°C)	North-south extent of isotherms ≤17°C (°S)	nm	n	Offshore distance of 20°C isotherm (nm) Min	Max	Mean	Mean SST (°C)
1983	Summer	1°39'-19°36'														25.2
	Autumn	3°25'-15°36'														26.0
	Spring	1°32'-18°32'	17	1,714	1	18	42	24	17	14°20'-14°31'	11	1	18	182	54	
					2	4	34	13	17	15°30'-15°58'	28					18.2
1984	Winter	3°25'-18°32'	16	668	1	6	74	40	16	8°18'-8°59'	41	1	14	82	52	
			17	28,645					16	10°22'-11°00'	38					
									16	14°32'-14°58'	26					16.9
									17	5°21'-16°48'	687					
1985	Summer	1°38'-18°34'	17	456	1	3	9	7	17	8°22'-8°52'	30	1	8	45	30	19.5
	Autumn	1°36'-17°31'	16	1,969	1	13	106	58	16	16°20'-16°42'	22	1	16	205	166	
			17	9,342	2	18	85	36	16	7°15'-8°01'	46	2	43	119	80	
					3	7	24	16	17	5°12'-5°59'	47					
					4	22	64	28	17	6°40'-8°28'	108					17.6
									17	15°08'-15°41'	33					
									17	16°14'-16°48'	34					
	Winter	1°39'-18°35'	15	5,116	1	25	272	84	15	8°13'-9°00'	47					
			16	30,478					15	15°10'-16°20'	70					
			17	56,132					16	4°20'-5°18'	58					
									16	6°24'-11°20'	296					16.6
									16	11°48'-14°00'	132					
									16	14°48'-16°58'	130					
									17	4°20'-17°21'	781					
	Spring	3°30'-13°36'	16	925	1	15	62	54	16	7°25'-8°15'	50	1	11	74	45	
			17	13,765	2	14	54	29	17	4°29'-5°49'	80	2	60	192	107	
					3	32	61	45	17	6°51'-10°35'	224					17.6
									17	12°11'-13°04'	53					

n = The number of isotherms of 17°C and 20°C that were measured per season.

came steadily closer inshore, from 300 nautical miles offshore distance in winter 1981 to zero in summer 1983.

We conclude that mean values of SST data referring to the entire Peruvian coast can be used for estimating the location of the ≤17°C and 20°C isotherms, which have been considered as characteristic for (i) the cold coastal upwelling area and (ii) the warmer oceanic waters of the outer half of the continental shelf.

Referring to species habitats, 17°C represents the mean preferred sea temperature of anchoveta and 20°C that of mackerel and horse mackerel (Zuta et al. 1983).

Increases in SST, during summer or El Niño events, are correlated with:

- an onshore movement of the 17°C and 20°C isotherms;
- a decrease in the size of the area ≤17°C; and
- a southward shift of the northern boundary of the cold water area.

For purposes of ecosystem modelling, the regressions presented in Table 2 can be used to assess the variation of the habitat size of anchoveta and its main predators.

Muck et al. (1987) put forward the hypothesis that changes in the spatial parameters area (alongshore, extent, onshore-offshore distance) of the cold and warm water habitats off Peru control - or at least influence - the migration and concentration pattern of anchoveta and of mackerel and horse mackerel, resulting, e.g., in changes of anchoveta vulnerability to predation, to egg and larval cannibalism and to the fishery.

This hypothesis is supported by Ware and Tsukayama (1981) who noted that anchoveta concentration increases with positive temperature anomalies. A direct relationship between water temperature and anchoveta density can also be shown to exist (Fig. 4).

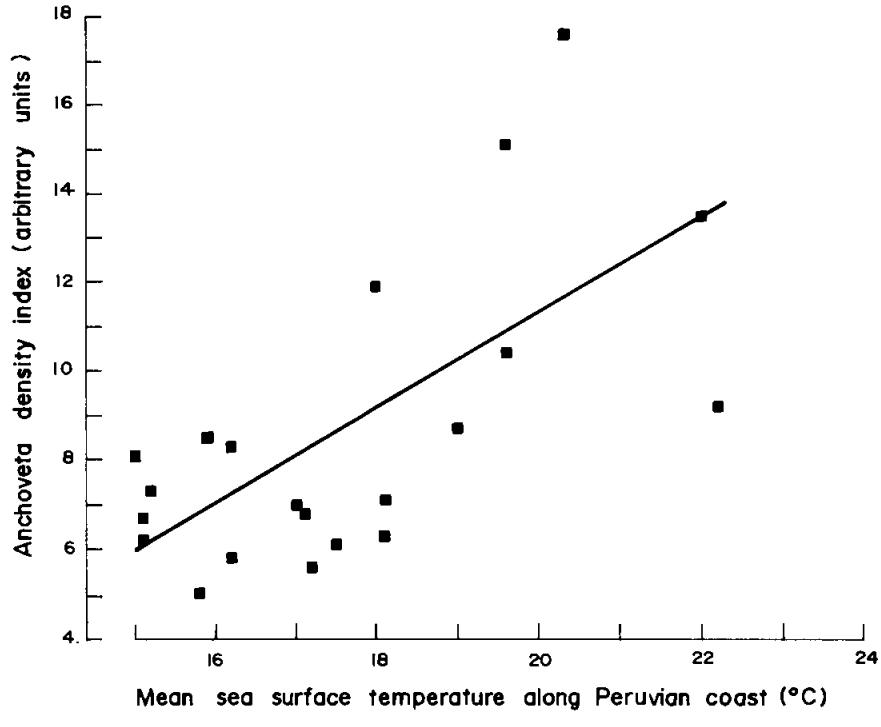

Fig. 4. Relationship between anchoveta density and SST off Peru (based on data in Table 3).
Fig. 4. Relación entre la densidad de la anchoveta y TSM frente al Perú (basados en datos de tabla 3).

Changes in anchoveta density imply changes of anchoveta biomass and/or of the size of anchoveta distribution area. Analysis of the data in Table 3 shows that the anchoveta distribution area is significantly correlated ($P < 0.05$; $r = 0.42$) with the area of water ≤17°C, and with anchoveta biomass (B) as well ($P < 0.005$; $r = 0.62$).

Table 2. Statistics of linear relationships between sea surface temperature off Peru and some dependent variables (see also Fig. 2).[a]
Tabla 2. Estadísticas de relaciones lineales entre la temperatura superficial del mar frente al Perú y algunas variables dependientes (ver también Fig. 2).

Plot in Fig. 1	Dependent variables (units)	Intercept (a)	Slope (b)	S.E. of b	Correlation coefficient (r)[c]	Degrees of freedom
A	Sea area (10^3 * Nm^2)[b] ≤17°C	420	-21.4	4.37	0.71	26
B	Offshore extent of area ≤17°C (Nm)	264	-12.5	3.06	0.63	27
C	Alongshore extent of area ≤17°C (Nm)	4,440	-226	33.5	0.81	26
D	Northern limit of area ≤17°C (° South)	-46	3.03	0.42	0.85	23
E	Offshore extent of area ≤20°C (Nm)	220	-8.74	2.22	0.64	24

[a]Based on seasonal means for 1970 to 1985 (in Table 1).
[b]Here and elsewhere, nm refers to nautical mile, i.e., 1,852 km.
[c]All correlation coefficients are significant ($P < 0.05$).

Table 3. Data for establishing relationships between sea surface temperature off Peru and the distribution area and density of anchoveta.
Tabla 3. Datos para establecer relaciones entre la temperatura superficial del mar frente al Perú y el área de distribución y densidad de la anchoveta.

Date	SST[a] (°C)	Sea area ≤17°C[b] (10^3 Nm^2)	Anchoveta distribution area[c] (10^3 Nm^2)	Anchoveta biomass[d] (10^6 t)	Anchoveta density index[c]
Jan-73	23.2	0.0	10.5	2.9	9.2
Jan-76	17.2	36.8	31.3	16.4	8.3
Feb-69	19.0	9.3	12.2	9.1	11.9
Feb-71	19.1	7.8	28.7	16.9	6.3
Feb-72	20.6	0.0	13.8	5.3	10.4
Feb-73	23.0	0.0	5.9	3.5	13.5
Feb-74	18.2	21.5	21.5	3.8	5.6
Feb-75	18.1	23.1	16.3	3.2	6.8
Mar-68	18.5	16.9	34.8	14.7	6.1
Mar-70	20.0	0.0	19.7	15.9	8.7
Mar-76	21.3	0.0	14.3	5.1	17.6
Mar-77	20.6	0.0	5.4	1.0	15.1
Mar-79	19.2	19.2	10.1	2.3	-
Aug-66	16.2	52.1	24.6	15.5	7.3
Aug-67	15.4	64.3	21.5	20.5	7.3
Aug-68	16.0	55.2	34.2	13.0	8.1
Aug-70	16.9	41.4	14.9	14.4	8.5
Aug-71	18.0	24.6	49.2	14.0	7.0
Aug-74	16.8	42.9	21.9	3.0	5.0
Aug-75	16.1	53.6	14.9	1.6	6.2
Aug-76	19.1	7.8	18.7	4.4	7.1
Sep-69	17.2	36.8	17.7	4.3	5.8
Sep-72	18.9	10.8	12.2	2.1	-
Sep-73	15.7	59.7	22.7	2.8	4.3
Sep-74	16.1	53.6	14.8	3.9	6.7
Sep-76	17.6	30.7	11.4	3.9	-

[a]From Pauly and Tsukayama (1987b), and pertaining to the Peruvian coast from 4° to 14°S.
[b]From Fig. 2A and corresponding regressions in Table 2; predicted areas < 0 were set = 0; 1 Nm^2 = 3.43 km^2.
[c]From Zuta et al. (1983).
[d]From Pauly et al. (1987).

However, predictions can be markedly improved by combining three variables into a log-linear model, e.g., into

$$\log_{10}A = 0.8177 + 0.3492 \log_{10}B + 0.1396 \log_{10}(C + 1) \quad ...1)$$

where A is the anchoveta distribution area (in 10^3 Nm^2) off Peru,
B the biomass of anchoveta (in $t \cdot 10^6$)
and C the area of water ≤17°C (in 10^3 Nm^2)

This model, based on the data of Table 3, has a multiple correlation coefficient R = 0.794 and explains 62.1% of the variance in the data set. Both of its partial slope are significantly different from zero ($P < 0.01$; d.f. 23).

As an alternative, one can replace the variable (C) in equation (1) by the SST values from which the C-values were computed (see Table 3) and this yields

$$\log_{10}A = 3.23 + 0.3483 \log_{10}B - 1.797 \log_{10} SST \quad ...2)$$

where R = 0.780 ($R^2 = 0.608$) and where both slopes are significant ($P < 0.01$), and which applies, as did equation (2), to the stretch of the Peruvian coast between 4° and 14°S.

The good fit of these models to the available data validates the concept of a Main Anchoveta Area (MAR), first proposed and used as a constant by Muck and Sánchez (1987), and now shown to be an SST-dependent variable.

The interrelationships between SST, anchoveta concentration and the spatial characteristics of its habitat imply an increase of anchoveta mortality by predators and the fishery when the distribution area of mackerel and horse mackerel overlaps with that of anchoveta (Muck and Sanchez 1987), especially during El Niño events.

This is also a time when the anchoveta schools are concentrated close to the coast and hence highly vulnerable to the purse seiner fleet. Valdivia (1978) reports that during the El Niño event of 1971-1972 anchoveta were so concentrated that 170,000 t of them were caught in a single day, in March 1972 (see also Csirke, this vol.).

When an El Niño event, however, becomes so strong that the cold waters completely disappear (as is nearly the case in Fig. 1 lower panel), anchoveta vulnerability to the fishery fleet abruptly drops to near-zero values because of the vertical displacement of the pelagic schools out of the purse seiners' range. This has been observed during the last very strong El Niño event of 1982-1983 and is also reported in Muck and Vilchez (1986).

Changes in the area of the cold water habitat also influence anchoveta recruitment. Csirke (1980), who added to the standard stock/recruitment model of Ricker (1954) an "anchoveta concentration index", found that an increase in the concentration of the parent stock during spawning resulted in less recruits in the next year which suggests a density-dependent egg and larvae cannibalism. Ware and Tsukayama (1981), who used a bioenergetics model of anchoveta recruitment suggested that increases of anchoveta concentration during spawning cause reduced egg production (via crowding effects) and/or lead to food competition between the spawning stock and its progeny, which may result in reduced larval survival.

Thus, the dynamics of SST-related parameters such as the area of water ≤17°C, and the onshore and alongshore extent of the 17°C and 20° isotherms for which several expressions are given in the present contribution, appear to be of crucial importance for anchoveta population growth and should be taken in account when modelling the Peruvian upwelling ecosystem.

References

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population, p. 307-313. *In* A. Saville (ed.) The assessment and management of pelagic fish stocks. Rapp. P.-V. Réun. CIEM 177.

Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and G. Sanchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and R. Vilchez. 1986. Biomasa y su distribucción en el espacio y tiempo - Perú, p. 110-119. *In* O.A. Mathisen and I. Tsukayama (eds.) Bases biológicas y marco conceptual para el manejo de los recursos pelágicos en el Pacífico Suroriental. Documento de Pesca No. 001, Organización Latinoamericana de Desarrollo Pesquero, Lima, Perú.

Muck, P., O. Sandoval de Castillo and S. Carrasco. 1987. Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Perú, p. 268-275. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama, Editors. 1987a. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama. 1987b. On the implementation of management-oriented fishery research: the case of the Peruvian anchoveta, p. 1-13. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987. VPA Estimates of the monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Ricker, W.E. 1954. Stock and Recruitment. J. Fish. Res. Board Can. 11: 559-623.

Urquizo, W., C. Wosnitza-Mendo, E. Valdivia and C. Moreno. 1987. Catálogo de datos oceanográficos (T,S y O_2) por estaciones del año en diferentes profundidades frente a la costa Peruana, período 1970-1985. Bol. Inst. Mar, Volúmen Extraordinario. 445 p. Instituto del Mar del Perú (IMARPE), Callao, Perú.

Valdivia, J. 1978. The anchoveta and "El Niño", Rapp. P.-V. Réun. CIEM 173: 196-202.

Villavicencio, Z. and P. Muck. 1985. The importance of temperature and plankton biomass changes for the production and mortality of anchovy. (*Engraulis ringens*) and sardine (*Sardinops sagax*), p. 119-128. *In* W. Arntz, A. Landa and J. Tarazona (eds.) "El Niño", su impacto en la fauna marina. IMARPE Boletín Volumen Extraordinario, 222 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany.

Ware, D.M. and I. Tsukayama. 1981. A possible recruitment model for the Peruvian anchovy, p. 55-61. Bol. Inst. Mar, Volúmen Extraordinario. Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá and Instituto del Mar del Perú (IMARPE), Callao, Perú.

Zuta, S., I. Tsukayama and R. Villanueva. 1983. El ambiente marino y las fluctuaciones de las principales poblaciones pelágicas de la costa peruana. p. 179-254. *In* G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species of Neritic Fish Resources, San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. No. 291, Vol. 2, Rome.

Are Peruvian El Niño Events Transmitted by Coastal Kelvin Waves?

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Abstract

The hypothesis that the poleward propagation of El Niño events along the coast of South America is due to Kelvin waves lacks stringent confirmation by observation. Observations are discussed which refute the Kelvin wave model. An alternative concept of poleward propagating shock waves is proposed. Some of its basic features and advantages are discussed.

Resumen

La hipotesis que la propagaciòn de los fenomenos de El Niño a lo largo de la costa de America del Sur es debido a las "ondas de Kelvin" adolece de una confirmación concluyente por medio de mediciones. Las observaciones que refutan el modelo des "ondas de Kelvin" estan discutidas. Un concepto alternativo de propagación de "onda shock" es propuesto. Se discute algunas de sus caracteristicas básicas y ventajas.

Introduction

Southern oscillation events are linked to equatorial Kelvin waves crossing the Pacific towards South America (see, e.g., Cane 1983; Käse 1985). The equatorial current system creates Kelvin waves by shear instability (Philander et al. 1985). The South American coast acts as wave guide for Kelvin waves of about 5 to 10 days period, more than 1,000 km wave length and 2.5 ms^{-1} phase velocity (Romea and Smith 1983). Equatorial Kelvin waves, incident on the South American coast, give rise to coastal Kelvin waves propagating poleward (Anderson and Rowlands 1976; Brink et al. 1983).

El Niño southern oscillation events propagate poleward along the coasts of Ecuador and Peru with phase velocities similar to those of coastal Kelvin waves (Smith 1983). The problem to be considered here is: are the dynamics of the southward propagating El Niño events those of a Kelvin wave as suggested by Cane (1983)? The Kelvin wave hypothesis seems to be acceptable because it provides both a reasonable estimate of the mean speed of alongshore propagation of the El Niño events and also provides a triggering mechanism. However, observations and theoretical considerations can be assembled which, together, indicate that the Kelvin wave hypothesis may be too restrictive and should be replaced by a more general concept.

Theoretical Considerations

A Kelvin wave has several main features which do not depend on the technique used to derive the solutions from the governing equations. The current amplitude u decreases with increasing offshore distance y (x is the alongshore distance, t the time). If H is the vertical displacement of the isotherms, then the proportionality

$$u(x, y, t) \simeq \partial/\partial y\, H(x, y, t) \qquad \ldots 1)$$

holds. The alongshore propagation of the wave is like a gravity wave, thus there is a proportionality such as

$$\partial/\partial t\, u(x, y, t) \simeq \partial/\partial x\, H(x, y, t) \qquad \ldots 2)$$

The phase speed of the Kelvin wave is nondispersive. Thus its propagation speed is independent of wave frequency. Therefore, a general-wave like solution of (1) and (2) may be obtained by:

$$u(x, y, t) = U(y) * F(x - ct) \qquad \ldots 3)$$
$$H(x, y, t) = H(y) * F(x - ct),$$

where c is the phase speed and x - ct the phase (abbreviated below as s). From (3) and (2) follow the proportionalities:

$$-c * U(y) * \partial/\partial s\, F(s) \simeq H(y) * \partial/\partial s\, F(s)$$
$$\text{or } c \simeq H(y)/U(y) \qquad \ldots 4)$$

H (y) and U (y) differ by a constant factor, and, using (1), are exponentially decreasing with increasing offshore distance.

$$U(y) \simeq \exp(-y/1)$$
$$H(y) \simeq \exp(-y/1) \qquad \ldots 5)$$

The constant 1 can be identified as the Rossby radius of deformation (Krauss 1973).

Data off Peru to test these main characteristics of currents and isopycnal depths (equations (1), (2), or derived proportionalities) are, to the authors' knowledge, not yet available. Thus, the Kelvin wave character of the motion is still hypothetical. However, the data from which Brainard and McLain (1987) derived the monthly mean depths of the 14-degree isotherm may be rearranged to test whether the proportionality of equation (6), which combines equation (1) and (2), holds.

$$\partial/\partial x\, H(x, y, t) \simeq \partial/\partial t\ \partial/\partial y\, H(x, y, t) \qquad \ldots 6)$$

If this proportionality holds and if likewise the nondispersive character of the phase speed is shown, then the linear Kelvin wave character of the El Niño events along the coasts of Peru could be demonstrated.

The linearity of the motion is implicit due to the form of equation (3). The linearity of the wave may be questioned. The poleward increasing influence of the earth rotation causes an increasing trapping of the wave energy against the shoreline. The Rossby radius decreases by a factor of two from either 2.5°S to 5°S, or 5°S to 10°S, or 10°S to 20°S. Therefore, a longshore gradient of the mean current amplitude will build up if not balanced by, e.g., frictional dissipation. Otherwise the motions will be subject to nonlinear accelerations.

Observational Considerations

Observations made during El Niño events are presented below which do not agree with the notion of one long, linear Kelvin wave propagating along the coast.

a) Posner (1957) reported that the 1953 El Niño advanced twice and retreated twice during the observation period from 10 March to 21 May 1953. Wooster and Guillén (1974) reported for the 1972 El Niño event "no systematic progression of anomalous conditions southward along the coast"

b) Smith (1983) described the 1982 El Niño event linked to a rapid, stepwise increase of the currents (Fig. 1) in 100 m depth: "the alongshore current, averaged over 1, 8, and 64 days before 7 October, was poleward at 18.9, 18.0, and 4.2 cm/s, respectively. Mean alongshore current abruptly accelerated to 35.8 cm/s poleward on 7 October, and current averaged over following 8 and 64 days remained poleward at 30.1 and 25.3 cm/s." Temperature (see his Fig. 2) increased steplike, first in small (from early October to mid-November), then in large steps. Furthermore, strong temperature changes were found in different depths (Knoll et al. 1987: p. 33 - end of March 1983, p. 113 - October 1982, p. 117 - April and May 1983) which neither occurred in phase nor had smooth forefronts. Both features are not consistent with a Kelvin wave dynamic.

The sea level changes at Santa Cruz and Callao in 1982 and 1983 were fluctuating stepwise, as shown by Cane (1983). Single steps may be smoothed to give the impression of a monotone mean rise like Cane's figure of the canonical El Niño. However, an approximation by a stepping function would probably be more appropriate (Fig. 2).

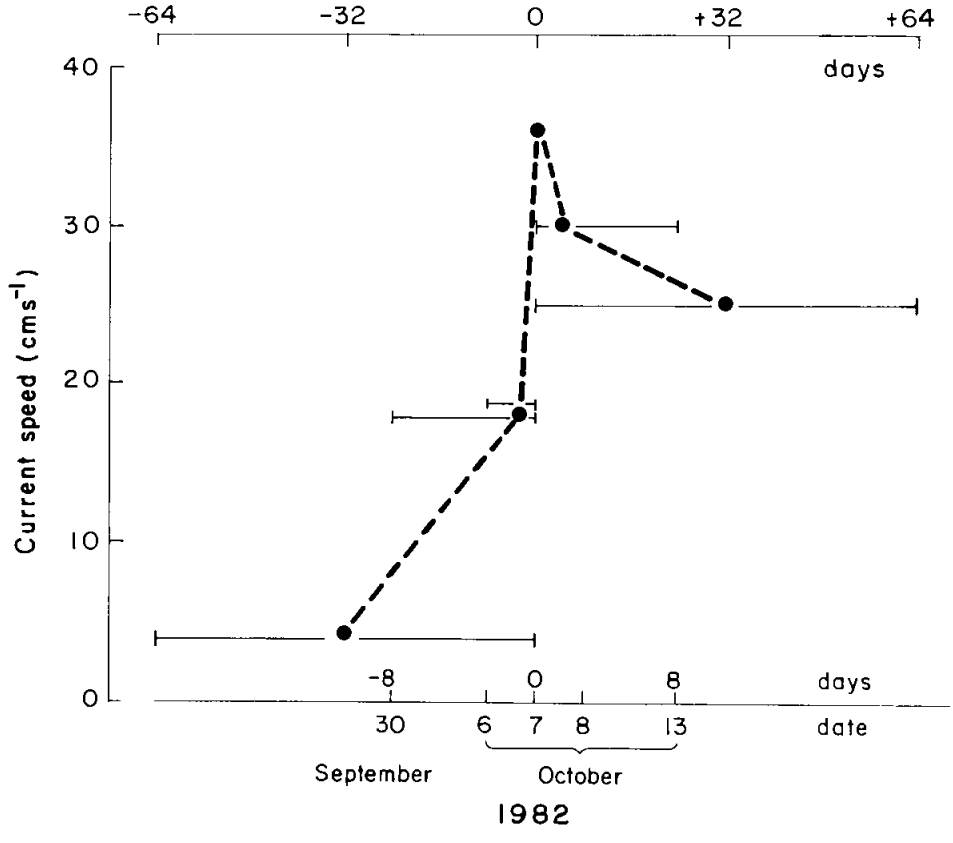

Fig. 1. Averaged current speeds observed at 10°S in 100 m depth (bottom depth 150 m) by Smith (1983) around 7 October 1982. Horizontal bars give the time intervals for which the mean values (vertical axis) have been calculated. Note the uneven scaling of the time axis. The broken line indicates how the mean currents would change for an evenly scaled time axis (upper line).

Fig. 1. Velocidades de corriente promediadas a 10°S y 100 m de profundidad (profundidad del fondo 150 m) de Smith (1983) alrededor del 7 de Octubre 1982. Las barras horizontales dan intervalos de tiempo del cálculo medio de las corrientes (línea vertical). Notar la desigualdad regular de la línea del tiempo. La línea puntillada indica como las corrientes medias podrian cambiar para una escala de tiempo equidistante (línea superior).

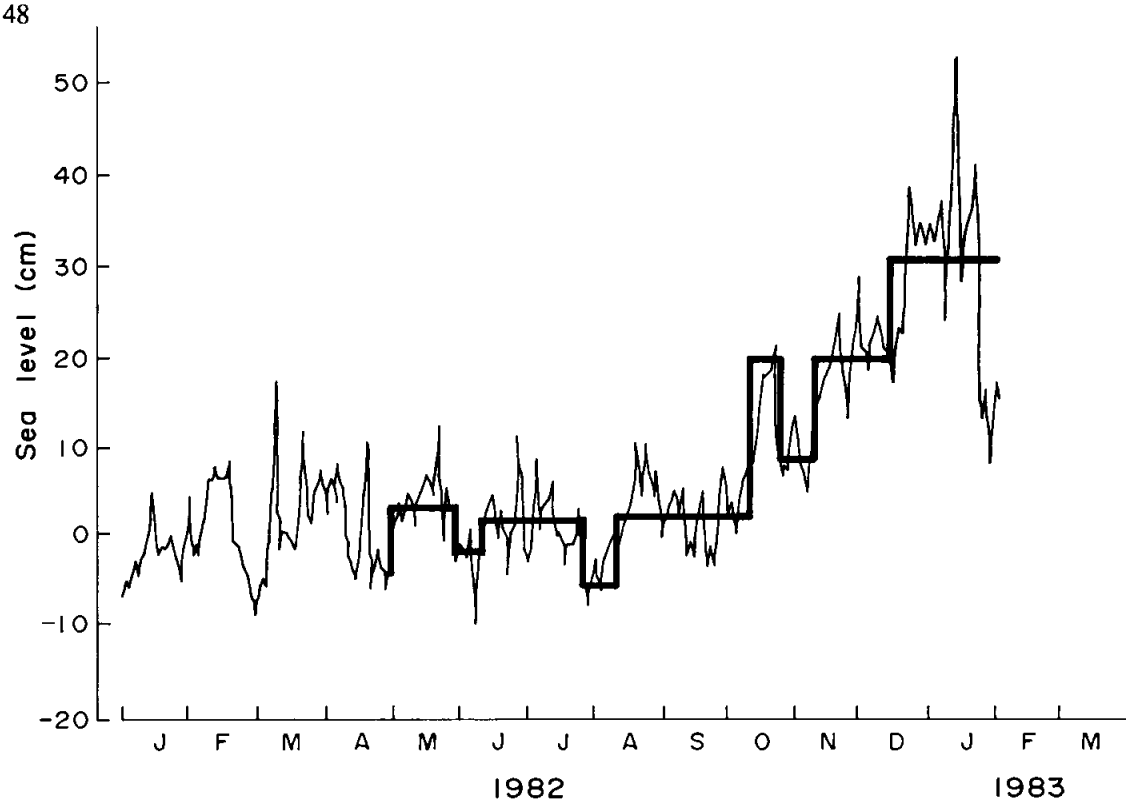

Fig. 2. Sea level changes at Callao (redrawn from Cane 1983). Superimposed is a suggestive stepwise approximation, contrasting with the common interpretation of smooth changes.
Fig. 2. Variaciones del nivel del mar en Callao (redibujado de Cane, 1983). La línea superimpuesta es una sugestiva aproximación de pasos en contraste con la interpretación común de cambios suavizados.

Discussion

The observations presented above imply a motion expressed by nonlinear, steplike changes and intermittence. These are features which do not match simple wave dynamics. Furthermore, a stringent confirmation of the Kelvin wave hypotheses by observations is lacking. Thus, it seems reasonable to suggest that the dynamic features of the El Niño events off Peru should be reanalyzed. Of special importance is the question whether the poleward propagating motion is a single or a composed signal and how linear the event is. The latter characteristic would determine to which degree locally remotely and remotely forced motions may interact, e.g., exchange energy.

A possible dynamic concept, including the Kelvin wave concept to a certain degree, is implied in the nonlinear model developed by Nof (1987a, 1987b) and applied to various hydrodynamic problems (Nof 1987a, 1987b; Nof and Van Gorder 1987), and which implies the possibility of boundary currents supporting propagating, frontlike disturbances, dissipating shock waves, e.g., steplike increases of the surface layer depth or the current speed.

Results obtained for the Mediterranean outflow (Nof 1987a, 1987b) may apply, after proper scaling, to the Peruvian Undercurrent. However, only the concept of shock waves itself needs to be discussed here. The model predicts that these shock waves will more rapidly than a Kelvin wave downstream from the front. An upstream Kelvin wave will catch up with the front. Thus, the front does not disintegrate in alongshore direction and will be maintained against frictional losses and offshore oriented Rossby wave dispersion by energy radiating from an upstream source. The alongshore penetration length of single shock wave will depend on the relative strength of the shock itself and on dissipation or dispersion. The generation of poleward propagating shock waves may be due to the observed pulsation of the Equatorial Current System (Lukas 1986). El Niño signals may be caused by these pulses especially if combined with the downwelling stroke of the isopycnals occurring east of the Galapagos Islands in early autumn and spring (Lukas 1986).

The sequence of shock waves, eventually followed up by Kelvin waves, may serve as a conceptual model. Each El Niño event can be assumed to be built by a particular sequence of shock waves. This would explain both the intermittence and the characteristics of particular El Niño events. Furthermore, the shock wave concept offers the possibility to analyze the observed nonlinear kinematic features. The nonlinear dynamics of the concept suggest that a free superposition of different motions may not be possible. Thus, a particular feedback between locally forced motions and remotely triggered waves may be possible.

References

Anderson, D.L.T. and P.B. Rowlands. 1976. The role of inertia-gravity and planetary waves in the response of the tropical ocean to the incidence of an equatorial Kelvin wave on a meridional boundary. J. Mar. Res. 34(3): 295-312.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984, p. 14-45. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Brink, K.H., D. Halpern, A. Huyer and R.L. Smith. 1983. The physical environment of the Peruvian upwelling system. Progr. Oceanogr. 12: 285-305.

Cane, M.A. 1983. Oceanographic events during El Niño. Science 222(4629): 1189-1195.

Käse, R.H. 1985. El Niño. Geowissenschaften in unserer Zeit. 3(4): 113-119.

Knoll, M., Th. Paluszkiewicz, G. Pittock, R.E. Still, R.L. Smith and A. Huyer. 1987. Current measurements off the west coast of South America, November 1981 - March 1985. College of Oceanography, Oregon State University, Data Report 140: 84-31. 271 p.

Krauss, W. 1973. Methods and results of theoretical oceanography. I. Dynamics of the homogeneous and the quasihomogeneous Ocean. Gebruder Bomtraeger Berlin. 302 p.

Lukas, R. 1986. The termination of the equatorial undercurrent in the Eastern Pacific. Progr. Oceanogr. 16: 63-90.

Nof, D. 1987a. Outflow dynamics. Geophy. Astro. Fluid Dynamics 30(3-4): 165-193.

Nof, D. 1987b. Penetrating outflows and the dam-breaking problem. J. Mar. Res. 45: 557-577.

Nof, D. and S. Van Gorder. 1987. The propagating of gravity currents along continental shelves. (Preprint, Department of Oceanography, Florida State University, Tallahassee).

Philander, G., D. Halpern, D. Hansen, R. Legeckis, L. Miller, C. Paul, R. Watts, R. Weisberg and M. Wimbush. 1985. Long waves in the Equatorial Pacific Ocean. Eos 66(14): 145.

Posner, G.S. 1957. The Peru current. Bulletin of the Bingham Oceanographic Collection 16(2): 106-1703.

Romea, R.D. and R.L. Smith. 1983. Further evidence for coastal trapped waves along the Peru coast. J. Phy. Oceanogr. 13(8): 1341-1356.

Smith, R.L. 1983. Peru coastal currents during El Niño: 1976 and 1982. Science 221: 1397-1399.

Wooster, W. and O. Guillén. 1974. Characteristics of El Niño in 1972. J. Mar. Res. 32(3): 387-404.

The Potential Primary Production of the Peruvian Upwelling Ecosystem, 1953-1984

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Abstract

A model was used to estimate the potential primary production of the Peruvian upwelling ecosystem from 1953 to 1984. A monthly time series of thermocline depth was converted to nitrate concentration at 60 meters using an empirical relationship between the depth of the thermocline and the concentration of nitrate at 60 m. A time series of new production was created using the time series of nitrate concentration at 60 m and a monthly time series of upwelling rates coupled with a Redfield ratio conversion of nitrogen to carbon. The new production time series was converted to primary production using the "f" ratio, 0.75 for the coast of Peru. The estimates of primary production were compared to values obtained using C-14 uptake and the results were similar. The interannual variability in new production generally followed the expected pattern, with lower new production during El Niño and higher new production during cool years. The level of new primary production of the Peruvian upwelling ecosystem is substantially higher than previous estimates and has remained relatively constant through time. The overall results are encouraging but the model still requires adjustment for the area over which the new production is realized.

Resumen

Se usó un modelo para estimar la producción primaria potencial del ecosistema de afloramiento junto a la costa del Perú, entre 1953 y 1984. La serie de tiempo mensual de la profundidad de la termoclina fué convertida a concentración de nitrato a 60 metros usando una relación empírica entre la profundidad de la termoclina y la concentración de nitrato a 60 metros. Se calculó una serie de tiempo de nueva producción primaria usando la serie de tiempo de nitrato a 60 metros y una serie de tiempo de afloramiento, junto con una conversión Redfield de nitrógeno a carbono. La nueva producción primaria se convirtió a producción primaria total, usando un valor de "f" de 0.75. Se compararon los valores estimados usando esta técnica con valores obtenidos usando la incorporación de C-14 por fitoplancton y los resultados fueron similares. La variabilidad interanual de la nueva producción primaria siguió generalmente el patrón esperado, con producción más baja durante El Niño y más alta durante los años frios. La magnitud de la producción primaria del ecosistema de afloramiento junto a la costa del Perú es sustancialmente más elevada que los estimados previos y se ha mantenido relativamente uniforme con el tiempo. Los resultados preliminares son alentadores, pero el modelo requiere mayor atención a los aspectos físicos que modulan el afloramiento y el área que es afectada por este fenómeno.

Introduction

The southeastern tropical Pacific produces a significant proportion of the global pelagic fish harvest (FAO 1983). The richness of living resources is a consequence of high levels of primary production which result from abundant concentrations of inorganic plant nutrients at the surface in a tropical setting (Ryther 1969; Cushing 1971). Primary production in the ocean, however, is highly variable in space and time (Steele 1977). On the other hand, temporal and spatial observations of primary productivity in the ocean are relatively few. Because of the high

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variability in primary productivity in space and time and the few direct observations of primary productivity, it is important to develop indirect methods of estimating primary productivity which integrate over space and time. One such indirect approach involves using upwelling models (Chavez and Barber 1987).

New primary production is primarily supported by upwelling which provides the euphotic zone with nitrate from below the thermocline (Dugdale and Goering 1967). The potential new production of a region is therefore determined by the amount of nitrate upwelled into the euphotic zone. An estimate of the potential new production can be made by estimating the nitrate concentration of the upwelled water and estimating the volume of water upwelled. Wyrtki (1963) estimated the volume of water upwelled for a region in the southeastern tropical Pacific from 6°S to 24°S to be 1.0 x 10^{14} m^3/year. Using the Wyrtki (1963) estimate of the volume of water upwelled and assuming a nitrate concentration of 25 µg-at./l in the source water, a potential new production of 2.0 x 10^{14} gC/year was estimated (Chavez and Barber 1987). The calculation assumes all upwelled nitrate is taken up by phytoplankton and uses a Redfield ratio conversion of nitrogen to carbon.

As part of a multidisciplinary effort designed to study the variability of living resources along the coast of Peru, long time series of monthly averages of physical and biological parameters have been compiled (Pauly and Tsukayama 1987). The spatial domain over which the multidisciplinary effort concentrates is the region along the coast of Peru from 4°S to 14°S. The temporal domain is from 1953 to 1982 and in some cases until 1985. Following a logic similar to that outlined below for the Wyrtki (1963) estimate of upwelling (Fig. 1) we have taken the upwelling time series compiled by Bakun (1987)[a] and the thermocline depth time series compiled by Brainard and McLain (1987) as part of the multidisciplinary study and converted them to a time series of new primary production (sensu Dugdale and Goering 1967).

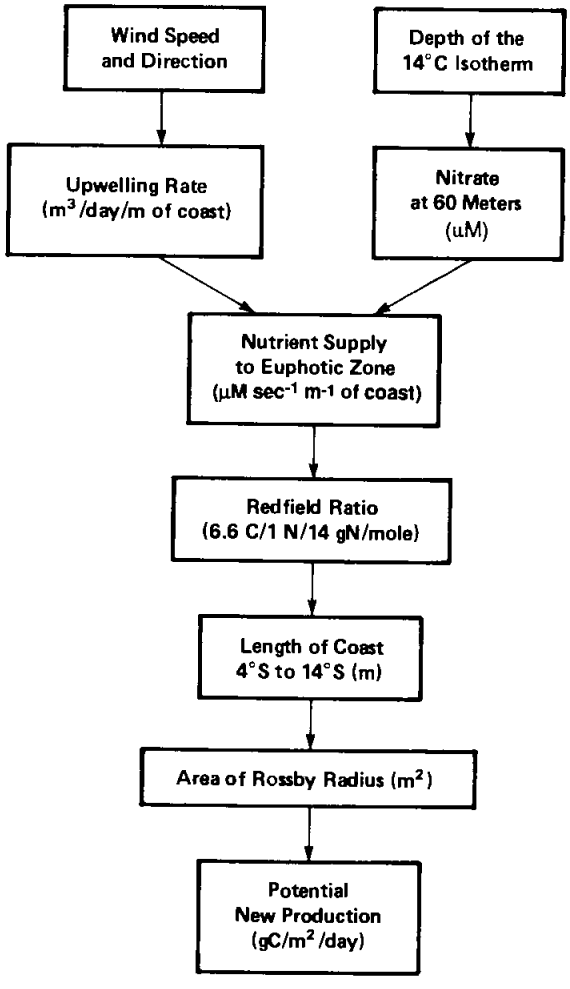

Fig. 1. Flow chart showing the logic involved in converting wind speed and direction and the depth of the 14°C isotherm to potential new production (µM = µg - at./l).

Fig. 1. Carta de flujo mostrando la lógica utilizada en convertir la velocidad y dirección del viento y la profundidad de la isoterma de 14°C, a nueva producción potencial (µM = µg - at./l).

[a]Editors' note: The use of Bakun's (1987) series implies a slight bias, not likely to affect final results (see Bakun and Mendelssohn, this vol.).

Materials and Methods

Barber and Smith (1981) have estimated that water upwelled along the coast of Peru comes from between 50 and 75 m, therefore the nitrate concentration at 60 m is a good proxy for the nitrate concentration of the upwelled water. During the period 1982-1984 the nitrate concentration at 60 m at Paita, Peru (5°S) was found to be a function of sea level and thermocline depth (Fig. 2). Long time series of nutrient concentrations for the coast of Peru do not exist; however, a long monthly time series of thermocline depth (the depth of the 14°C isotherm) has been compiled by Brainard and McLain (1987) from the US Navy Fleet Numerical Oceanography Center (FNOC) Master Oceanographic Observations Data Set (MOODS). The concentration of nitrate in the upwelled source water can be estimated by finding a relationship between the depth of the 14° isotherm (a proxy for the depth of the thermocline) and the nitrate concentration at 60 m. Using data collected on cruises during November and December 1981 and February, November, and December 1983, a significant relationship between the depth of

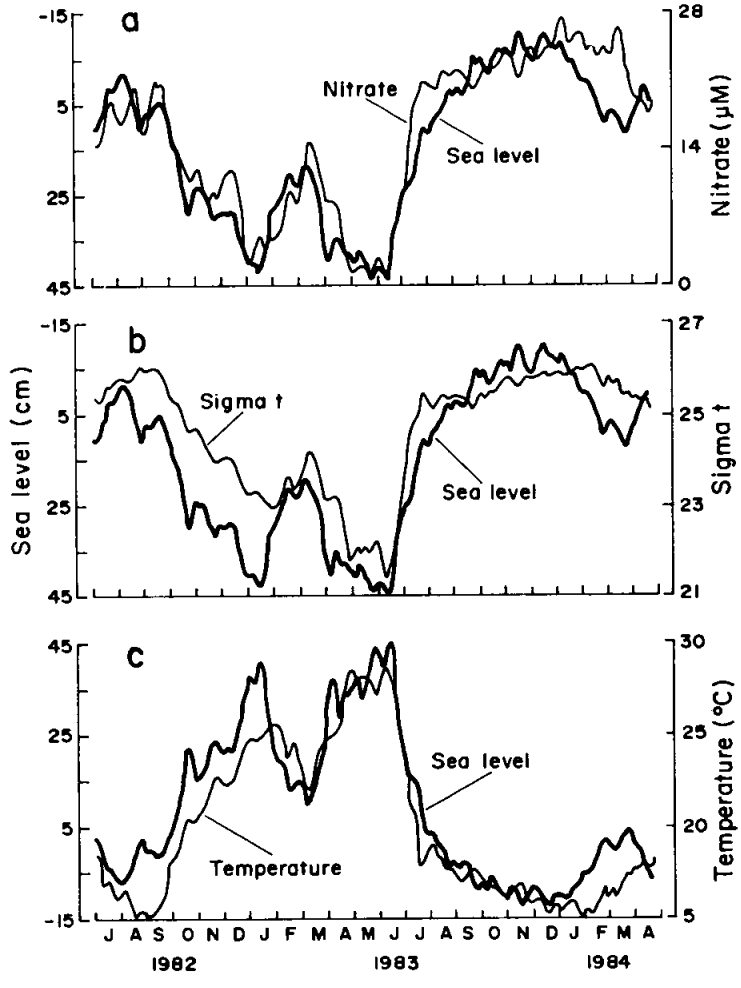

Fig. 2. Relationship between sea level measured at a pier in Paita, Peru (5°03'S, 81°07'W) and (a) nitrate at 60 m, (b) sigma-t at 60 m, and (c) temperature at 60 m measured at an offshore station (5°05'S, 81°15'W) during 1982, 1983, and 1984. Sea level was measured continuously by David Enfield of Oregon State University. Daily values were smoothed with a normal filter (Holloway 1958) to suppress frequencies of less than one week. The nitrate, sigma-t, and temperature were measured three times a week, interpolated to daily values (Stineman 1980) and smoothed as the sea level.

Fig. 2. Relación entre el nivel de mar medido en el muelle de Paita, Perú (5°03'S, 81°07'W) y (a) nitrato a 60 m; (b) sigma-t a 60 m y (c) temperatura a 60 m medida en una estación fuera de la costa (5°05'S, 81°15'W) durante 1982, 1983 y 1984. El nivel de mar fué medido continuamente por David Enfield de la Universidad del Estado de Oregón. Los valores diarios fueron suavizados mediante un filtro normal (Holloway 1958) para suprimir frequencias de menos de una semana. El nitrato, sigma-t, y la temperatura se midieron tres veces por semana, se interpolaron a valores diarios (Stineman 1980) y se suavizaron como los del nivel de mar.

the 14° isotherm and the nitrate concentration at 60 m was found. The regression equation of nitrate on the depth of the 14° isotherm was: nitrate = 44.15 - (0.20 x depth of the 14° isotherm) with a regression coefficient of -0.82 and a slope which is significantly different from zero at $P < 0.01$. Using this equation, the long monthly time series of the mean depth of the 14° isotherm created by Brainard and McLain (1987) was converted to concentrations of nitrate at 60 m.

There are several factors which have not been considered in the present analysis and could potentially bias the calculations. No correction is applied for denitrification. Denitrification has a similar effect on new primary production as El Niño: it reduces the concentration of nitrate in the upwelled water. Stations which exhibited strong denitrification were excluded from the regression between nitrate at 60 m and the depth of the 14°C isotherm. In addition shortly after the 1982-1983 El Niño waters of very high salinity and abnormal nitrate to temperature relationship (i.e., low temperatures and low nitrate concentration) remained close to the coast. These stations also were not considered in the present analysis.

The second parameter needed to estimate potential new production is the amount of water upwelled. A long time series (1953-1984) of monthly upwelling rates has been constructed by Bakun (1987). The upwelling rates are calculated from maritime measurements of wind speed and direction (Bakun et al. 1974) and the units are m^3/sec/m of coast. To see how the volume of upwelling calculated from the upwelling rate compared to other estimates of the volume of water upwelled along the coast of Peru (Wyrtki 1963) we estimated the mean volume of water upwelled for the stretch of coast from 4° to 14°S using the upwelling rates. From the upwelling time series we calculated a mean upwelling rate of 2.17 m^3/sec/m of coast. The calculated mean volume of water upwelled for the length of the coast (4°S to 14°S) for the period from 1953 to 1984 is 7.6×10^{13} m^3/year. The volume calculated here is very similar to that estimated by Wyrtki (1963) using geostrophy, supporting this method of calculation of upwelling volume. A potential bias of using upwelling models which depend solely on the wind (Bakun 1987) is that there are times when upwelling favorable winds along the coast of Peru produce no upwelling (Huyer et al. 1987). This happens at times during El Niño and perhaps during summer months.

Following the logic outlined in Fig. 1, the long time series of nitrate concentration and upwelling rate coupled with a Redfield ratio conversion of nitrogen to carbon were used to construct a long time series of potential new production. Since the theoretical offshore dimension of coastal upwelling is the Rossby radius of deformation (Yoshida 1967) an estimate of the area affected by coastal upwelling between 4°S and 14°S can be made. Taking the total productivity of the length of the coastline and dividing by the area we converted the production into daily or yearly rates per m^2 so that comparisons to productivities measured using other techniques could be made (Table 1).

The thermocline depth time series was incomplete so that smoothing and time series analysis could not be easily performed. In order to fill in the gaps we searched for relationships between thermocline depth and other physical variables. A multiple regression using the mean Peru SST and an index of the Southern Oscillation (Brainard and McLain 1987) gave a regression coefficient of 0.63 which was significant ($P < 0.001$). The missing thermocline depths were found using the multiple regression equation. With the complete series we were able to smooth the data in order to suppress the annual cycle, using a 13-month running mean.

In order to investigate the higher frequency variability, time series analysis was performed on the long monthly time series. In order to determine seasonal cycles in the time series the long-term means of individual months were calculated. Trend analysis was also performed on the time series data in order to investigate long-term trends of the data. Spectral analysis was used to identify the important frequencies of the time series.

Results

The grand mean concentration of nitrate at 60 m for the entire time series is 22.21 μM. This together with the mean upwelling rate converts to a mean potential new production of 844 gC/m^2/year. Chavez and Barber (1987) have estimated a mean total production of 834 gC/m^2/year for 1983, 1984, and 1985 using C-14 carbon uptake experiments. Others (Walsh 1975, 1981; Cowles et. al. 1977; Shushkina et. al. 1978; Barber and Smith 1981; Chavez and

Barber 1985; and Barber et. al. 1986) have also estimated total primary production for the Peruvian upwelling system. In order to compare the new production estimates to total production estimates it is necessary to convert new production to total production. Although new production is a fraction of total production, for the coast of Peru this fraction is high and has been estimated as 0.75 (Dugdale 1985). Using Dugdale's (1985) estimate of the "f" factor (the ratio of new to total production) for the Peruvian upwelling system, the potential new production was converted to total production. Comparison of estimates made in this paper to estimates made using C-14 uptake (Table 1) shows the estimates made using the physical data and those from C-14 measurements are very similar. There is then good agreement between the estimates from the physical data sets and those from C-14 uptake experiments.

Table 1. Comparison of published estimates of production for the Peruvian upwelling system to the estimates made from our method of calculation. The potential new production was converted to total production using a ratio of new to total production (the "f" factor) of 0.75 (Dugdale 1985).
Tabla 1. Comparación de estimaciones publicadas de producción del sistema de afloramiento peruano con las estimaciones obtenidas con nuestro método de calculación. La nueva producción potencial fué convertida a producción total, usando una relación entre la producción nueva y la total de 0.75 (el factor "f") (Dugdale 1985).

Date	Productivity $gCm^{-2}day^{-1}$ This study	Others	Source
April 1969	3.35	4.82	(Chávez and Barber 1985)
April 1969	2.84	5.16	(Barber and Smith 1981)
June 1969	2.66	1.30	(Walsh 1975)
February 1974	4.10	4.16	(Shushkina et al. 1978)
April 1975	3.86	3.80	(Cowles et al. 1977)
April 1976	3.13	1.70	(Barber and Smith 19871)
August 1976	2.85	3.20	(Walsh et al. 1980)
April 1977	2.99	1.90	(Barber and Smith 1981)
November 1977	3.06	3.19	(Barber et al. 1986)
March 1978	3.27	4.30	(Barber and Smith 1981)
Nov 1983 - Sept 1987 (mean)	2.81	2.29	(Chávez and Barber 1987)
MEANS	3.18	3.26	

Interannual Variability

The time series of depth of the 14° isotherm shows that the isotherm is deepest during periods of El Niño Southern Oscillation (see Fig. 3 and Brainard and McLain 1987). From 1956 through 1961 the depth of the 14° isotherm remained relatively constant at about 120 m. The depth of the 14° isotherm during El Niño ranged from 120 m in 1957 to 160 m in 1983. The average depth of the 14° isotherm during non-El Niño years is about 100 m.

The nitrate concentration at 60 m, a mirror image of the depth of the 14° C isotherm, has minima during the El Niño years (Fig. 4). The lowest value occurred in 1983 where the concentration of nitrate was about 13 µM. The highest concentration of nitrate occurred in 1971 at 27 µM. Just like the depth of the 14° isotherm, the nitrate concentration data had a relatively constant value of about 21 uM between 1956 and 1961.

The time series of the rate of upwelling showed peaks during El Niño years (Fig. 5) supporting the observations of Enfield (1981) who first suggested that during El Niño the coastal winds which drive upwelling intensify. During normal time periods, the average upwelling rate is about 2.0 m^3/sec/m of coast. The lowest rate being about 1.5 m^3/sec/m of coast occurred in 1959 and the strongest rate of 3 m^3/sec/m of coast occurred in 1983. The range of upwelling rate during El Niño years is from 2 to 3 m^3/sec/m of coast occurring in 1969 and 1983, respectively.

The time series of new production (Fig. 6) shows that production is lower than the mean during El Niño years except during part of 1957 when the production was about 2.6 gC/m^2/day. During the other El Niño years, the production ranged from 1.7 gC/m^2/day in 1983 to about 2.2

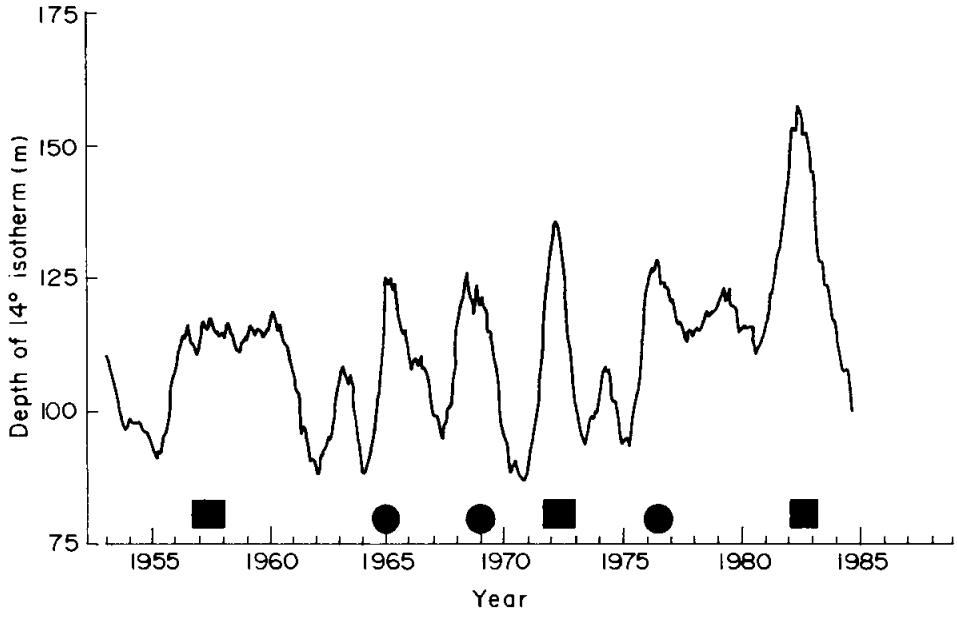

Fig. 3. Time series of the depth of the 14° isotherm (m). The time series was smoothed using a 13-month running mean and the tickmarks on the x-axis represent the middle of the year. The highest peaks on the graph represent the deepest depths; these occur during El Niño years. The 14°C isotherm is from Brainard and McLain (1987). The periods of El Niño are represented by darkened squares for strong and darkened circles for weak El Niño events.

Fig. 3. Serie de tiempo de la profundidad (m) de la isoterma de 14°C. La serie de tiempo fué suavizada usando promedios móviles de trece meses y las marcas en el eje horizontal representan la mitad del año. Los picos mas altos en el grafico representan las mayores profundidades; estas ocurren durante los años El Niño. La isoterma de 14°C es de Brainard and McLain (1987). Los cuadrados representan los Niños fuertes y los círculos representan los Niños más débiles.

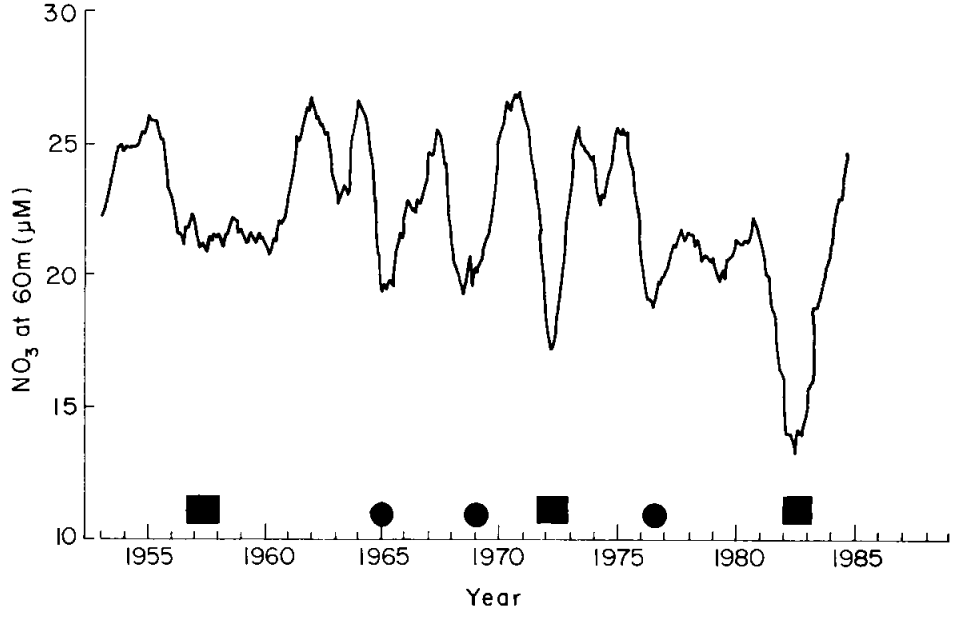

Fig. 4. Time series of the concentration of nitrate at 60 m (μM). The monthly time series was smoothed with a 13-month running mean and the tickmarks on the x-axis represent the middle of the year. This graph shows that during El Niño years the nitrate concentration at 60 m is lower than normal (or cool) years. The filled squares represent the periods of the strong El Niño events of 1957-58, 1972-73 and 1982-83 and the filled circles represent the periods of the weaker El Niño events of 1965, 1969 and 1976.

Fig. 4. Serie de tiempo de la concentración de nitrato a 60 m (μM). La serie de tiempo mensual fue suavizada usando promedios móviles de trece meses y las marcas en el eje horizontal representan la mitad del año. Esta gráfica muestra que durante los años El Niño, la concentración de nitrato a 60 m es más baja que en los años normales (o frios). Los cuadrados representan los Niños fuertes de 1957-58, 1972-73 y 1982-83 y los círculos representan los Niños más débiles de 1965, 1969 y 1976.

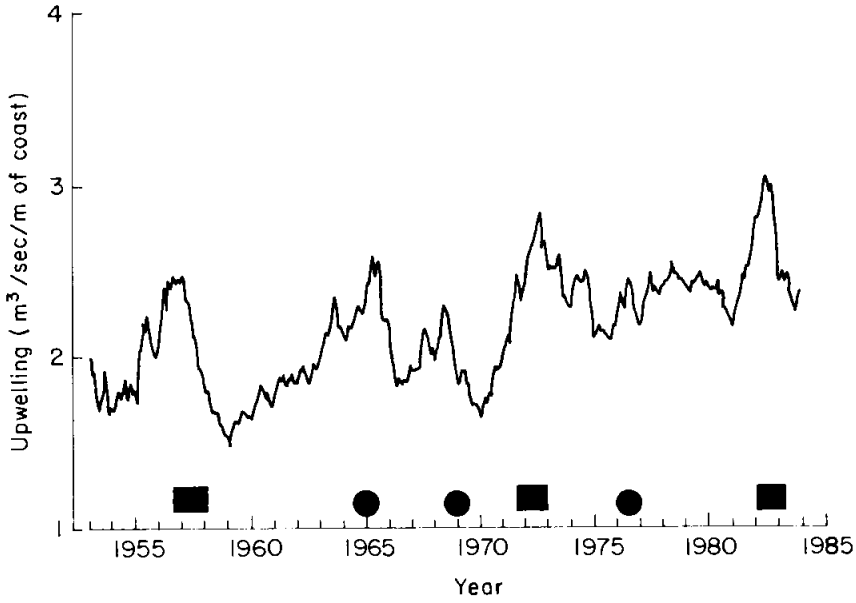

Fig. 5. Time series of upwelling rate (m^3/sec/m of coast). The time series was smoothed using a 13-month running mean and the x-axis tickmarks represent the middle of the year. This graph shows that the upwelling rate is stronger during El Niño events than it is during normal conditions. The upwelling rate is from Bakun (1987). The filled squares represent the periods of the strong El Niño events of 1957-58, 1972-73 and 1982-83 and the filled circles represent the periods of the weaker El Niño events of 1965, 1969 and 1976.

Fig. 5. Serie de tiempo del índice de afloramiento (m^3/seg/m de costa). La serie de tiempo fué suavizada usando promedios móviles de trece meses y las marcas en el eje horizontal representan la mitad del año. Esta gráfica muestra que el afloramiento es más fuerte durante los eventos El Niño que durante condiciones normales. El índice de afloramiento es de Bakun (1987). Los cuadrados representan los Niños fuertes de 1957-58, 1972-73 y 1982-83 y los círculos representan los Niños más débiles de 1965, 1969 y 1976.

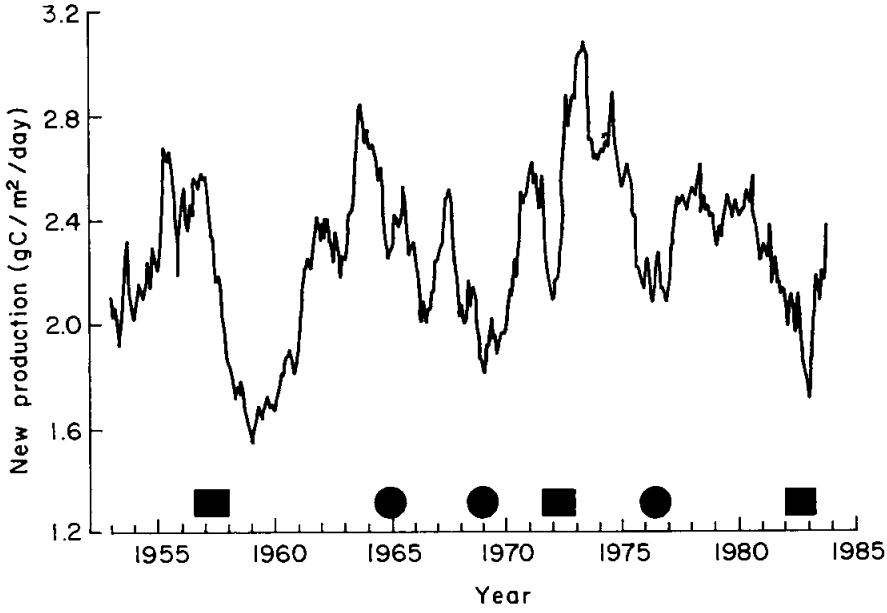

Fig. 6. Time series of new production (gC/m^2/day) from 1953 to 1984. The time series was smoothed using a 13-month running mean and the x-axis tickmarks represent the middle of the year. The 1957-62 negative anomaly is visible as are the valleys of low production during El Niño years except 1957. The filled squares represent the periods of the strong El Niño events of 1957-58, 1972-73 and 1982-83 and the filled circles represent the periods of the weaker El Niño events of 1965, 1969 and 1976.

Fig. 6. Serie de tiempo de nueva producción (gC/m^2/day) desde 1953 a 1984. La serie de tiempo fué suavizada usando promedios móviles de trece meses y las marcas en el eje horizontal representan la mitad del año. La anomalía negativa de 1957-62 es visible asi como lo son los valles de baja producción durante los años El Niño excepto 1957. Los cuadrados representan los Niños fuertes de 1957-58, 1972-73 y 1982-83 y los círculos representan los Niños más débiles de 1965, 1969 y 1976.

gC/m²/day in 1965. Lowest production for the smoothed time series occurred in 1959 at 1.5 gC/m²/day and highest production occurred in 1973 at 3.1 gC/m²/day. There was a strong negative anomaly in new production starting in late 1957 and ending in 1962. New production dropped to its lowest rate of 1.5 gC/m²/day in 1959. The 1957-1962 anomaly was the result of weak upwelling coupled with a relatively deep thermocline. The thermocline deepened during the 1957 El Niño and remained deep until 1962.

Seasonal Cycles

The depth of the 14° isotherm fluctuates irregularly throughout the year. In January it is at about 100 m and gets deeper in February and levels off at 120 m for March, April, and May. In June it rises to 108 m and then drops to lower than 120 m in July. By August the depth of the 14° isotherm rises to about 115 m. It levels off at 100 m for September, October, and November, then it deepens to 110 m in December (Fig. 7).

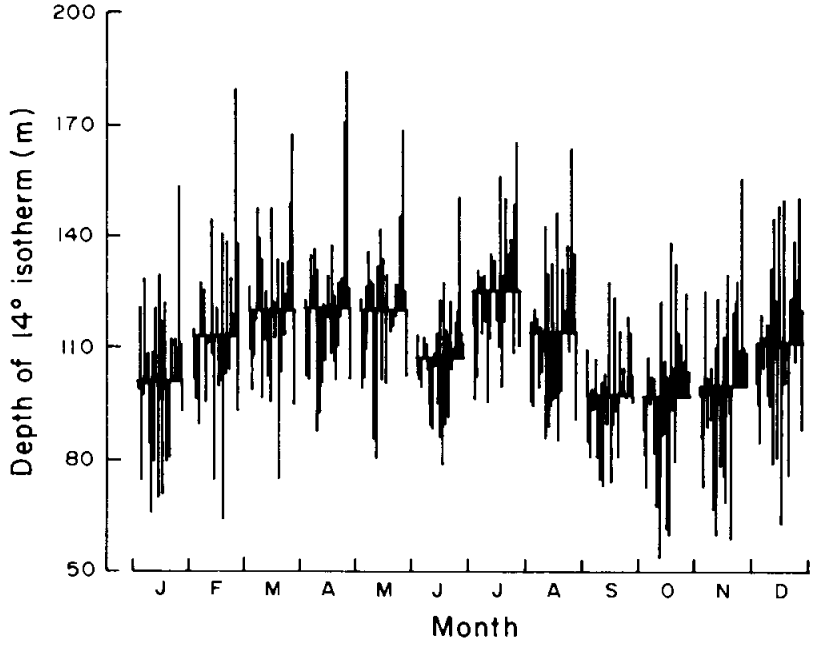

Fig. 7. Monthly plot of the depth of the 14° isotherm (m). The horizontal lines represent the average value for the month and the vertical lines represent the difference from the average to the actual value for each observation. The 14°C isotherm is from Brainard and McLain (1987).
Fig. 7. Representación mensual de la profundidad (m) de la isoterma de 14°C. Las líneas horizontales representan el valor promedio del mes y las líneas verticales representan la diferencia entre el promedio y el valor actual de cada observación. La isoterma de 14°C es de Brainard and McLain (1987).

The upwelling rate exhibits a more regular annual cycle. In January, upwelling is at its weakest, about 1.4 m³/sec/m of coast. The upwelling rate steadily increases by about 0.2 to 0.4 m³/sec/m of coast every month until July. In July, August, and September the upwelling rate is strongest at 2.8 m³/sec/m of coast. In October the rate decreases to 2.2 m³/sec/m of coast and decreases steadily until it reaches 1.6 m³/sec/m of coast in December (Fig. 8).

New production is lowest in December, January and February when it has a mean of around 1.6 gC/m²/day. These months also appear to have the least interannual variability in new production. Production increases steadily until it reaches 2.8 gC/m²/day in June. In July it decreases to 2.5 gC/m²/day and is back to 2.8 gC/m²/day in August. By September, productivity reaches its highest peak of 3.3 gC/m²/day. It then decreases steadily to reach 1.7 gC/m²/day in December (Fig. 9).

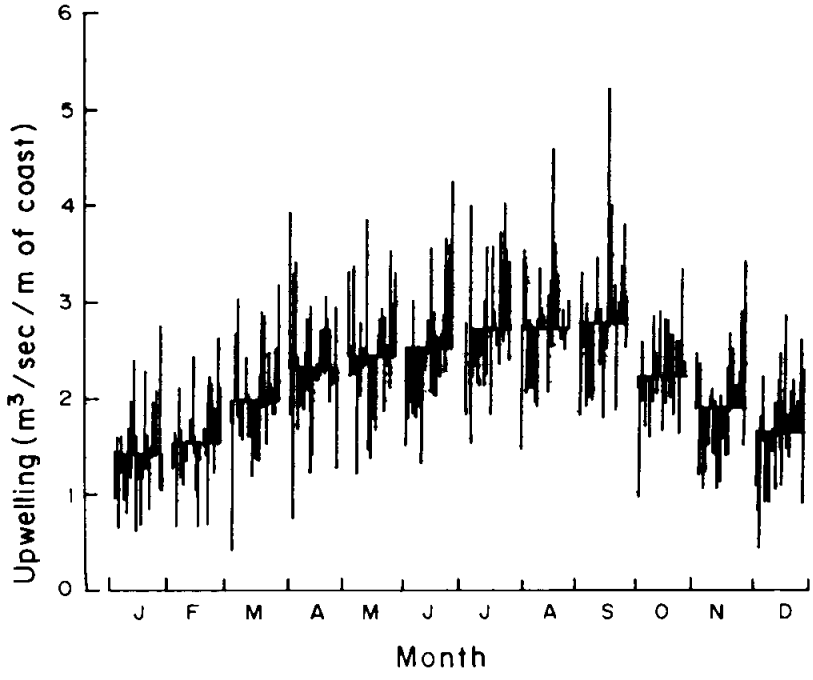

Fig. 8. Monthly plot of the upwelling rate (m^3/sec/m of coast). The horizontal lines represent the average value for the month and the vertical lines represent the differences from the average to the actual value for each observation. The upwelling rate is from Bakun (1987).

Fig. 8. Representación mensual del índice de afloramiento (m^3/seg/m de costa). Las líneas horizontales representan el valor promedio del mes y las líneas verticales representan la diferencia entre el promedio y el valor actual de cada observación. El índice de afloramiento es de Bakun (1987).

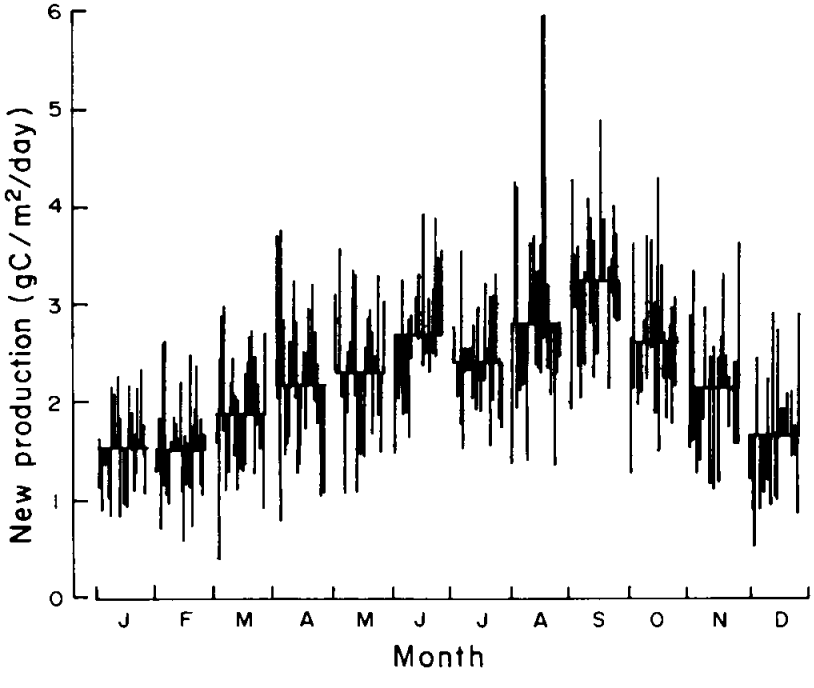

Fig. 9. Monthly plot of new production (mgC/m^2/day). The horizontal lines represent the average value of the month and the vertical lines represent the differences from the averages to the actual value for each observation.

Fig. 9. Representación mensual de la nueva producción (mgC/m^2/dia). Las líneas horizontales representan el valor promedio del mes y las líneas verticales representan las diferencias entre los promedios y el valor actual de cada observación.

Spectral Analysis

The annual cycle of the thermocline depth in the eastern tropical Pacific is apparently driven by remote annual changes in the trade winds; however it is typically believed that the important periodicities are annual and semi-annual (Myers 1979). The power spectrum for the depth of the 14° isotherm (Fig. 10) has strong variance peaks at 12 months, 4 months and 2.33 months and a surprisingly weak peak at 6 months. Nutrient observations along 85°W also suggest that the semi-annual cycle of the 14°C isotherm determined by Myers (1979) can be decomposed into three deepenings (Chavez 1987a). The variation in the depth of the thermocline along the coast of Peru may be a result of local (see below) and remote wind forcing.

The power spectrum of the upwelling rate (Fig. 11) has strong signals at 12 and 6 months. The existence of a six-month cycle in the coastal winds is probably related to the large-scale annual variations of the southeast trade wind field (Goldberg and O'Brien 1981). The power spectrum of new production is very similar to the power spectrum of the upwelling rate (Fig. 12).

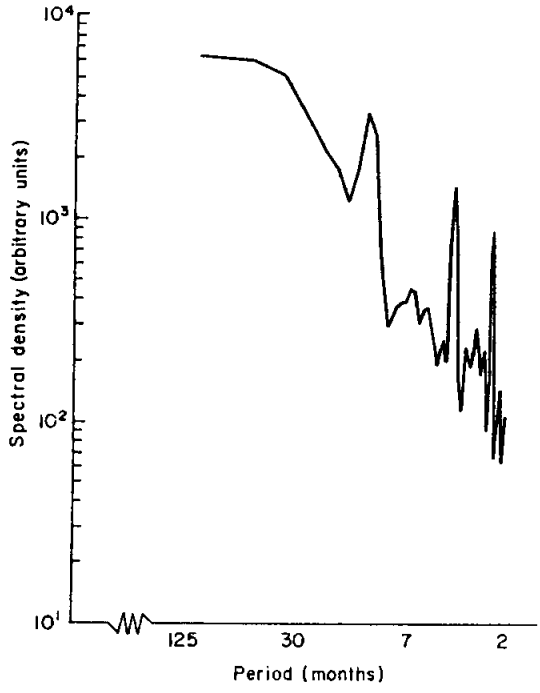

Fig. 10. Spectral analysis of the depth of the 14° isotherm showing strong 12 months, 4 months and 2.3 month cycles.
Fig. 10. Análisis espectral de la profundidad de la isoterma de 14°C mostrando ciclos fuertes de 12 meses, 4 meses y 2.3 meses.

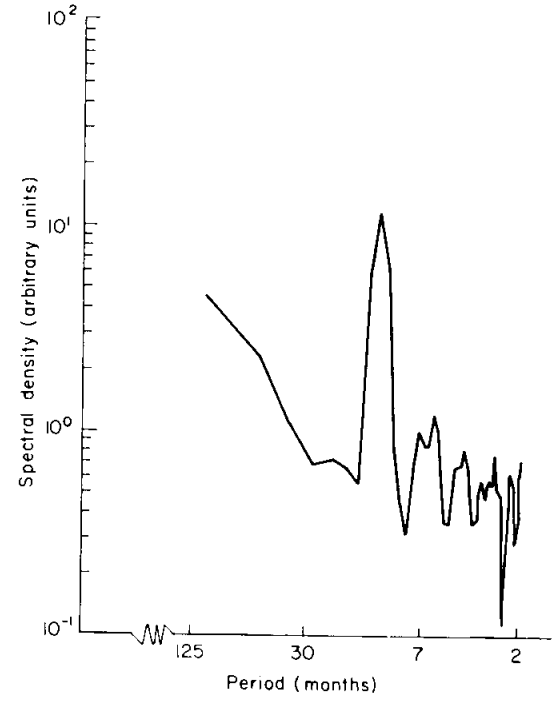

Fig. 11. Spectral analysis for the upwelling rate showing a strong 6-month cycle and a stronger 12-month cycle.
Fig. 11. Análisis espectral del índice de afloramiento mostrando un fuerte ciclo de 6 meses y un ciclo de 12 meses aún más fuerte.

Trends

The trend line equation for the depth of the 14° isotherm was 101.5 + 0.05T. The linear regression of the depth on time (T) gave a regression coefficient of $r = 0.26$; this was significant ($P < 0.01$) suggesting that over the course of the thirty-year period covered here the thermocline depth had progressively deepened. A similar trend analysis was performed on the Southern Oscillation index. The Southern Oscillation showed a significant long-term trend towards lower values. The deepening of the thermocline may be a result of the weakening of the pressure gradient which is believed responsible for maintaining the cross basin tilt in the thermocline (Wyrtki 1975).

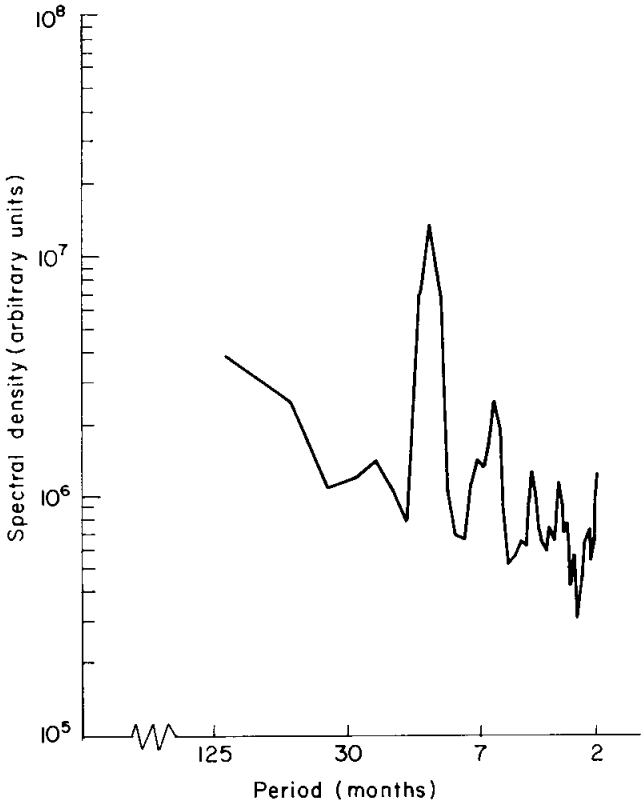

Fig. 12. Spectral analysis for new production showing a strong 6-month cycle and a stronger 12-month cycle.
Fig. 12. Análisis espectral de la nueva producción mostrando un fuerte ciclo de 6 meses y un ciclo de 12 meses aún más fuerte.

The trend line equation for the rate of upwelling was 1.80 + 1.89T (in months). The linear regression on time gave a regression coefficient of 0.28; this was also significant at the $P < 0.01$ level. Since upwelling along the coast of Peru is directly related to wind speed the long-term trend is for stronger winds and stronger upwelling. These findings support the observations of Whysall et al. (1987) who found a long-term trend of increasing winds in the eastern and central Pacific. Again this appears related to changes in the Southern Oscillation.

New production had a trend line equation of 2,134 + 0.71T (in months). The new production data were regressed on time and the resulting correlation coefficient was $r = 0.09$, which was not significant ($P < 0.05$). The trend analysis shows that during the course of thirty years the depth of the 14° isotherm and the upwelling rate increased with time, while new production remained constant over this same period. The trends in thermocline depth and upwelling rate affect new production in opposite directions. A deeper thermocline means less nitrate in the upwelled water while stronger upwelling implies that a larger volume of water is upwelled.

Discussion

Potential new production depends on the depth of the thermocline (nutricline) and on the upwelling rate. These two properties tend to be coupled temporally along the coast of Peru. They vary in such a manner that variations in the amount of nutrients supplied to the euphotic zone, and therefore potential new production, are minimized. When the thermocline is deep, such as during El Niño, upwelling is stronger and when the thermocline is shallow, during cool conditions, then upwelling is typically weaker. Enfield (1981) has determined a physical basis for these observations. When the thermocline is deep there is also warmer sea surface temperature (SST), partially a result of the deeper thermocline (see Cane 1983 for a review of the physical nature of El Niño). During periods of warmer SST (and lesser cloud cover) the land-sea temperature difference drives stronger coastal winds. Conversely periods of shallow thermocline and cool SST would be associated with weaker coastal winds.

The coastal wind scenario can be taken to the scale of the Southern Oscillation. The long-term (thirty-year) trend in the Southern Oscillation and the thermocline depth is for a weaker pressure difference and a deeper thermocline. The deeper thermocline (through increased upper ocean heat content) would result in stronger coastal winds and stronger upwelling following the logic of Enfield (1981). It is important to note that others (e.g., Rasmusson 1987) do not find a similar trend in the Southern Oscillation and have suggested that the trends in the wind data (Whysall et al. 1987) may be a result of changes in the methods of measuring winds. The trend in the depth of the thermocline, the measurement of which appears free of systematic sampling artifacts, supports the trend in the coastal winds.

The level of new production supported by upwelling along the coast of Peru has thus remained relatively constant over the thirty-year period. Periods of deeper thermocline (nutricline) are somewhat balanced by stronger upwelling. The combination of stronger winds and deeper thermocline, however, raises questions regarding the size of the area over which the new production is realized. The area calculated using the Rossby radius is the spatial domain of vertical motion or upwelling. Stronger winds and greater offshore advection should increase the area over which the new production is realized. Thus, although a similar quantity of nitrate is upwelled, the primary production driven by the upwelled nitrate would probably occur over a larger area. This would decrease the intensity (per m^2) of primary production. The long-term trend and the El Niño condition would result in a decrease in the intensity of primary production and therefore reduced fish production (Ryther 1969). Similarly during the winter months when upwelling is strongest the method of calculating the intensity of primary production appears biased toward larger values.

The species composition of the phytoplankton should also be affected by the long-term trends and El Niño. A deeper thermocline implies stronger poleward transport. Increased poleward currents appear to favor small offshore organisms as opposed to diatoms. Dinoflagellates are favored by weak winds (Chavez 1987b). The long-term trends suggest that conditions unfavorable to diatoms and dinoflagellates are developing. Colonial diatoms are considered the organisms which are most efficiently converted to fish production (Ryther 1969) so the long-term trend would be for less efficient conversion of primary production into fish production. The decrease in the abundance of dinoflagellates would lower larval anchoveta

Table 2. Potential primary production of the Peruvian upwelling ecosystem, 1953 to 1984 (in gC * $year^{-1}$ * 10^{-12}).
*Tabla 2. Producción primaria potencial del ecosistema de afloramiento peruano, 1953 a 1984 (en gC*año^{-1}*10^{-12}).*

Year	Jan	Feb	Mar	Apr	May	Month Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	95	75	92	220	180	88	160	83	110	150	170	72
1954	65	110	25	120	150	120	140	250	250	74	89	55
1955	88	44	140	46	160	120	120	250	200	210	200	33
1956	51	69	170	220	210	130	140	120	170	130	95	100
1957	84	150	170	160	120	190	210	120	210	150	120	140
1958	82	87	100	130	110	110	100	160	140	120	76	94
1959	90	63	65	86	64	150	90	140	120	110	84	55
1960	06	62	74	92	110	110	120	130	160	130	87	83
1961	50	57	75	96	150	120	150	130	140	120	110	84
1962	130	94	130	150	150	170	140	120	190	170	170	64
1963	110	93	140	130	150	95	150	84	190	210	130	71
1964	120	110	120	190	190	170	150	210	240	210	130	130
1965	90	95	85	120	190	140	120	170	230	130	110	83
1966	130	100	120	160	120	160	160	220	170	150	70	57
1967	110	89	65	76	65	170	110	200	210	210	140	170
1968	50	130	99	81	89	180	170	140	130	150	150	100
1969	59	65	77	110	87	190	120	190	160	110	67	60
1970	76	35	88	130	120	150	130	140	150	180	130	94
1971	56	96	80	150	110	230	110	210	190	250	140	160
1972	90	89	130	100	85	140	130	130	280	90	71	110
1973	130	68	140	150	150	150	190	350	280	200	160	98
1974	99	150	150	170	170	160	150	150	200	170	190	110
1975	110	90	160	170	170	180	150	240	220	160	130	110
1976	65	44	130	190	160	130	92	140	190	130	140	110
1977	76	100	74	120	98	150	180	190	120	110	130	120
1978	97	110	140	160	130	180	180	160	200	130	110	100
1979	120	140	130	140	140	230	120	120	180	160	130	84
1980	110	96	100	100	190	140	190	150	200	170	120	120
1981	140	68	90	110	110	190	190	160	230	110	140	86
1982	86	110	100	62	110	200	140	81	220	180	110	100
1983	100	62	55	61	88	170	110	130	180	130	93	52
1984	63	98	160	65	180	210	100	140	170	160	210	170

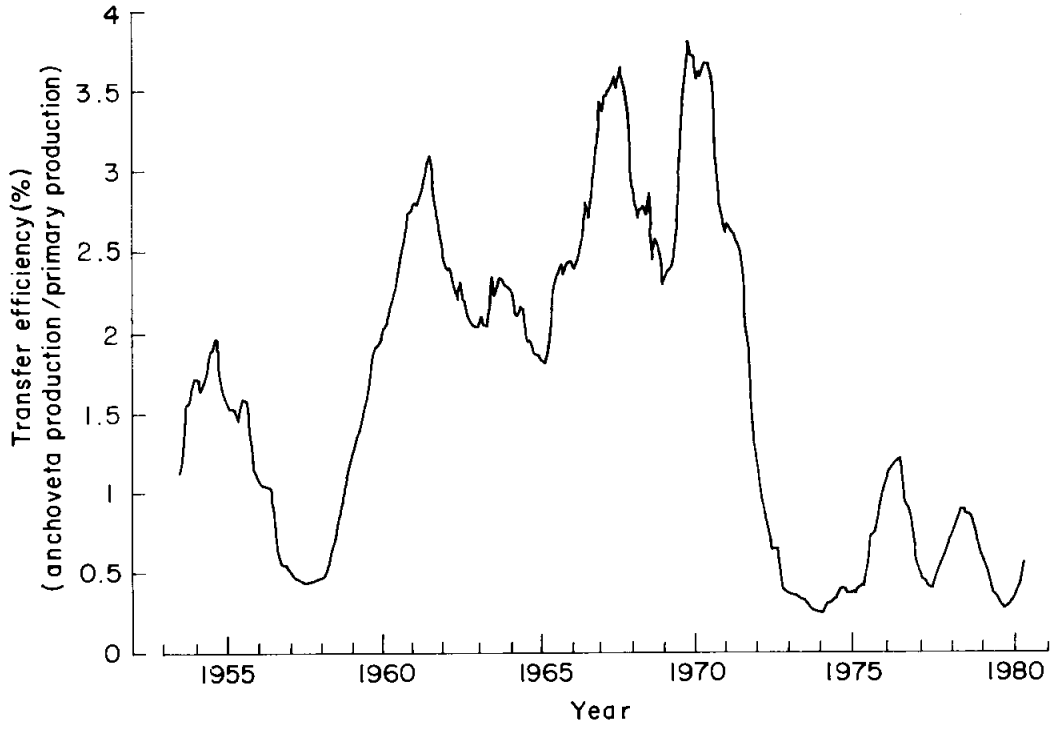

Fig. 13. Efficiency of transfer of primary production to anchoveta production (both in gC/year) with monthly values smoothed using a 13-month running mean. Note that transfer efficiency was 2-3% during the period of high anchoveta biomass and production (i.e., the 1960s).

Fig. 13. Eficiencia con que la nueva producción se convirtió a producción de anchoveta (ambos en gC/año) con los valores mensuales suavizados usando promedios móviles de 13 meses. Nótese que la eficiencia de transferencia fué de 2-3% durante el período de alta biomasa y producción de anchoveta (ej. los años de 1960).

survival, since dinoflagellates are the preferred food of the larvae (Lasker 1978), and eventually affect recruitment levels.

The results summarized in Table 1 suggest that the estimates of primary productivity calculated using the methods developed here are accurate. The results confirm that the primary production of the Peruvian upwelling system is substantially higher than that estimated by Ryther (1969) and Cushing (1971) (Chavez and Barber 1985). With the more accurate monthly estimates of primary production in Table 2 it is now possible to determine the proportion of primary production which was converted into anchoveta production for the entire time series. To estimate production of anchoveta (P), we have multiplied the monthly anchoveta biomass (B, wet weight) estimates of Pauly et al. (1987) by their estimates of total mortality (Z = fishing mortality + natural mortality from all causes), and estimated production as P = Z * B (Allen 1971). These estimates were then turned into carbon production estimates, using as conversion factor the average of Ryther's (10) and Cushing's (17.85) factor of carbon to wet weight (0.072gC = 1 g ww). The percentage that this represents of the total production is plotted in Fig. 13. This suggests that during the periods of maximum anchoveta biomasses, 2-3% of the total primary production was converted to anchoveta production.

Assuming that the gross food conversion efficiency of anchoveta is between 10 and 20% (Walsh 1981), the 2-3% converted to anchoveta flesh would correspond to between 10 and 30% of primary production. However, this range which would have applied during the period of maximum anchoveta abundance (in the 1960s) is realistic only if anchoveta fed exclusively on phytoplankton (which is not the case, see Rojas de Mendiola, this vol., Alamo, this vol. and Pauly et al., this vol.). Walsh (1981) suggested that the changes in anchoveta biomass which occurred in the early seventies would result in increased carbon accumulation in the sediments. However, the changes in the carbon flow from primary production to anchoveta production do not appear to be of sufficient magnitude to support this hypothesis which was also rejected by Henrichs and Farrington (1984), based on the lack of notable differences in the sediment organic carbon deposition rates before and after 1971.

References

Allen, K.R. 1971. Relation between production and biomass. J. Fish. Res. Board Can. 28: 1573-1581.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Bakun, A., D.R. McLain, F.V. Mayo. 1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. US Fish. Bull. 72(3):843-844.

Barber, R.T., J.E. Kogelschatz and F.P. Chavez. 1986. Productividad primaria en las aguas costeras entre los 5°-15°S del Pacifico suroriental, p. 33-37. *In* O.A. Mathisen and I. Tsukayama (eds.) Bases biológicas y marco conceptual para el manejo de los recursos pelágicos en el Pacífico suroriental. Documento de Pesca No. 001, Organización Latinoamericana de Desarollo Pesquero, Lima, Perú.

Barber, R.T. and R.L. Smith. 1981. Coastal upwelling ecosystems, p. 31-68. *In* A.R. Longhurst (ed.) Analysis of marine ecosystems. Academic Press, New York.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability of Peru, 1952 to 1984, p. 14-45. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Cane, M.A. 1983. Oceanographic events during El Niño. Science 222: 1189-1195.

Chavez, F.P. 1987a. The annual cycle of SST along the coast of Peru. Tropical Ocean-Atmosphere Newsletter 37: 4-6.

Chavez, F.P. 1987b. Ocean variability and phytoplankton community structure. Duke University, North Carolina, U.S.A. Ph.D. Dissertation.

Chavez, F.P. and R.T. Barber. 1985. La productividad de las aguas frente a la costa del Perú. CPPS, Boletin ERFEN 15: 9-13.

Chavez, F.P. and R.T. Barber. 1987. An estimate of new production in the equatorial Pacific. Deep-Sea Res. 34: 1229-1243.

Cowles, T.J., R.T. Barber and O. Guillen. 1977. Biological consequences of the 1975 El Niño. Science 195: 285-287.

Cushing, D.H. 1971. Upwelling and the production of fish. Adv. Mar. Biol. 9: 255-334.

Dugdale, R.C. 1985. The effects of varying nutrient concentrations on biological production in upwelling regions. CalCOFI Rep. 26: 93-96.

Dugdale, R.C. and J.J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr. 12: 196-206.

Enfield, D.B. 1981. Thermally driven wind variability in the planetary boundary layer above Lima, Peru. J. Geophys. Res. 86: 2005-2016.

FAO. 1983. Review of the state of world fishery resources. FAO Fish. Circ. 710, Revision, Rome, 42 p.

Goldberg, S.B. and J.J. O'Brien. 1981. Time and space variability of tropical Pacific wind stress. Mar. Wea. Rev. 109: 1190-1207.

Henrichs, S.M. and J.W. Farrington. 1984. Peru upwelling region sediments near 15°S. 1. Remineralization and accumulation of organic matter. Limnol. Oceanogr. 29(1): 1-19.

Holloway, J.L. 1958. Smoothing and filtering of time series and space fields. Adv. of Geophys. 4:351-389.

Huyer, A., R.L. Smith and T. Paluszkiewicz. 1987. Coastal upwelling off Peru during normal and El Niño times, 1981-1984. S. Geophys. Res. 92: 14297-14308.

Lasker, R. 1978. The relation between oceanographic conditions and anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-V. Réun. Cons. int. Explor. Mer. 173: 212-230.

Myers, G. 1979. Annual variation in the slope of the 14°C isotherm along the equator in the Pacific Ocean. J. Phys. Oceanogr. 9: 885-891.

Pauly, D. and I. Tsukayama (eds.). 1987. The anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987. VPA estimates of the monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Rasmusson, E.M. 1987. Tropical Pacific variations. Nature 327: 192.

Ryther, J.H. 1969. Photosynthesis and fish production in the sea. Science 166: 72-76.

Shushkina, E.A., M.Y. Vinogradov, Y.I. Sorokin, L.P. Lebedeva and V.N. Mikheyev. 1978. Functional characteristics of planktonic communities in the Peruvian upwelling region. Oceanology 18: 579-589.

Steele, J.H. 1977. Some comments on plankton patches, p. 1-20. *In* J.H. Steele (ed.) Spatial pattern in plankton communities. Plenum Press, New York.

Stineman, R.W. 1980. A consistently well-behaved method of interpolation. Creative Computing 6: 54-57.

Walsh, J.J. 1975. A spatial simulation model of the Peru upwelling ecosystem. Deep-Sea Res. 22: 201-236.

Walsh, J.J. 1981. A carbon budget for overfishing off Peru. Nature 290:300-304.

Walsh, J.J., T.E. Whitledge, W.E. Esaias, R.L. Smith, S.A. Huntsman, H. Santander and B.R. de Mendiola. 1980. The spawning habitat of the Peruvian anchovy, *Engraulis ringens*. Deep-Sea Res. 27A: 1-27.

Whysall, K.D.B., N.S. Cooper and G.R. Bigg. 1987. Long-term changes in the tropical Pacific surface wind field. Nature 327: 216-219.

Wyrtki, K. 1963. The horizontal and vertical field of motion in the Peru Current. Bull. Scripps Inst. Oceanogr. 8: 313-346.

Wyrtki, K. 1975. El Niño - the dynamic response of the equatorial Pacific Ocean to atmospheric forcing. J. Phys. Oceanogr. 5: 572-584.

Yoshida, K. 1967. Circulation in the eastern tropical oceans with special reference to upwelling and undercurrent. Jap. J. Geophys. 4: 1-75.

Time Series of Upwelling Nitrate and Primary Production off Peru Derived from Wind and Ancillary Data, 1953-1982

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Abstract

Different models of upwelling nitrate flux along the Peruvian coast are derived and compared. It emerged that realistic estimates of nitrate flux, and hence of new primary production, can be obtained only if the selected model incorporates a realistic gradient of nitrate concentrations, a variable upwelling depth and a variable width of the upwelling area along the Peruvian coast. Model outputs, i.e., monthly estimates of primary production for the period 1953 to 1982 are provided in tabular form for different parameterizations.

Resumen

Diferentes modelos para la surgencia de flujos de nitratos a lo largo dc la costa peruana son derivados y comparados. Se encontró que estimaciones realistas de flujo de nitratos, y a partir de este de la de nueva producción primaria, pueden ser obtenidas solamente si el modelo seleccionado incorpora un gradiente realista de concentraciones de nitratos, una profundidad variable de surgencia y una anchura variable del area de surgencia a lo largo de la costa. Los resultados del modelo, es decir, estimaciones mensuales de producción primaria, para el período de 1953 a 1982 son proporcionados en forma tabular para las diferentes parametrizaciones.

Introduction

The primary production in the Peruvian upwelling system is known to fluctuate widely. Estimates vary more than one order of magnitude (see, e.g., Guillén and Calienes 1981; Feldman 1986) and are not available on routine basis. However, routine measurements of physical parameters, such as local wind speed, are available. Physical data recently made available by Pauly and Tsukayama (1987) may be used to parameterize newly upwelling nitrate. Thus, based on wind data and some ancillary data, Chavez et al. (this vol.) derived time series of the potential new production of the Peruvian upwelling ecosystem, with a mean of about 3.2 gC m^{-2} day^{-1}.

Here we compare three models and two sets of physical parameters used to compute the upwelling nitrate in coastal and oceanic zones off Peru. The approach of Chavez et al. (this vol.) shall herein be referred to as Model I.

Data

The physical data used are time series of monthly mean of upwelling index, sea surface temperature, and depth of the 14°C isotherm. The upwelling indexes have been calculated from wind measurements at Trujillo (8°S) on the Peruvian shore (Mendo et al. 1987) and ship measurements in Peruvian coastal waters from 4°-14°S (Bakun and Mendelssohn, this vol.). Local and spatially averaged SST are given by Pauly and Tsukayama (1987) and Bakun (1987) respectively and isotherm depths by Brainard and McLain (1987) for coastal Peruvian waters. The chemical data are measurements of nitrate concentration (and SST) taken on cruises carried out by IMARPE during 1981-1987.

Theory

The parameterization of primary production relies on the assumption that the upwelled waters contain a limiting nutrient (nitrate) required by phytoplankton. New primary production will therefore be proportional to the upwelled water mass and the concentration of nitrate. The first step in modelling new primary production is thus to parameterize the upward flux of nitrate.

The divergence-induced upwelling in depths of the Peruvian coastal current system is the source of the upwelled water masses. Their actual upwelling to the surface is due to the wind-induced Ekman pumping. Consequently, upwelling depths change as a function of the wind (Guillén and Calienes 1981).

Model I relies on the correlation of the depth of the 14°C isotherm and nitrate concentration in 60-m depth. Also, the time series of isotherm depths was interpreted as a measure of the mean nitrate concentration of the upwelled water masses. The product of the upwelling index, basically the square of the wind speed, and isotherm depth would thus be a measure of the upwelled nitrate which may then be converted into an estimate of new primary production.

Our model of the vertical nitrate flux differs in three elements from Model I. First, the nitrate concentration above the thermocline changes with depth; it is lowest near the surface. Second, the water masses upwelled to the surface originate from different depths depending on the actual wind speed. Third, the width of the upwelling region, measured by the internal Rossby radius of deformation, changes with the thermal stratification. This model, described below, leads in contrast to Model I, to a measure of the vertical nitrate flux which is proportional to the third power of the ratio of wind speed and depths of the 14°C isotherm divided by the surface temperature.

The concentration of nitrate (µM) at 60 m depth is, in Model I, linearly correlated with the depth of the 14°C isotherm ("D_{14}").

$$C_{NO_3} = a - b * D_{14} \qquad \text{... 1)}$$

where a = 44.15 µM and b = 0.20 $\mu M m^{-1}$ and r = -0.82.[a]

The vertical nitrate flux per unit length of coast line as a function of the upwelling "Up" ($m^3 sec^{-1} m^{-1}$) is:

$$F_{NO_3} = C_{NO_3} * Up \qquad \text{... 2)}$$

The strength of the upwelling is proportional to the longshore wind speed squared. The nitrate concentration at the surface is generally considerably less than in deeper waters (Calienes and Guillén 1981). The difference is most pronounced during periods of warm anomalies, i.e., El Niño events. Thus it might be assumed, as a first approximation that the surface concentration is negligible when compared to the concentration in deeper waters. However, it would be better to parameterize the surface nitrate concentrations by the surface temperature. Using data collected

[a]Chavez et al. (this vol.) use micromolar (µM) to express concentrations (i.e., µg-at./l); further below we use the equivalent $mmol.m^{-3}$.

in the region 7°-10°S by IMARPE (during February and August 1981, December 1982, January 1983, February, July and August-September 1985, April-May 1986 and February 1987) suggests the parameterization (Fig. 1):

$$\log(C(O)) = \log(A) - B * \log(SST) \quad \text{... 3)}$$

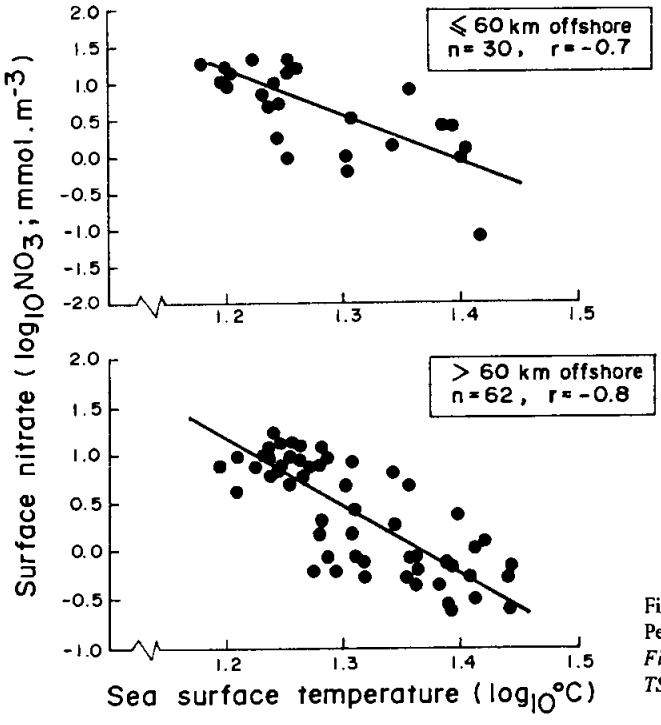

Fig. 1. Regression of nitrate concentration in surface waters *vs.* SST off Peru. Above: coastal zone. Below: oceanic zone.
Fig. 1. Regresión de concentración de nitratos en agua superficial vs. TSM frente a Perú. Arriba: zona costera. Abajo: zona oceánica.

where the units are $mmol.m^{-3}$ and °C, and
where the parameters "a" and "b" vary with offshore distance, i.e.,
≤ 60 km offshore: log(a) = 8.57 b = -6.18
> 60 km offshore: log(a) = 9.48 b = -6.93

The 14°C isotherm generally occurs at depths around 120 m. Thus, taking the estimates of nitrate concentration at the surface and at 60 m depth, the vertical profile of newly upwelled nitrate above the thermocline may be approximated as

$$C(z) = C(O) + 2 * (C_{NO_3} - C(O))/D_{14} * z \quad \text{... 4)}$$

where z is the depth and which reduces, for vanishing surface concentration, to

$$C(z) = 2 * C_{NO_3}/D_{14} * z \quad \text{... 5)}$$

The upwelling of subsurface water takes place at the bottom of the wind driven Ekman layer. Its thickness "D_E" can be estimated as a function of the wind speed (U) using scaling laws given by Csanady (1982):

$$D_E = c * U \quad \text{... 6)}$$

Thus, the nitrate concentration in the upwelled water is

$$C(D_E) = (C(O) + 2\,(a - b * D_{14} - C(O)/D_{14}) * c * U \quad \text{... 7)}$$

with

$a = 44.15$ mmol.m^{-3}
$b = 0.20$ mmol.m^{-3}
$c = 6.222$ s

The vertical flux of nitrate per unit length of the coast line can be compared to equation (2):

$$F_{NO_3} = C(DE) * Up \qquad \text{... 8)}$$

The internal Rossby radius "R_i", the measure of the width of the upwelling zone, can be estimated using different approaches, depending on the physics to be described. Here we use a formula which assumes two-layered stratification: a warmer upper layer of thickness "h_1" extending from the surface down to the depth of the 14°C isotherm, and a colder lower layer of thickness "h_2" extending from the 14°C isotherm, down to the bottom. The interface is described by its depth (D_{14}) and a normalized mean density difference "e" which is a function of the temperatures of the top and the bottom layers. The first is understood as a function of SST and the latter is set to 12°C.

Density differences depending on salinity changes are not incorporated because of lack of data. The temperature and salinity ranges found offshore of Peru (Guillén et al. 1977; Zuta et al. 1978) indicate that density differences are mainly a function of temperature. However, the estimate of the internal Rossby radius given below is nothing more than a first order approximation formulated such as to vary with season and the occurrence of El Niño events:

$$R_i = (g * e\,(h_1 * h_2/h_1 + h_2))^{1/2}/f \qquad \text{... 9)}$$

$e = E * (Ta^2 - 8° * Ta - 4° * 12°)$
$Ta = (14° + SST)/2$
$h_1 = D_{14}$
$h_2 = 250\text{ m} - D_{14}$
$E = 7.3\ 10^{-6}$ (°C^{-2})
$g = 9.81$ (ms^{-2})
and $f = 2.283 * 10^{-5}$ (rad s^{-1}; at 10°S)

The mean reference bottom depth of 250 m has been chosen as reference value for the entire region to which the model is applied. This value fits the nearshore (shelf) conditions but is too low for offshore conditions over the continental slope.

Some comments on the Rossby radius should be made. It is a measure of the width of the coastal upwelling zone, i.e., there is an exponential decrease of the upwelling to 25% over distances of the order of one Rossby radius.

Estimates of the Rossby radius based on equation (9) are most sensitive to changes of the interface depth if the reference bottom depth is about twice the interface depth. If the reference bottom depth is several times larger than the interface depth, then estimates of the Rossby radius of deformation are not too sensitive to different values for the reference bottom depth. Here, the seasonal fluctuations of the Rossby radius as a function of the changing stratification is the feature to be parameterized. Thus, the parameterization of the Rossby radius is set to mirror temperature-dependant changes of stratification.

A constant estimate of Rossby radius derived from the phase speed (about 2.5 ms^{-1}) of internal Kelvin waves (Romea and Smith 1983) has been used in Model I. Estimates of average Rossby radius for regions of large latitudinal extent in low latitudes, as in this case, must be very approximate. The Rossby radius in 5° and 15°S is about 220 km and 73 km, respectively, if derived from the internal phase speed of Kelvin waves. These estimates are several times higher than those which will be used here (Fig. 2), because they rely on a dynamic (Kelvin wave) which is sensitive to the abyssal depths off the continental margin. This would be meaningful if the coastal upwelling is due to Kelvin waves and not due to deep divergence of the Peruvian coastal current system and to Ekman pumping. However, in view of the latitudinal dependence of the Rossby radius, any useful parameterization should be such that it is not too sensitive to the mean value of the Rossby radius, but rather responds to its temporal, especially seasonal, changes (Fig. 2).

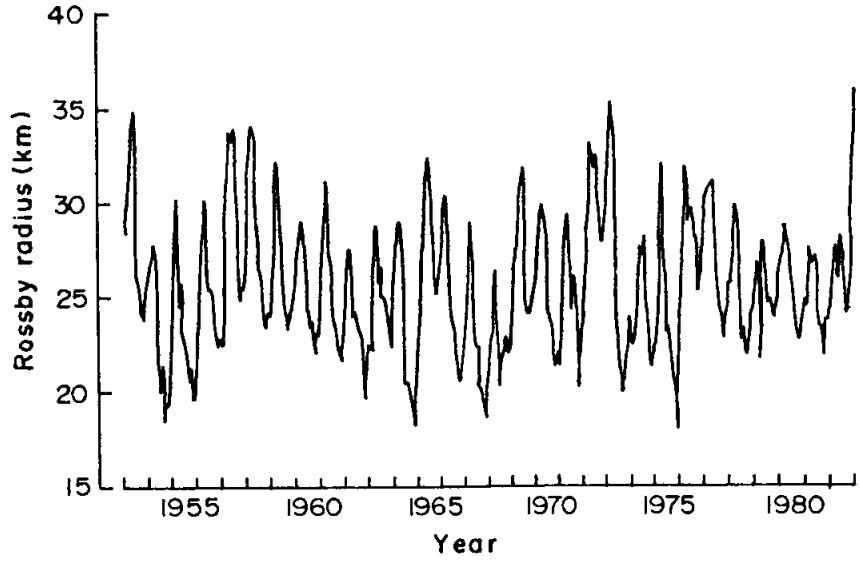

Fig. 2. Time series of the mean Rossby radius of deformation for the area 4-14°S off Peru, as estimated with local SST and depth of the 14°C isotherm.
Fig. 2. Series de tiempo del radio de deformación de Rossby medio para el área 4°-14°S frente a Perú, calculadas con TSM local y profundidad de la isoterma de 14°C.

Upwelling decreases from the coastline. The latter is, in this context, the isobath for which the surface wave field is not yet influenced by the bottom topography (this starts at about 50 m), or the isobath which separates roughly the nonhydrostatic inshore from the hydrostatic offshore dynamics. The strength of the upwelling will be about 5% of its maximum value, which occurs at the coast line, at positions three times the Rossby radius seaward of the coast line. The strength of the upwelling is measured by the upwelling index which gives the mass flux by unit length of coast line. Thus, the nitrate flux per unit surface will be obtained for both models of the nitrate flux per unit coast line (equations 2 and 8) via:

$$f_{NO_3} = F_{NO_3}/(R_i * 3) \qquad \text{... 10)}$$

The estimates of nitrate flux per unit surface depends on (1) the model of the nitrate concentration at depth and (2) the parameterization of the upwelling. The version of our model following most closely that in Model I is characterized by homogeneous nitrate concentration and a fixed upwelling depth. This model will be called here the "constant depth model" or "CDM". Our complete model includes nitrate concentration which increases with depth and a variable depth from which the water is upwelled by Ekman pumping. This model will be labeled "variable depth model" or "VDM". Both models are used together with an upwelling zone of variable width (three Rossby radii), thus incorporating lateral variability. In this context, Model I is characterized as: homogeneous nitrate concentration, fixed upwelling depth and fixed width of the upwelling region. The three models thus form a hierarchy of models of increasing complexity (Model I < CDM < VDM).

Results and Discussion

In the following, the models of the vertical nitrate fluxes are compared, and differences due to the use of two distinct descriptions of the wind field will be presented. In a second step, we convert the nitrate fluxes to the new primary production of organic carbon by the Redfield ratio and a global efficiency factor of 0.75. These estimates are then compared to independently obtained measurements of primary production.

In order to compare correctly, one has to consider (1) that the regressions between nitrate concentration and temperature or isotherm depths are only crude estimates (the square of the correlation coefficients is about 0.5, thus only 50% of the variance is explained), and (2) that the model contains several more or less unknown parameters whose values may be selected such as to "tune" the model to any preselected conditions. Therefore, even if we trust the model itself, we cannot expect to find close agreement to observations. However, the key features of the model outputs should be consistent with observations.

The time series of surface nitrate concentrations were estimated by regression (equation 3) from the time series of the spatial mean SST and local SST (mean of values off Talara, Chimbote and Callao). Fig. 3, which shows their long periodic variability (twelve-monthly running mean), implies that the upwelling at the coast (<=60 km offshore) is stronger than in the oceanic zone (>60 km offshore). Minima of the nitrate concentrations occur during periods of maximal SST (El Niño events). The difference in surface nitrate concentrations in the coastal and in the oceanic zone appear to have increased since the late 1960s. This feature is due to the different behavior of the time series of local and mean SST since the late 1960s (see Brainard and McLain 1987).

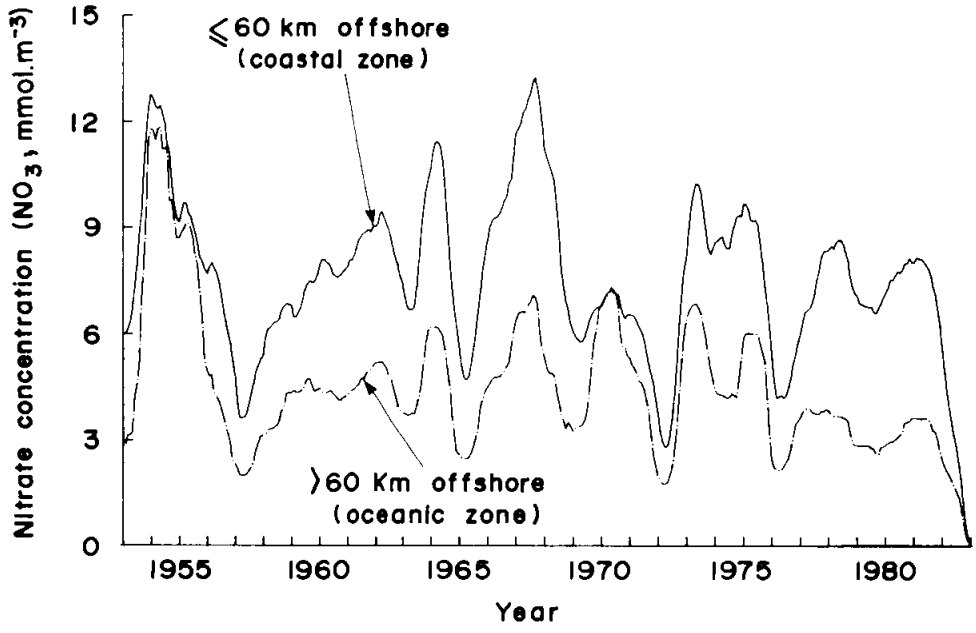

Fig. 3. Smoothed time series of nitrate concentration in Peruvian surface waters (coastal and oceanic zones, 4-14°S). Note impact of El Niño events (arrow).

Fig. 3. Series de tiempo suavizadas de concentración de nitrato en aguas superficiales peruanas (zonas costera y oceánica, 4°-14°S). Notar el impacto del evento El Niño (flecha).

Thus, the time series of nitrate concentration behave reasonably and match concepts and observations (Calienes et al. 1985). This result justifies the use of two different sets of upwelling indexes, one for the coast (Trujillo upwelling) and one for the oceanic zone (Bakun's upwelling), to describe the vertical fluxes. Therefore, both models will be applied to two different regimes, one determined by the coastal parameter setting (SST to NO_3, Trujillo winds) and the other determined by the oceanic parameter setting (SST to NO_3, Bakun's winds). In both cases, the same estimates of the Rossby radius (Fig. 2) have been used.

It should be noted that most of the variability of the Rossby radius is due to seasonal fluctuations; the seasonal estimates differ roughly by a factor of 1.5; and minimum and maximum values are about 20 km and 30 km, respectively. This means that the width of the upwelling zone (equation 9) varies between 60 and 90 km. This seems to be a reasonable estimate if compared to observations of the width of the coastal zone of high productivity (Calienes et al. 1985) or low SST (Zuta et al. 1978). Also, the seasonal variability of the Rossby radius and of the wind-induced upwelling is well reproduced in the monthly fluctuations of nitrate flux (Fig. 4).

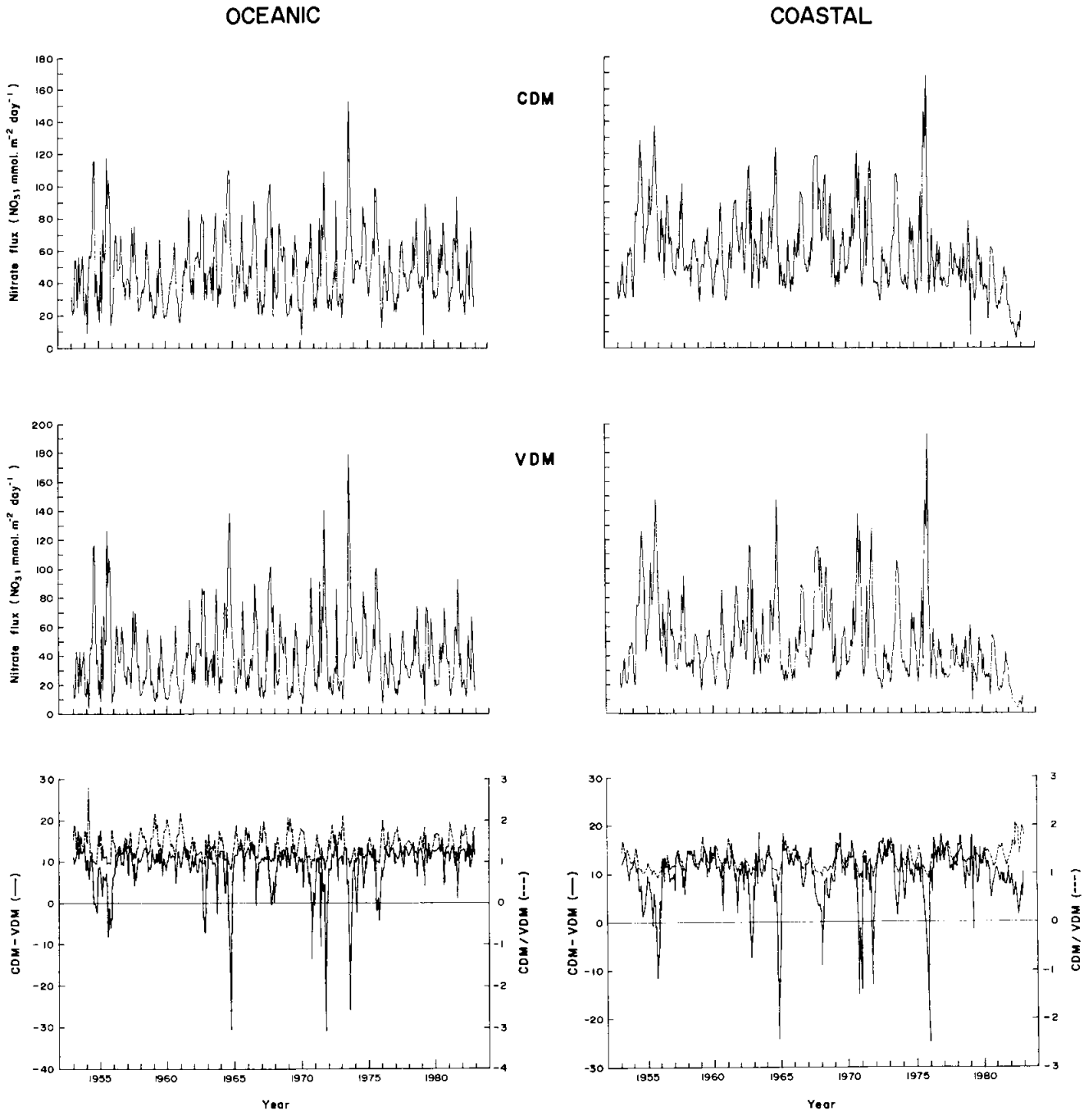

Fig. 4. Upper and central graphs: monthly estimates of upwelled nitrate off Peru, as obtained from "constant depth model" (CDM) and "variable depth model" (VDM), for oceanic and coastal settings. Lower graphs: relationship between CDM and VDM estimates.

Fig. 4. Gráficos arriba y centro: estimaciones mensuales de nitratos frente al Perú, obtenido del "modelo a profundidad constante" (CDM) y el "modelo a profundidad variable" (VDM), usando parámetros oceanicos y costeros. Gráficos abajo: relación entre las estimaciones con CDM y VDM.

The complete, variable upwelling depth model (VDM) yields nitrate fluxes which are generally lower than those using the constant upwelling depth model (CDM) (Figs. 4 and 5). Similar estimates obtained by the CDM are obtained for situations of high nitrate fluxes and this feature is independent of the use of coastal or oceanic parameter setting.

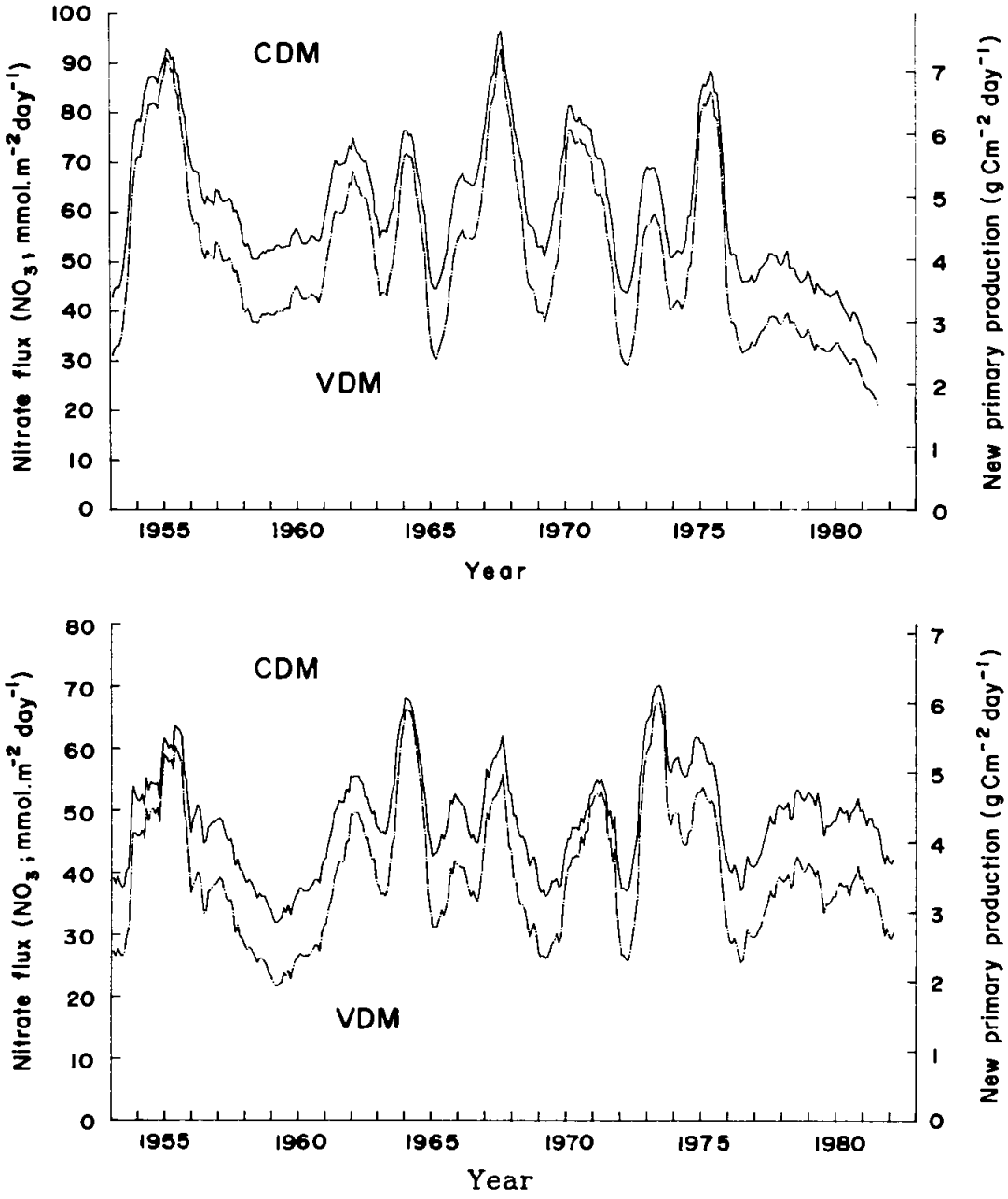

Fig. 5. Smoothed nitrate fluxes per unit sea area off Peru. Above: coastal zone (based on Trujillo upwelling index). Below: oceanic zone (based on Table 1 in Bakun and Mendelssohn, this vol.). The right scale (see text) expresses the same data as time series of new primary production.

Fig. 5. Flujos de nitrato suavizados por unidad de área frente a Perú. Arriba: zona costera (basado en el índice de surgencia de Trujillo). Abajo: zona oceánica (basado en Tabla 1 en Bakun y Mendelssohn, este vol.). La escala a la derecha (ver texto) expresa los mismos datos de las series de tiempo de nueva producción primaria.

Thus, seasonal variability is increased if nitrate concentrations as a function of depth and variable upwelling depths are included in the model. The differences concern mainly lower estimates of upwelled nitrate per unit surface for southern hemisphere summer. Calienes et al. (1985) report ratios of mean seasonal surface concentration of nitrate summer to winter of about 1 to 3. This seems to be closer to the range given by the VDM, but the CDM does not fall off significantly. Seasonal variability is slightly higher for the coastal than for the ocean parameter setting.

The smoothed time series (twelve-month running mean) of the nitrate fluxes per unit surface (Fig. 5) show that both models give the same mean estimate for well established "cool events" but differ considerably for "warm events", (i.e., El Niño events) and this obviously also applies

to our estimates of new primary production which are mathematically nothing more than re-scaled estimates of nitrate flux (see Fig. 5). The mean values of both models could have been tuned to match each other by, e.g., plugging a higher constant "c" in the parameterization of the depth from which the water is taken by Ekman pumping. However, this would only mask the systematic differences between both models.

Fig. 5 also shows the net effects of the coastal and oceanic parameter setting. Mean levels of nitrate flux or new primary production are higher for the coastal setting. However, the differences are about 1 $gCm^{-2}d^{-1}$, which is within the range of differences between the two models. The sequence of peak and troughs in the time series differ, especially for the 1960s. This indicates, if it is assumed that both parameter settings really depict coastal and oceanic conditions, that nitrate upwelling and primary production have different temporal changes near- and offshore. This, too, appears consistent with the spatial variability of the physics of the Peruvian upwelling system (Brink et al. 1983).

Guillén et al. (1977) report a ratio of primary production between "normal" and the 1972 El Niño event of about 4 to 1. This ratio is higher than any modeled peak to trough ratio found for the smoothed time series but could be met by the peak to trough ratios of the unsmoothed monthly values. However, the mean values estimated by the model, about 4 gCm^{-2} d^{-1} or 2 gCm^{-2} d^{-1}, are much higher than the observations (a problem which could be circumvented by selecting a different factor for converting nitrate flux to primary production - see above).

Comparing both models in terms of monthly mean values of the daily new production per m^2 illustrates (see Fig. 4C, D) the features discussed above. The new primary production is

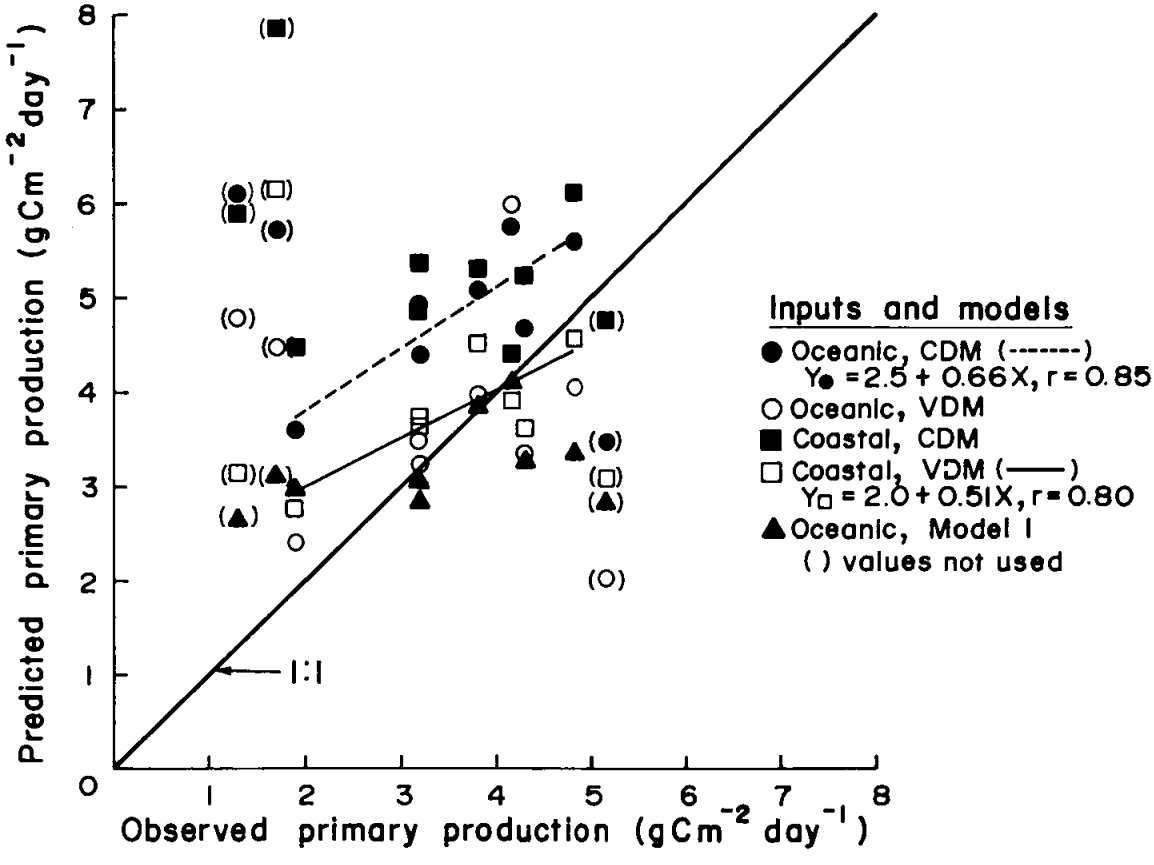

Fig. 6. Estimates of primary production relationships between observed (C_{14} method) and predicted primary production. The two regressions and their correlation coefficients refer to the two significant correlations of models and observations. Some observations (in brackets) were not used in the regression (see text for details).

Fig. 6. Estimaciones de producción primaria: Relaciones entre valores observados (método del C_{14}) y producción primaria pronosticada. Las regresiones y sus coeficientes de correlación se refieren a las dos correlaciones significantes de los modelos y observaciones. Algunas observaciones (en paréntesis) no fueron usadas en la regresión (ver texto para detalles).

Table 1. Comparison of observed and modelled estimates of primary production in $gCm^{-2}day^{-1}$ (unsmoothed) in the Peruvian upwelling system. Models have been used for two parameter settings (coastal, oceanic) and rely on two hypotheses: (a) upwelling from fixed depth (CDM), and (b) upwelling from variable depth and vertical profile of nitrate concentration (VDM). The potential new production was converted to total production using a ratio of new to total production of 0.75 (Dugdale 1985). Dates marked "*" refer to measurements performed under conditions not compatible with the models (see text for details).

Tabla 1. Comparación de estimaciones de producción primaria en $gCm^{-2}día^{-1}$ (no suavizadas) observadas y modeladas en el sistema de afloramiento peruano. Se usaron modelos para dos parámetros (costero, oceánico) y se basan en dos hipótesis: (a) Surgencia desde una profundidad fija (CDM), y (b) surgencia de profundidades variables y perfiles verticales de concentración de nitratos (VDM). La producción nueva potential fue convertida a producción total usando un factor de conversión de producción nueva a total de 0.75 (Dugdale, 1985). Fechas marcadas con "" se refieren a medidas hechas bajo condiciones no compatibles con los modelos (ver texto para detalles).*

	MODELS				
	Oceanic		Coastal		
Date	CDM (1)	VDM (2)	CDM (3)	VDM (4)	Observed values[a]
April 1966	5.60	4.05	6.12	4.56	4.82
April 1969 *	3.47	2.03	4.76	3.08	5.16
June 1969 *	6.11	4.80	5.09	3.15	1.30
February 1974	5.76	5.99	4.41	3.91	4.16
April 1975	5.08	3.97	5.31	4.51	3.80
April 1976 *	5.73	4.48	7.87	6.16	1.70
August 1976	4.40	3.25	5.37	3.73	3.20
April 1977	3.59	2.41	4.48	2.76	1.90
November 1977	4.92	3.49	4.87	3.64	3.19
March 1978	4.67	3.35	5.24	3.61	4.30
median (all obs.)	5.00	3.73	5.17	3.69	3.50
median (without *)	5.60	4.05	5.31	3.91	3.80

[a]From Table 1 in Chávez et al. (this vol.)

generally about 1 $gCm^{-2}d^{-1}$ higher if parameterized via the CDM. The ratios of model estimates scatter less for the coastal setting. This feature is reasonable because upwelling is strongest near the coast and vertical gradients are therefore less pronounced. The VDM estimates the highest production, about 1 to 2 $gCm^{-2}d^{-1}$ higher than the CDM does during pronounced cool events. A spectacular difference of both model is found for the coastal setting in southern hemisphere winter 1982. Both estimates differ by a factor of more than 2 for several months compared to an overall ratio of about 1.5. This feature indicates important changes of the nitrate concentration with depth and weak upwelling. Upwelling indexes at Trujillo are small, about 25% of their normal values (Mendo et al. 1987), the 14°-isotherm is relatively deep (150 m), about 20 m below normal, and SST is relatively high (16°C), about 1°C above normal (Brainard and McLain 1987). The nitrate profile corresponding to these values is steeper than normal and upwelling is from depths above 60 m. Thus, the CDM should overestimate the vertical nitrate fluxes during the onset of the 1982-1983 El Niño event. CDM and VDM show no different estimates for the oceanic setting, because winds are about normal (Bakun 1987).

Using Dugdale's (1985) estimate of the "f" factor for the Peruvian upwelling system, the new production was converted to total production in order to compare our estimates to estimates made using C_{14} uptake reported in Chávez and Barber (1987). Numbers are given in Table 1 and refer to unsmoothed monthly estimates. Their relationships, compared to the expected slope of one, are shown in Fig. 6. This figure shows estimated production *vs.* measured production. Any good approximation of the measurements by the model should yield a scatter of points about a line with slope one.

First, Model I (constant upwelling depth and fixed width of the upwelling zone) and our models CDM and VDM used with coastal and oceanic parameter setting respectively, do not describe the tendency found in the C_{14} uptake measurements (i.e., the linear regressions lead to

Table 2. Monthly estimates (unsmoothed) of new production in $gCm^{-2}day^{-1}$ for the Peruvien upwelling system using coastal parameterization, CDM (see text) and upwelling from Trujillo for 1953-1982.

Tabla 2. Estimaciones mensuales (no suavizadas) de producción nueva en $gCm^{-2}dia^{-1}$ para el sistema de afloramiento peruano usando parametrización costera, CDM (ver texto) y surgencias de Trujillo para 1953-1982.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
1953	3.22	2.38	2.62	3.38	4.20	2.86	2.51	2.42	3.30	4.63	4.48	4.92	3.41
1954	4.61	2.92	2.39	4.53	6.67	6.42	6.73	8.42	10.16	9.01	7.70	5.44	6.25
1955	4.13	5.18	5.63	6.00	8.26	6.46	6.87	8.13	9.13	10.87	8.93	7.15	7.23
1956	5.98	4.47	4.20	6.71	5.25	5.94	3.25	5.19	7.47	6.92	5.00	5.41	5.48
1957	5.16	4.44	3.84	3.67	3.52	4.78	4.85	4.34	7.14	6.29	8.05	5.09	5.10
1958	3.73	3.80	4.03	3.70	4.01	4.07	2.94	4.71	5.32	5.24	4.66	4.25	4.21
1959	4.35	2.75	2.26	3.57	4.06	4.08	3.87	5.17	5.04	5.86	4.53	4.36	4.16
1960	4.33	3.53	2.45	3.18	3.82	4.36	4.02	5.12	7.10	6.34	5.38	3.49	4.43
1961	3.54	2.30	2.42	3.24	4.52	5.18	3.86	4.52	6.66	7.19	7.22	5.69	4.70
1962	5.36	4.60	4.94	5.67	6.16	4.53	3.63	4.79	6.84	8.66	8.96	5.06	5.77
1963	7.67	2.89	3.86	5.35	5.04	4.06	3.81	2.88	4.96	6.66	4.44	3.86	4.62
1964	4.51	4.20	3.85	5.07	6.82	6.07	4.82	6.71	7.01	9.83	8.50	5.61	6.08
1965	4.51	3.08	4.16	3.35	2.99	3.64	2.87	3.14	5.27	4.07	3.59	2.74	3.62
1966	3.51	3.03	5.32	4.59	4.42	5.83	4.49	7.64	7.54	7.31	5.71	4.08	5.29
1967	4.11	3.72	3.75	4.50	4.00	5.44	4.67	8.87	9.38	9.42	9.43	6.75	6.17
1968	7.83	7.63	5.19	5.42	8.14	8.52	5.51	5.42	5.28	6.96	7.55	3.40	6.40
1969	3.92	5.75	2.96	3.57	3.19	3.82	3.09	5.04	4.97	5.84	4.81	3.59	4.21
1970	4.02	3.83	4.35	5.43	4.92	6.84	5.32	5.90	8.75	9.77	6.84	8.92	6.24
1971	6.82	3.90	3.00	3.76	4.65	7.93	3.84	5.79	8.72	9.19	6.70	5.93	5.85
1972	4.70	3.19	3.25	3.14	3.23	2.75	2.28	2.99	5.00	4.21	4.37	3.62	3.56
1973	4.15	2.93	3.10	4.46	4.91	5.43	5.56	8.50	8.57	8.03	6.06	4.32	5.50
1974	3.58	3.31	3.15	3.10	3.66	3.08	2.81	3.95	6.39	5.10	6.01	5.07	4.10
1975	4.26	3.20	2.67	3.98	5.36	7.69	2.95	8.21	11.61	9.80	13.39	7.43	6.71
1976	5.74	2.69	3.74	5.90	4.55	4.25	2.78	4.03	5.25	3.98	4.99	3.30	4.27
1977	3.49	3.03	3.50	3.36	3.07	3.01	3.02	4.06	5.21	5.12	3.65	3.58	3.68
1978	4.67	4.23	3.93	4.00	3.47	4.52	2.94	3.65	5.13	3.82	3.17	4.00	3.96
1979	6.23	4.95	0.62	3.97	3.56	3.01	2.29	2.92	5.49	4.34	4.56	3.09	3.75
1980	4.43	3.26	2.81	3.17	2.90	3.07	1.43	2.93	4.94	4.90	4.70	3.66	3.52
1981	3.07	2.10	1.89	2.33	2.14	2.23	3.04	2.86	4.00	3.51	3.51	2.07	2.73
1982	2.14	2.04	1.37	1.13	1.26	1.16	0.72	0.47	1.17	1.26	0.85	1.80	1.28
Mean	4.59	3.64	3.37	4.11	4.42	4.70	3.69	4.96	6.43	6.47	5.93	4.59	

Table 3. Monthly estimates (unsmoothed) of new production in $gCm^{-2}day^{-1}$ for the Peruvian upwelling system using coastal parameterization, VDM (see text) and upwelling from Trujillo for 1953-1982.

Tabla 3. Estimaciones mensuales (no suavizadas) de producción nueva en $gCm^{-2}dia^{-1}$ para el sistema de afloramiento peruano usando parametrización costera, VDM (ver texto) y surgencias de Trujillo para 1953-1982.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
1953	2.27	1.42	1.60	2.26	3.06	1.94	1.68	1.72	2.42	3.74	3.57	3.94	2.47
1954	3.58	1.96	1.56	3.63	5.96	5.91	6.11	8.32	10.03	8.78	7.28	4.74	5.65
1955	3.37	4.51	4.95	5.48	8.33	5.98	6.43	7.96	9.30	11.78	9.38	6.80	7.02
1956	5.89	3.57	3.13	6.04	4.20	5.05	2.33	4.22	6.81	6.20	4.25	4.69	4.70
1957	4.35	3.92	2.75	2.51	2.39	3.79	3.91	3.39	6.56	5.53	7.58	4.16	4.24
1958	2.55	2.61	2.86	2.51	2.86	2.97	1.99	3.73	4.41	4.29	3.79	3.31	3.16
1959	3.32	1.68	1.28	2.42	2.82	2.90	3.12	4.27	4.24	4.61	3.51	3.21	3.11
1960	3.25	2.26	1.57	2.26	2.89	3.44	3.32	4.14	6.91	5.38	4.33	2.54	3.52
1961	2.36	1.34	1.55	2.34	3.21	4.00	3.01	3.86	5.86	7.06	6.46	4.81	3.82
1962	4.60	3.65	3.96	5.15	5.10	3.57	2.91	3.95	6.73	9.26	9.07	4.45	5.20
1963	7.31	2.07	2.74	4.72	3.54	3.15	2.99	2.17	4.09	5.75	3.61	2.87	3.74
1964	3.35	2.93	2.76	4.02	6.22	5.46	4.48	6.08	6.99	11.75	9.00	4.95	5.66
1965	3.89	2.34	2.69	2.17	1.77	2.47	1.81	2.20	4.13	2.96	2.56	1.83	2.57
1966	2.42	1.92	4.25	3.42	3.35	4.76	3.79	7.08	6.95	6.61	4.76	3.13	4.37
1967	3.13	2.64	2.51	3.66	3.22	4.58	4.14	8.48	9.01	9.15	9.14	6.59	5.52
1968	8.55	7.55	4.52	4.75	7.40	8.13	5.13	4.89	4.53	6.17	6.90	2.74	5.94
1969	2.92	4.44	1.82	2.31	1.98	2.36	2.30	4.11	4.23	4.77	3.92	2.63	3.15
1970	2.87	2.80	3.30	4.09	3.66	6.16	4.29	5.14	9.19	10.97	6.93	10.01	5.78
1971	6.55	2.80	2.03	2.68	3.97	7.03	2.98	5.13	7.69	10.22	6.61	5.53	5.28
1972	3.96	2.36	2.33	1.90	1.95	1.73	1.34	2.00	3.77	2.96	3.29	2.28	2.49
1973	2.83	1.69	1.96	3.32	3.64	4.77	5.03	8.39	8.10	7.25	4.77	3.32	4.59
1974	2.75	2.93	2.76	2.27	2.46	1.99	1.98	3.21	5.54	4.50	5.27	4.09	3.31
1975	3.38	2.36	1.72	3.38	4.25	6.87	2.52	7.85	11.76	10.13	15.34	7.09	6.39
1976	4.80	1.96	3.25	4.62	3.18	3.08	1.83	2.80	4.09	3.00	3.56	2.12	3.19
1977	2.50	1.95	2.24	2.07	1.95	2.07	2.17	3.12	4.41	4.06	2.73	2.59	2.66
1978	3.78	2.96	2.71	2.59	2.48	3.50	2.28	3.11	4.20	2.99	2.45	3.25	3.02
1979	4.88	3.52	0.75	2.72	2.37	2.15	1.67	2.21	4.29	3.41	3.53	2.16	2.81
1980	3.23	2.17	1.95	2.16	1.96	2.23	1.05	2.35	4.33	4.21	3.87	2.78	2.69
1981	2.25	1.34	1.24	1.53	1.35	1.57	2.26	2.25	3.40	2.78	2.60	1.49	2.00
1982	1.48	1.24	0.81	0.72	0.62	0.58	0.38	0.34	0.71	0.64	0.45	0.99	0.75
Mean	3.75	2.70	2.45	3.12	3.40	3.81	2.98	4.29	5.82	6.03	5.35	3.83	

Table 4. Monthly estimates (unsmoothed) of new production in $gCm^{-2}day^{-1}$ for the Peruvian upwelling system using oceanic parameterization, CDM (see text) and Bakun's upwelling for 1953-1982.

Tabla 4. Estimaciones mensuales (no suavizadas) de producción nueva en $gCm^{-2}dia^{-1}$ para el sistema de afloramiento peruano usando parametrización oceánica, CDM (ver texto) y surgencias de Bakun para 1953-1982.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
1953	2.56	1.63	1.84	4.34	4.30	2.01	4.53	2.50	3.30	3.61	4.57	1.94	3.11
1954	1.61	2.80	0.73	3.72	4.57	4.43	4.89	9.12	9.24	2.55	3.65	1.78	4.09
1955	2.56	1.22	4.98	1.73	5.86	4.23	4.70	9.39	6.85	8.31	7.19	1.10	4.84
1956	1.62	1.81	4.06	5.59	5.47	3.85	3.85	3.95	5.57	4.36	3.04	3.24	3.87
1957	2.41	3.14	3.47	3.38	2.39	4.28	5.96	4.22	5.99	4.34	3.41	3.53	3.88
1958	1.83	1.91	2.18	2.90	2.72	3.07	3.03	5.24	4.46	4.05	2.30	2.82	3.04
1959	2.39	1.50	1.50	2.14	1.66	3.83	2.53	5.37	3.62	3.01	2.09	1.45	2.59
1960	1.64	1.56	1.90	2.49	3.20	3.16	3.65	3.90	5.22	4.08	2.67	2.41	2.99
1961	1.40	1.23	1.90	2.46	3.83	3.56	4.44	3.91	4.61	6.83	3.55	2.62	3.36
1962	3.54	2.41	3.62	4.48	4.40	4.76	4.21	3.93	6.60	6.25	6.22	2.36	4.40
1963	3.72	2.44	3.58	3.64	4.03	2.69	4.22	2.32	5.68	6.66	3.81	2.00	3.73
1964	3.16	2.62	3.07	4.94	6.31	5.93	5.12	7.38	8.77	8.54	4.73	4.46	5.42
1965	2.83	2.36	1.95	2.66	4.16	3.56	2.96	4.34	6.57	3.93	3.08	2.23	3.38
1966	3.26	2.45	3.23	4.20	3.39	4.75	4.91	7.27	5.98	5.48	2.34	1.66	4.08
1967	2.88	2.26	1.64	2.16	2.02	5.42	3.75	7.07	7.43	8.05	5.40	5.95	4.50
1968	1.57	4.01	2.77	2.40	2.80	6.15	5.62	4.57	4.24	5.01	4.90	2.81	3.90
1969	1.58	1.69	1.74	2.60	1.96	4.58	3.45	5.54	4.73	3.31	2.08	1.81	2.92
1970	1.94	0.68	2.12	3.31	3.32	4.48	3.90	4.20	5.03	6.37	4.52	3.51	3.61
1971	1.83	2.55	1.95	3.49	2.84	6.39	3.02	6.07	5.29	8.68	4.83	4.78	4.31
1972	2.50	1.92	2.69	2.22	1.84	3.04	3.82	3.23	7.27	2.38	2.04	2.67	2.97
1973	2.67	1.43	2.97	3.96	4.19	5.02	5.93	12.10	9.40	6.38	4.58	3.22	5.15
1974	3.20	4.32	4.15	4.30	4.28	3.86	4.06	4.56	6.98	5.95	6.17	3.82	4.64
1975	3.42	2.53	3.38	3.81	4.44	5.40	4.49	7.87	7.79	5.80	5.24	3.89	4.84
1976	2.11	1.02	2.82	4.30	3.78	3.20	2.29	3.30	5.37	3.71	3.71	2.84	3.20
1977	1.81	2.26	1.77	2.69	2.44	3.79	5.00	5.29	4.02	3.45	3.69	3.27	3.29
1978	2.79	2.85	3.50	3.84	3.69	5.48	3.88	5.15	6.38	4.17	3.15	2.94	3.98
1979	3.29	3.56	0.66	4.43	7.10	6.28	3.34	4.30	5.96	4.76	3.93	2.44	4.17
1980	2.83	2.44	2.56	2.61	4.85	3.67	5.10	4.10	6.15	5.36	3.92	3.61	3.93
1981	3.81	1.69	2.45	3.00	2.95	5.29	5.40	4.70	7.44	3.29	4.23	2.38	3.88
1982	2.58	2.86	2.49	1.65	2.79	5.10	3.81	2.37	5.95	4.67	3.11	2.06	3.29
Mean	2.51	2.24	2.59	3.32	3.72	4.38	4.20	5.24	6.06	5.12	3.94	2.85	

Table 5. Monthly estimates (unsmoothed) of new production in $gCm^{-2}day^{-1}$ for the Peruvian upwelling system using oceanic parameterization, VDM (see text) and Bakun's upwelling for 1953-1982.

Tabla 5. Estimaciones mensuales (no suavizadas) de producción nueva en $gCm^{-2}dia^{-1}$ para el sistema de afloramiento peruano usando parametrización oceánica, VDM (ver texto) y surgencias de Bakun para 1953-1982.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
1953	1.67	0.88	1.01	3.44	3.14	1.15	3.45	1.54	2.32	2.82	3.44	1.11	2.17
1954	0.96	1.98	0.26	3.13	3.68	3.60	4.91	9.11	9.26	2.75	3.01	1.07	3.64
1955	1.86	0.69	4.85	1.22	5.42	3.77	4.13	10.04	6.95	8.56	7.66	0.62	4.65
1956	1.09	1.25	3.14	4.89	4.59	2.89	2.81	3.21	4.78	3.64	2.06	2.08	3.04
1957	1.56	2.62	2.49	2.29	1.40	3.46	5.65	3.48	5.55	3.64	2.55	2.67	3.11
1958	1.05	1.06	1.30	1.87	1.66	2.07	1.97	4.64	3.75	3.40	1.58	1.81	2.18
1959	1.53	0.74	0.70	1.20	0.87	2.82	1.75	4.34	3.08	2.15	1.27	0.82	1.77
1960	0.91	0.77	0.97	1.49	2.32	2.22	2.75	3.00	4.83	3.24	1.69	1.46	2.14
1961	0.70	0.57	1.07	1.50	2.69	2.69	3.42	3.04	3.94	6.25	2.68	1.69	2.52
1962	2.83	1.61	2.67	3.90	3.81	3.92	3.35	3.16	6.88	6.53	6.74	1.54	3.91
1963	3.41	1.45	2.51	2.82	3.04	1.93	3.46	1.54	5.00	6.86	2.86	1.14	3.00
1964	2.15	1.63	2.07	4.13	6.11	5.71	4.15	7.57	9.88	10.98	4.94	3.90	5.27
1965	2.08	1.42	1.05	1.75	3.08	2.55	1.89	3.23	6.17	3.04	2.18	1.23	2.47
1966	2.18	1.40	2.38	3.04	2.26	3.79	3.81	7.34	5.33	5.04	1.56	0.88	3.25
1967	2.01	1.40	0.83	1.27	1.19	4.59	2.83	6.70	7.36	8.10	4.98	5.96	3.94
1968	1.06	3.70	1.85	1.50	1.99	5.46	4.61	3.76	3.23	4.03	4.21	1.73	3.09
1969	0.76	0.97	0.86	1.52	1.11	3.60	2.47	4.98	4.07	2.41	1.31	1.04	2.09
1970	1.09	0.39	1.24	2.26	2.36	4.07	3.54	3.65	4.89	7.43	4.32	3.57	3.23
1971	1.48	1.70	1.18	2.62	2.00	7.24	2.23	5.87	4.93	11.13	4.81	4.69	4.16
1972	1.84	1.25	2.09	1.26	0.98	2.10	2.50	2.14	6.85	1.53	1.17	1.75	2.12
1973	1.75	0.68	1.91	2.95	3.16	4.66	5.52	14.16	9.98	6.15	3.88	2.39	4.77
1974	2.51	4.49	3.89	3.44	3.19	2.94	3.05	3.81	6.69	5.18	5.47	2.69	3.95
1975	2.38	1.60	2.39	2.98	3.32	4.84	3.44	7.69	7.94	5.69	5.57	3.43	4.27
1976	1.42	0.52	1.99	3.36	2.71	2.29	1.35	2.44	4.39	2.67	2.65	1.86	2.30
1977	1.05	1.33	0.96	1.81	1.55	2.67	4.07	4.51	3.36	2.45	2.62	2.24	2.38
1978	1.89	1.91	2.51	2.79	2.58	4.59	3.11	4.33	5.87	3.18	2.13	1.88	3.06
1979	2.32	2.69	0.36	3.42	5.80	5.54	2.34	3.36	5.13	3.80	2.93	1.46	3.26
1980	1.83	1.45	1.54	1.57	3.79	2.72	3.85	3.16	5.74	4.49	2.93	2.66	2.98
1981	2.83	0.88	1.41	1.89	1.93	4.38	4.72	3.76	7.35	2.44	3.24	1.37	3.02
1982	1.58	1.82	1.45	0.88	1.74	4.22	2.72	1.70	5.24	3.69	1.80	1.14	2.33
Mean	1.73	1.50	1.76	2.41	2.78	3.62	3.33	4.71	5.69	4.78	3.28	2.06	

slopes of about 0.1, while the correlation coefficients are about 0.6). Those are the best estimates (minimum confidence interval for r) which may be achieved after dropping of extreme values. Thus, no reasonable relation exists between measurements and model estimates.

Our models CDM and VDM used for the oceanic and coastal parameter setting respectively match the observations relatively well (see Fig. 6). The correlation coefficients, while not high, are in the order of those coefficients which relate the nitrate-temperature relationships. Also, the computed slopes are less than, but not statistically different from one. The slopes are different from slope zero at the 80% confidence level. However, care should be taken for any statistical interpretation because the number of points is low. It seems that both models underestimate high productivities and overestimate low productivities. This effect is stronger for the CDM, which as in Model I, incorporates the idea of a constant upwelling depth along with a variable width of the upwelling region. It is concluded that both variable upwelling depths and variable width of the upwelling zone are important features which are needed for correct representation of the processes described here.

Second, phenomena occurring in April and June 1969 as well as in April 1977 are outside the range of phenomena described reasonably well by the models. Two events resulting in low production were overestimated and one event in high production was underestimated.

Third, the model incorporating a variable width of the upwelling zone and a fixed upwelling depth overestimates primary production by about 1 $gCm^{-2}\ d^{-1}$, whether production is high or low. The median values (Table 1) of both models differ by about 1.6 $gCm^{-2}\ d^{-1}$. This difference is too low to be statistically significant, but the regression suggests systematic overestimation by the model using a constant upwelling depth.

The estimate of monthly new primary production provided here as Tables 2 to 5 should be used with the foregoing in mind.

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References

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984, p. 14-45. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Brink, K.H., D. Halpern, A. Huyer and R.L. Smith. 1983. The physical environment of the Peruvian upwelling system. Prog. Oceanogr. 12:285-305.

Calienes, R. and O. Guillén. 1981. Masas de agua y producción primaria en el Perú. Bol. Inst. Mar Perú-Callao, Volumen Extraordinario.

Calienes, R., O. Guillén and N. Lostaunau. 1985. Variabilidad espacio-temporal de clorofila, producción primaria y nutrientes frente a la costa peruana. Bol. Inst. Mar Perú-Callao. 10(1). 44 p.

Chavez, F.P. and R.T. Barber. 1987. An estimate of near production in the equatorial Pacific. Deep-Sea Res. 34(7): 1229-1243.

Csanady, G.T. 1982. Circulation in the coastal ocean. Reidel Publ. Company, The Netherlands.

Dugdale, R.C. 1985. The effects of varying nutrient concentrations on biological production in upwelling regions. CaLCOFI Reports 26:93-96.

Feldman, G.C. 1986. Variability of the productive habitat in the eastern equatorial Pacific. Eos 67(9):106-108.

Guillén O., R. Calienes and R. Rondán. 1977. Medio ambiente y producción primaria frente al área Pimentel - Chimbote. Bol. Inst. Mar Perú-Callao 3(4):107-159.

Guillén, O. and R. Calienes. 1981. Upwelling off Chimbote. Coast. Est. Sci. 1:312-326.

Mendo, J., L. Pizarro and S. Castillo. 1987. Monthly turbulence and Ekman transport indexes 1953 to 1985, based on local wind records from Trujillo and Callao, Peru, p. 75-88. *In* D. Pauly and I. Tsukayama (eds.). The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama. 1987. On the implementation of management-oriented fishery research: the case of the Peruvian anchoveta, p. 1-13. *In* D. Pauly and I. Tsukayama (eds.). The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Romea R. D. and R.L. Smith. 1983. Further evidence for coastal trapped waves along the Peru coast. J. Phys. Oceanogr. 13(8):1341-1356.

Zuta S., T. Rivera and A. Bustamante. 1978. Hydrologic aspects of the main upwelling areas off Peru, p. 235-257. *In* R. Boje and M. Tomczak. Upwelling ecosystems. Springer-Verlag, Berlin.

Alongshore Wind Stress, 1953-1984: Correction, Reconciliation and Update Through 1986

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Abstract

Corrected values are presented for the monthly series of Peruvian alongshore stress presented in the previous volume of this series. The series is updated through 1986. The faulty "old" and corrected "new" series are compared and found to have very similar properties. It is concluded that studies based on the "old" series will not be significantly in error.

Resumen

Se presentan los valores corregidos del esfuerzo del viento a lo largo de la costa peruana, para las series mensuales dadas en el Volumen previo a este. La serie ha sido actualizada hasta 1986. Se compara la serie "antigua" defectuosa con la serie "nueva" corregida, encontrándose que ambas tienen propiedades muy similares. Se concluye que los estudios basados en la serie "antigua" no contienen error significativo.

Introduction

Bakun (1987) presented monthly indicator series for a number of environmental processes affecting the habitat off Peru. An error has been discovered in the computer program used to generate one of the reported series, that of the alongshore component of wind stress on the sea surface. Here we present corrected values for that particular series and also update the series through 1986 (Table 1).

Alongshore wind stress is one of the most important forcing functions for dynamic processes in the coastal environment. For periods of variation longer than a half-pendulum day (2.9 actual days at 10° latitude), the offshore transport which is directly driven by the wind (the offshore Ekman transport) is directly proportional to the equatorward alongshore wind stress, the constant of proportionality (~3.95×10^4 sec. for the latitude range of this particular series) being the reciprocal of the Coriolis parameter. To the extent that the flow divergence at the coast due to offshore surface transport is not balanced by convergence of alongshore flow, the water transported offshore is replaced by upwelling of deeper waters to the surface. Thus, variability in alongshore stress is reflected in variability in intensity of locally wind-driven coastal upwelling. Interyear variability in alongshore stress, often expressed either in terms of offshore Ekman transport or in terms of an "upwelling index", has been found to correlate with recruitment variability in a number of neritic fish populations (Bakun and Parrish 1980; Shepherd et al. 1984; Bakun 1985).

The computations and procedures employed in generating the updated corrected series (Table 1) are those outlined by Bakun (1987), except that the data for 1985-86 is from the COADS dataset rather than from the TDF-11 dataset.

Table 1. Alongshore component (positive equatorward) of wind stress on the sea surface. Units are dynes per square centimeter. Values in this table multiplied by the factor 3.95 yield offshore Ekman transport in cubic meter per second across each meter width.
Tabla 1. Componente a lo largo de la costa (positivo con dirección ecuatorial) del esfuerzo del viento sobre la superficie del mar. Las unidades se dan en dinas por centímetro cuadrado. Los valores de esta Tabla al multiplicarse por 3.95 dan como resultado el transporte Ekman en metro cúbico por segundo por cada metroo de línea costera.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	.33	.27	.37	.79	.70	.29	.63	.32	.42	.46	.55	.24
1954	.21	.37	.09	.41	.46	.40	.46	.73	.76	.21	.32	.19
1955	.32	.14	.50	.18	.54	.38	.41	.76	.57	.60	.54	.10
1956	.15	.23	.59	.70	.71	.44	.59	.52	.57	.47	.40	.39
1957	.27	.43	.62	.71	.47	.66	.83	.51	.64	.49	.40	.51
1958	.36	.38	.40	.51	.48	.41	.47	.67	.45	.42	.23	.34
1959	.30	.26	.34	.37	.26	.55	.33	.67	.45	.38	.27	.20
1960	.21	.24	.36	.42	.46	.38	.51	.48	.45	.43	.29	.32
1961	.19	.22	.34	.41	.59	.41	.57	.42	.45	.58	.33	.27
1962	.38	.29	.41	.44	.43	.49	.52	.44	.53	.44	.45	.23
1963	.29	.34	.53	.40	.50	.28	.46	.40	.63	.62	.45	.32
1964	.43	.38	.44	.57	.52	.50	.53	.61	.64	.51	.31	.36
1965	.26	.35	.34	.46	.79	.50	.53	.70	.76	.55	.45	.43
1966	.53	.53	.42	.61	.51	.53	.64	.65	.53	.48	.24	.22
1967	.34	.32	.25	.26	.33	.62	.48	.62	.62	.63	.39	.50
1968	.13	.35	.32	.30	.29	.55	.76	.63	.57	.53	.45	.50
1969	.26	.23	.39	.48	.39	.74	.49	.59	.52	.37	.26	.34
1970	.29	.11	.35	.50	.49	.45	.49	.45	.41	.47	.38	.26
1971	.16	.32	.29	.50	.35	.60	.39	.69	.53	.60	.38	.40
1972	.25	.27	.45	.47	.35	.58	1.00	.70	1.14	.44	.35	.65
1973	.52	.34	.60	.60	.57	.47	.58	.98	.85	.60	.49	.33
1974	.28	.35	.39	.57	.60	.56	.61	.54	.65	.60	.59	.42
1975	.34	.31	.59	.51	.63	.53	.56	.77	.63	.46	.32	.31
1976	.19	.15	.42	.62	.61	.48	.50	.57	.70	.60	.54	.48
1977	.28	.46	.34	.49	.40	.56	.80	.69	.42	.41	.50	.46
1978	.33	.43	.54	.58	.50	.59	.53	.59	.63	.48	.45	.41
1979	.42	.45	.48	.59	.91	.76	.55	.70	.67	.56	.48	.43
1980	.39	.40	.42	.42	.73	.46	.81	.57	.63	.56	.42	.41
1981	.43	.25	.41	.46	.45	.71	.64	.52	.72	.37	.49	.34
1982	.32	.42	.52	.46	.57	.76	.76	.54	.80	.76	.84	.57
1983	.61	.55	.39	.63	.65	.91	.70	.56	.62	.51	.33	.20
1984	.23	.56	.73	.27	.70	.79	.54	.78	.53	.51	.70	.47
1985	.27	.27	.16	.65	.48	.38	.50	.50	.65	.36	.52	.34
1986	.35	.23	.30	.41	.44	.56	.58	.68	.85	.75	.74	.44

Comparison and Reconciliation of the Two Series

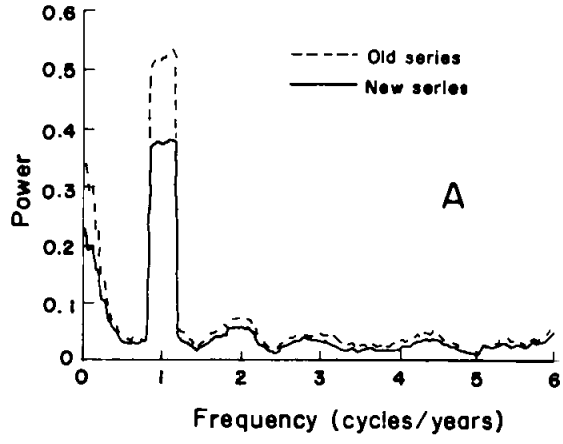
Resolution of the alongshore component of the wind stress, τ_a, is according to

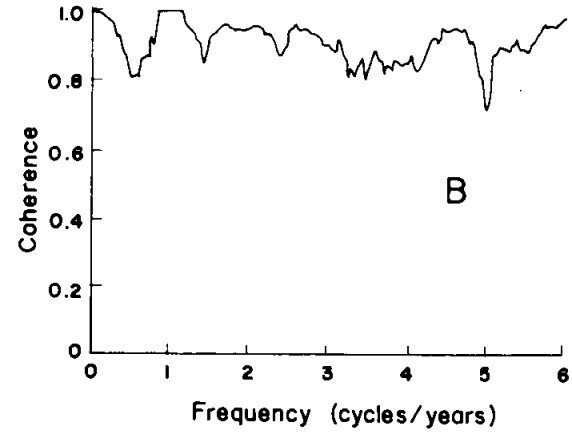
$$\tau_a = \alpha \tau_y - \beta \tau_x \qquad \text{... 1)}$$

where τ_y and τ_x are the respective northward and eastward stress components; $\alpha = \cos\phi$ and $\beta = \sin\phi$, where ϕ is the angle, counterclockwise from true north, of the large-scale coastline trend. For the Peruvian coast a compass direction of 332° ($\phi = 28°$) is chosen as the characteristic large scale coastline trend (i.e., $\alpha = 0.8829$, $\beta = 0.4695$).

In producing the series reported by Bakun (1987), the value 0.8829, appropriate to α, was also erroneously assigned to β. Since the wind stress off Peru is generally from the southwest (Bakun and Parrish 1982), τ_x would generally have a negative value. Thus the magnitude of the monthly estimate of τ_a would tend to have been amplified by the error. The computation of the onshore component of the wind stress and of the "wind cubed" index (Bakun 1987) are unaffected by this error.

Thus the power spectra of the "old" series from Bakun (1987) generally has higher values than the "new" corrected series (Fig. 1a). However, note that the shape of the spectra are quite similar, with high peaks at the annual frequency and the familiar "red noise" spectral shape at the low frequency end. Note also that the coherence (Fig. 1b) between the series is very high, being nearly 1.0 over the spectral peaks and falling somewhat lower only in spectral "gaps" where very little of the variance of the series is found. Also there is essentially no phase difference between the two series over the entire spectral range (Fig. 1c). Fig. 1 shows that the two series should be nearly equivalent for most applications, except in terms of magnitude.





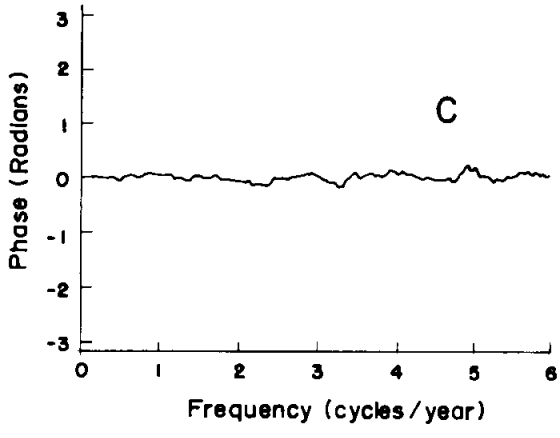


Fig. 1. "Frequency domain" comparison between the "old" monthly series of alongshore component of wind stress reported by Bakun (1987) and the "new" corrected series presented in Table 1: (a) Power spectra of the two series, (b) coherence, (c) phase.

Fig. 1. Comparación de la "frecuencia dominante" de la componente del esfuerzo del viento a lo largo de la costa, de la serie mensual "antigua" reportada por Bakun (1987) y la "nueva" serie corregida que se presenta en la Tabla 1: (a) Espectro de poder de las dos series, (b) coherencia, (c) fase.

For example, the seasonal pattern is very similar (Fig. 2), as are the major interannual features in the two series (Fig 3). Both series indicate seasonal maxima in alongshore stress during austral winter (peak in September) and minima in summer (lowest in January). Both series show increases in alongshore stress associated with El Niño episodes and some indication of a general linear upward trend from the mid-1950s to 1982-83.

For readers who may be more comfortable with correlation coefficients than with coherence spectra, regressing the "old" series on the "new" series yields a correlation of r = .975 and a regression line slope of b = 1.14. Transforming the two series to "anomalies", by subtracting the

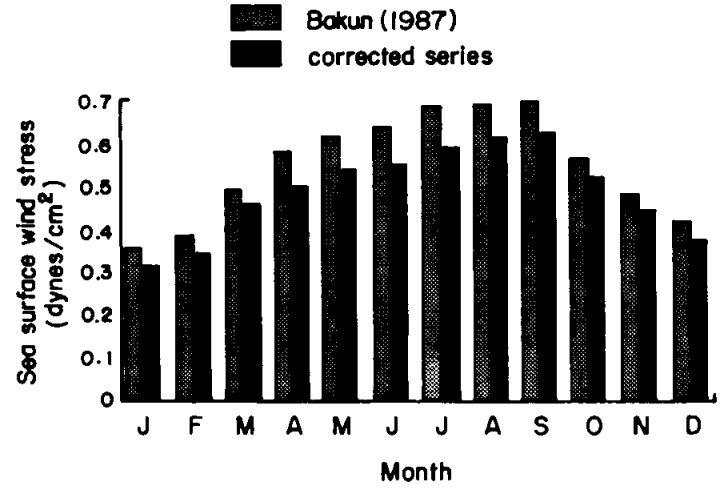


Fig. 2. Seasonal pattern (long term 1953-84 mean monthly values) of the "old" monthly series of alongshore component of wind stress reported by Bakun (1987) and of the "new" corrected series presented in Table 1.

Fig. 2. Patrón estacional (promedios mensuales a largo plazo 1953-84) de la serie "antigua" de la componente del esfuerzo del viento a lo largo de la costa reportada por Bakun (1987) y la "nueva" serie corregida presentada en la Tabla 1.

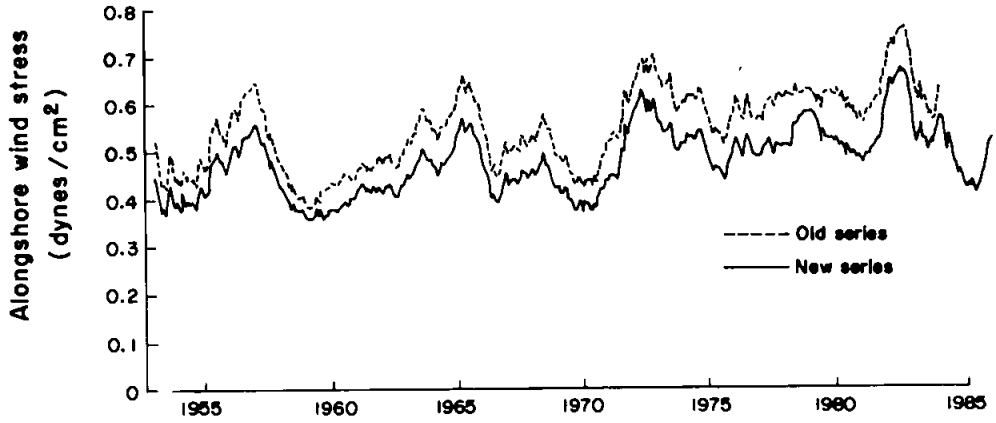


Fig. 3. Low-frequency nonseasonal variations: 12-month running means of monthly time series values of the "old" monthly series (dashed line) of alongshore component of wind stress reported by Bakun (1987) and the "new" corrected series (solid line) presented in Table 1.

Fig. 3. Variaciones de baja frecuencia no estacionales: promedios moviles de 12 meses de los valores de la "antigua" serie mensual (línea punteada) de la componente del esfuerzo del viento a lo largo de la costa, reportada por Bakun (1987) y la "nueva" serie corregida (línea solida) presentada en la Tabla 1.

appropriate 1953-84 long term monthly mean from each monthly value, yields r = .962 and b = 1.12. Removing the seasonal variation and the long term linear trend by "12th-differencing" each series (subtracting from each value the value for the same month one year earlier) yields r = .953 and b = 1.09. The regression line directly intersects the origin (intercept = 0.00) in all three cases.

Bohle-Carbonell (this volume), in examining the fractal dimensions of several series related to the anchoveta fisheries, uses the Bakun (1987) series. As discussed in Mendelssohn (this vol.), there is a close relationship between fractal dimension and fractal differencing in time series. Statistical estimates of the fractional differencing parameter *d* are determined from properties of the observed and theoretical spectrum. As the "old" and "new" series have similar spectra, there should be little change in these estimates, and the use of the "new" series should not affect Bohle-Carbonell's conclusions. (In fact, the estimate of fractional differencing for the "old" series is $d = .2212$, while for the "new" series it is $d = .2857$, see Mendelssohn (this vol.) for details).

Cury and Roy (1989) estimate optimal environmental windows for the Peruvian anchoveta, as well as for species from other eastern boundary current regions, using a turbulence index (wind speed cubed) as the environmental variable. Their study is unaffected by this correction, as they use the Trujillo series of Mendo et al. (1987). It is expected that other studies that may have used the earlier series will be similarly unaffected to any substantial degree.

References

Bakun, A. 1985. Comparative studies and the recruitment problem: searching for generalizations. CalCOFI Rep. 26: 30-40.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953-84, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bakun, A. and R.H. Parrish. 1980. Environmental inputs to fishery population models for eastern boundary current regions, p. 67-104. *In* G.D. Sharp (ed.) Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, Peru, 20 April-5 May 1980. IOC Workshop Rep. 28. UNESCO, Paris. 323 p.

Bakun, A. and R.H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. CalCOFI Rep. 23: 99-112.

Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46(4): 670-680.

Mendo, J., L. Pizarro and S. Castillo. 1987. Monthly turbulence and Ekman transport indexes, 1953 to 1985, based on local wind records from Trujillo and Callao, Peru. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Shepherd, J.G., J.G. Pope and R.D. Cousens. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-v. Réun. CIEM 185: 255-267.

Seasonal and Long-Term Variations of Zooplankton Volumes in the Peruvian Sea, 1964-1987

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CARRASCO, S. and O. LOZANO. 1989. Seasonal and long-term variations of zooplankton volumes in the Peruvian Sea, 1964-1987, p. 82-85. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Seasonally-averaged estimates of zooplankton volume (in ml/m^3) for the northern, central and southern part of the Peru coast (up to about 170 km offshore) are presented, based on 6,658 hauls with a Hansen net of 0.33 m^2 mouth area. Highest zooplankton biomasses occur in spring (October-December) in all three zones. Overall, zooplankton abundances are lowest off central Peru. There is a clear declining trend of zooplankton biomasses from the mid-1960s to the mid-1980s. The impact of various El Niño events on zooplankton abundance and composition is briefly discussed.

Resumen

Se presentan las variaciones estacionales, promedio de los volúmenes de zooplancton (en ml/m^3) para el área norte, centro y sur de la costa peruana (dentro de 170 km de la costa). Esta contribución se basa en 6,658 muestreos colectados con red Hensen de 0.33 m^2 de área de boca.

Las biomasas de zooplancton mas altas se presentan en la estación de Primavera (Octubre-Diciembre) en las tres zonas investigadas. En general estos volúmenes son menores en el área central del Perú. Entre la década del 60 a la década de 80 se observa una clara tendencia decreciente de los valores del zooplancton.

El impacto de diferentes eventos El Niño sobre abundancia y composición del zooplancton son discutidos.

Introduction

This contribution presents a time series, covering the years 1964 to 1987, of zooplankton volumes off Peru and attempts to identify some of the causes for the observed changes.

During the initial period covered by this time series (1974-1969), only two mild El-Niño events occurred (1965, 1969); thus, one may use this period as reference for the general pattern of zooplankton distribution off Peru. Subsequent El Niño events, notably that of 1982-1983, altered this pattern and reduced overall abundances (Carrasco and Santander 1988). The present contribution provides previously unpublished background material on these changes.

Materials and Methods

The basic material consists of 6,658 samples collected during research and survey cruises of the *Eureka* type, carried out by IMARPE from 1964 to 1987.

Samples were obtained from vertical hauls between a depth of 50 m and the sea surface, using a Hensen net of 0.33 m^2 mouth area and 300 μ mesh, and then fixed in 10% formaldehyde buffered with Borax.

Large coelenterates were removed by filtration (using mesh sizes of approximately 1 cm) prior to all zooplankton analyses. Then the fish eggs and larvae were set aside and the volume of the remaining zooplankters was determined using the displacement method (Kramer et al. 1972). All values are expressed in ml/m^3.

The sampling area (Fig. 1) covers the Peruvian coastline from 3°30'S to 18°30'S, and up to 170 km off the coast. Considering the characteristics of its fish populations and its oceanographic attributes, the Peruvian Coast has been divided into three zones:

Area "A" (03°30'-05°59'S), strongly influenced by equatorial surface waters (mainly in spring and summer). The coastal zone is also subjected to mixing processes during summer.

Area "B" (06°00'-13°59'S), wherein a widening of the shelf is observed, and with an upwelling area north of 09° S and another off Callao (12° S). The country's main pelagic fisheries are localized in this area.

Area "C" (14°00'-18°30'S), characterized by intense upwelling (Zuta and Guillén 1970) and high biological productivity (phytoplankton, zooplankton).

As data collection was not continuous, the zooplankton volumes obtained have been averaged by seasons: summer (January-March), autumn (April-June), winter (July-September) and spring (October-December).

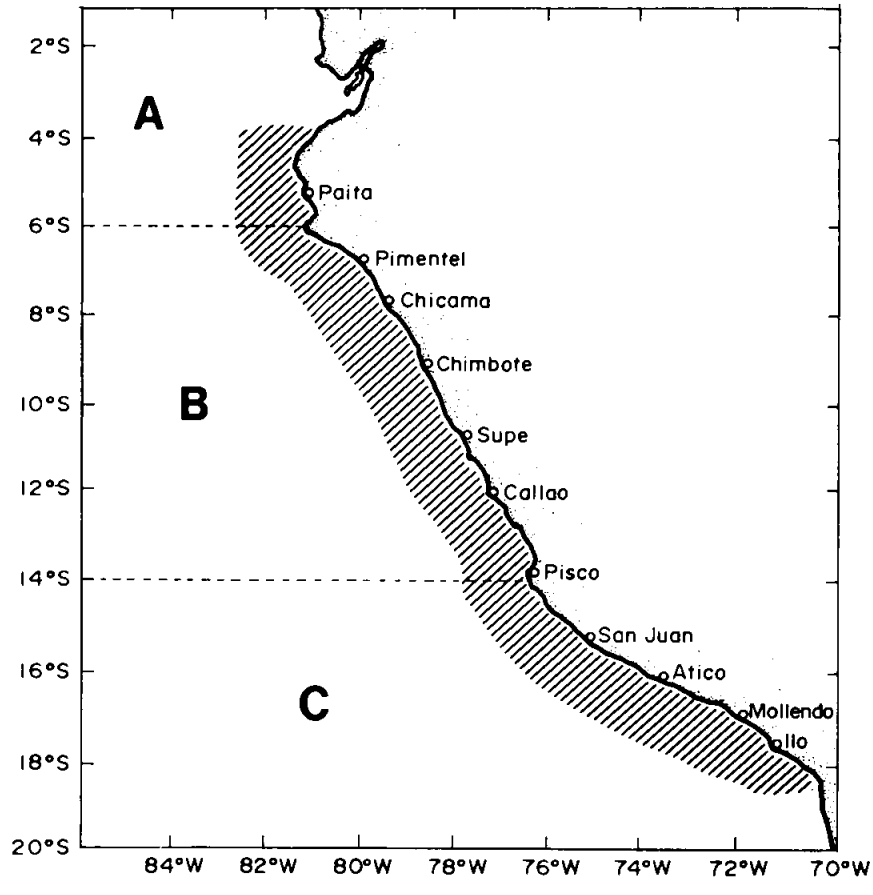

Fig. 1. Definition of sampling areas: A (3°30'-5°59'S), B (6°-13°59'S) and C (14°-18°30'S) off Peru. Seaward extension of sampling area is about 170 km on the average.

Fig. 1. Definición de las áreas de muestreo frente a la costa peruana: A (3°30'-5°59'S), B (6°-13°59'S) y C (14°-18°30'S). La extensión hacia fuera de la costa del área de muestreo es cerca de 170 km en promedio.

Results and Discussion

The zooplankton volumes, averaged by season, are presented in Table 1. In general, it can be seen that the volumes are higher during spring (see Fig. 2).

Comparatively, Area "A" (03°30'-05°59'S) presents the highest zooplankton volumes, a fact attributable to the influence in this area of equatorial surface water, which carries larger zooplanktonic organisms than the cold water of the coastal current.

The other matter to highlight with regard to these series is the notable reduction of the zooplankton volumes along the Peruvian coast, very evident since the El Niño event of 1972-1973. Volumes for the period 1972-1987 represent, on the average, around 30-40% of those observed for previous years (Fig. 3).

Carrasco and Santander (1988) pointed out that during the 1983 El Niño and for the area of 06o-12oS, copepod abundance decreased to 1/6 with respect to 1977 and 1981, and that generally, zooplankton volumes decreased drastically.

Table 1. Seasonal means of zooplankton volume off Peru, 1964-1987.
Tabla 1. Promedios estacionales de los volúmenes del zooplancton frente a la costa peruana, 1964-1987.

	Area A (3°30'-5°59'S)				Area B (6°-13°59'S)				Area C (14°-18°30'S)			
Year	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec
1964	1.14	0.70	1.44	2.43	0.90	0.75	0.66	1.00	–	0.25	2.36	3.50
1965	0.89	1.15	0.88	0.97	0.49	1.93	0.71	0.69	–	0.62	0.56	1.81
1966[a]	2.44	1.15	1.90	3.49	1.28	1.78	1.10	1.40	0.62	0.62	0.90	2.86
1967[a]	1.75	1.46	1.21	5.12	0.41	0.72	0.53	2.73	0.40	0.32	1.62	5.37
1968	–	–	0.59	–	0.46	–	0.83	–	0.93	–	–	–
1969	1.24	–	1.33	–	1.55	–	0.56	–	–	0.34	–	0.75
1970	–	0.49	0.60	1.97	–	0.67	0.50	1.01	–	–	0.60	0.64
1971	–	0.90	1.60	1.90	–	0.40	0.39	1.40	–	0.30	0.32	1.70
1972	1.41	–	1.09	0.80	1.36	–	0.54	0.84	1.43	–	1.21	–
1973	1.24	1.94	–	–	1.16	0.75	0.77	–	0.86	0.48	–	–
1974	0.13	–	–	–	0.14	0.91	0.18	–	–	0.74	0.07	–
1975	–	–	0.40	0.70	0.23	–	0.21	0.20	0.26	–	0.15	–
1976	0.35	0.22	–	0.29	0.19	0.11	–	0.15	0.30	–	–	–
1977	–	–	–	–	–	0.27	0.18	0.09	–	0.38	–	–
1978	–	–	–	0.29	0.32	–	–	0.22	0.38	–	–	–
1979	0.78	–	–	–	0.67	–	–	–	–	–	–	–
1980	–	–	0.10	–	–	–	0.28	–	–	–	0.40	–
1981	0.31	–	–	–	0.22	–	0.10	0.51	0.16	–	–	0.31
1982	–	–	0.09	–	–	–	0.90	0.26	–	–	0.65	0.34
1983	0.11	0.09	–	–	0.16	0.40	0.32	0.31	0.58	0.25	0.41	–
1984	–	0.15	0.74	0.24	–	0.23	0.27	0.15	–	0.16	–	–
1985	0.26	0.14	0.08	–	0.09	0.10	0.17	–	–	0.12	0.03	–
1986	–	0.20	–	–	–	0.14	–	0.37	–	–	–	0.24
1987	0.53	–	–	–	0.30	–	–	–	–	–	–	–
Mean	0.90	0.72	0.86	1.65	0.58	0.65	0.48	0.71	0.59	0.38	0.71	1.75
n	14	12	14	11	17	14	19	16	10	12	13	10
St. dev.	0.66	0.58	0.57	1.48	0.47	0.55	0.28	0.67	0.37	0.19	0.64	1.61

[a]Years used to illustrate seasonality of relative abundance (see Fig. 2).

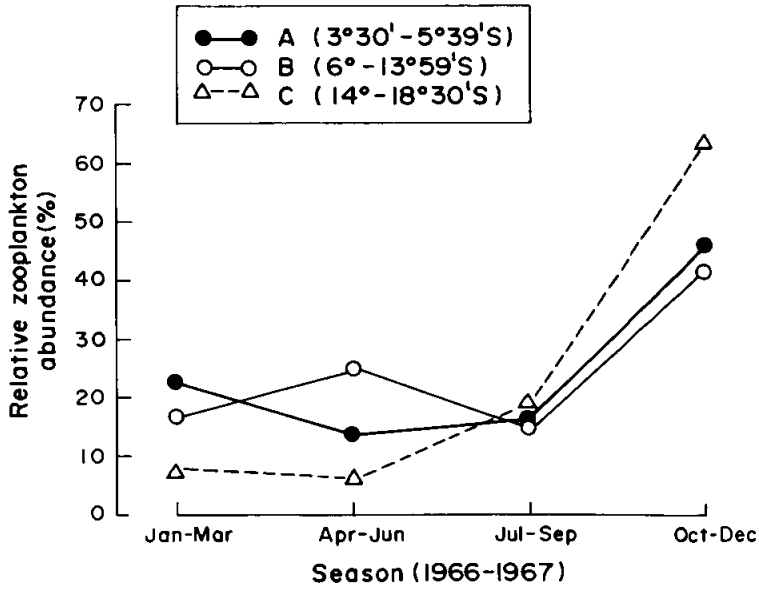

Fig. 2. Seasonal changes of zooplankton relative abundance for the years 1966 and 1967 (i.e., the only two years in Table 1 with samples from all seasons).
Fig. 2. Variaciones estacionales de la abundancia relativa del zooplancton para los años 1966 y 1967 (Enla Tabla 1, solo estos 2 años presentan muestreos en todas las estaciones).

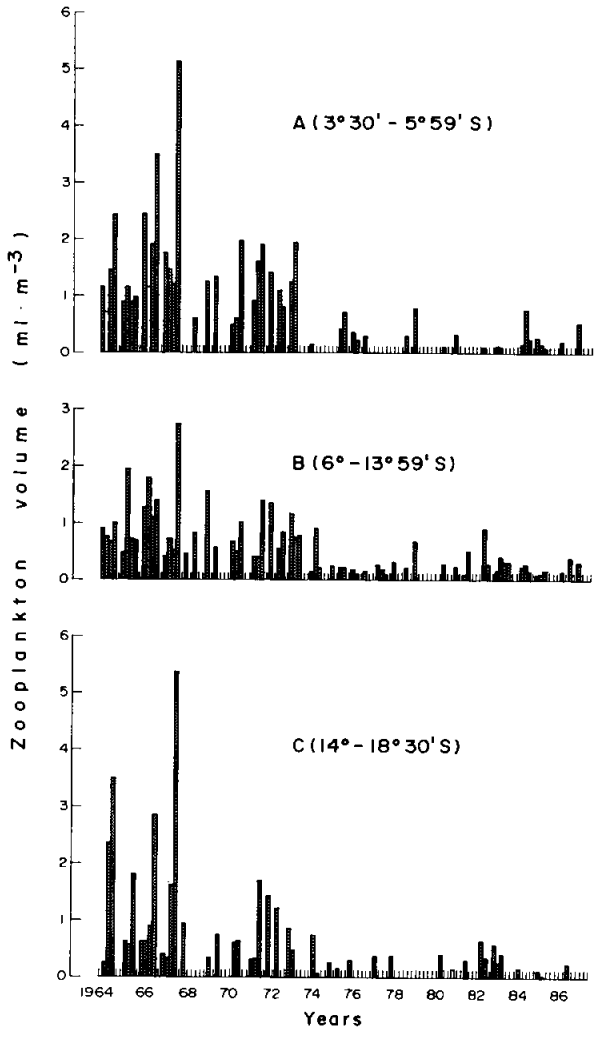

Fig. 3. Trend of zooplankton abundance off Peru, 1964 to 1987. Note strong decline in all three zones and overall lower biomasses in area B.
Fig. 3. Tendencia de la abundancia del zooplancton en el Perú, 1964 a 1987. Notar la fuerte disminución de la biomasa en las tres zonas y los valores más bajos en área B.

The observed decline of zooplankton volumes, assuming that it reflects a real decrease of zooplankton biomass, is probably related to the observed changes in the southeastern Pacific ecosystem - coincidental with the 1972-1973 El Niño - which led to a drastic decrease of the anchoveta stock and to the associated increase of other species, such as sardine, horse mackerel and mackerel (Zuta et al. 1983).

These changes in the ecosystem would have generated a greater zooplankton consumption by these predator species. Muck and Sanchez (1987) showed that the contribution of anchoveta to the diet of horse mackerel *Trachurus murphyi* and mackerel (*Scomber japonicus*) decreased during the 1976-1982 period. Also, the results of stomach content analyses presented in Muck (this vol.) suggest a switch from anchoveta to a zooplanton diet for both predators after 1980. Hence, it is reasonable to assume that there has been a greater zooplankton contribution to the diet of horse mackerel and mackerel during this period, leading to a decline of zooplankton biomasses.

References

Carrasco, S. and H. Santander. 1988. El Niño event and its influence on the zooplankton in the Peruvian coast. J. Geophys. Res. 92:14405-14410.

Kramer, D., M.J. Kalin, E.G. Stevens, J.R. Thrailkill and J. R. Zweifel. 1972. Collecting and processing data on fish eggs and larvae in the California Current Region. NOAA Tech. Rep. NMFS Circ-370:1-38.

Muck, P. and G. Sánchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15.

Zuta, S. and O. Guillén. 1970. Oceanografía de las aguas costeras del Perú 2(5):154-324.

Zuta, S., I. Tsukayama and R. Villanueva 1983. El ambiente marino y las fluctuaciones de las principales poblaciones pelágicas de la costa peruana, p. 179-254. *In* G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species of Neritic Fish Resources, 18-29 April 1983, San José, Costa Rica. FAO Fish. Rep. No. 291. Vol. 2. Rome.

Comparative Studies on Feeding in Larval Anchoveta *(Engraulis ringens)* and Sardine *(Sardinops sagax)**

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Abstract

The diet and morphological parameters (mouth width, gut length, eye pigmentation and mouth function) of larval anchoveta (*Engraulis ringens*) and sardine (*Sardinops sagax*) of the Peruvian upwelling system were studied, based on samples obtained in February/March 1982. The relationships body length/mouth width and body length/gut length show significant differences: an anchoveta has a larger mouth than a sardine of the same size but a shorter gut; the two species also differ in a number of morphological characteristics. Species and size composition of prey in the guts of first feeding larvae (anchoveta: 3-3.5 mm; sardine: 4-4.5 mm) are significantly different: the former feeds almost exclusively on a pure phytoplankton diet (phytoflagellates, dinoflagellates; 30 µm width) whilst the latter feeds almost exclusively on zooplankton (copepod eggs and nauplii; 70 µm width).

These findings for first feeding larvae suggest a high larval mortality for anchoveta during El Niño periods when primary production is reduced drastically; they also agree with the hypothesis that differences in larval mortality during El Niño events are one of the decisive factors for the transition from anchoveta to sardine in the Peruvian upwelling system.

For older anchoveta and sardine larvae (>5.5 mm), there is a wide diet overlap for all stages of calanoid copepods, and phytoplankton becomes less important as an energy source.

Resumen

Se estudia la dieta y los parámetros morfológicos (ancho de boca, longitud de intestino, pigmentacion de ojo, y función de la boca) de las larvas de anchoveta *(Engraulis ringens)* y sardina *(Sardinops sagax)* del sistema de afloramiento peruano, basados en muestras obtenidas en febrero/marzo de 1982. Las relaciones del cuerpo longitud/ancho de boca, longitud del cuerpo/longitud de intestino, muestran diferencias significativas: una anchoveta tiene la boca mas larga que una sardina de la misma talla, pero un intestino corto; las dos especies también difieren en un número de características morfológicas. La composición de tamaño de presas y de especies en los intestinos de la primera alimentación larval (anchoveta: 3-3.5 mm; sardina: 4-4.5 mm) son significativamente diferentes: las anchovetas se alimentan casi exclusivamente de una dieta pura de fitoplancton (fitoflagelados, dinoflagelados: 30 µm de ancho) mientras que las sardinas se alimentan casi exclusivamente de zooplancton (huevos de copépodos y nauplios: 70 µm de ancho).

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Estos resultados de la primera alimentación de larvas sugieren una alta mortalidad larval para la anchoveta durante períodos de El Niño cuando la producción primaria se reduce drásticamente. Ellos también concuerdan con la hipótesis de que las diferencias en la mortalidad larval durante los eventos de El Niño sea uno de los factores decisivos en la transición de anchoveta a sardina en el sistema de afloramiento peruano. Para las anchovetas viejas y larvas de sardina (> 5.5 mm) hay un amplio traslape de dietas para todos los estadíos de copépodos calanoides y el fitoplancton es menos importante como fuente de energía.

Introduction

Survival rate during the larval stage of fishes has been suggested for over 70 years (Hjort 1914) to be a decisive factor controlling recruitment and thus the population density of stocks.

Studies on clupeoid fish larvae show that early stages can only survive approximately 1.5-3.5 days without food (Lasker et al. 1970; Houde 1974, 1978; Rojas de Mendiola and Gómez 1980). This period, however, becomes much shortened when water temperatures become abnormally high, as was the case in the upper 70 m of the Peruvian upwelling system during the "El Niño" event of 1982-1983, when temperatures of 26-30°C were reached (Villavicencio and Muck 1983). Therefore, the chances of survival of the individual larval stages appear to be largely dependent on strategy and efficiency of food uptake (May 1974). This applies in particular to the first larval stages following the absorption of the yolk sac, whose feeding success is often extremely poor (Braum 1967; Rosenthal and Hempel 1970; Blaxter and Staines 1971; Hunter 1972).

The aim of this study is to identify the food niches and feeding strategies of anchoveta (*Engraulis ringens*) and sardine larvae (*Sardinops sagax*) by gut content analysis as well as through the comparison of morphological parameters. This study follows up on contributions on the feeding behavior of *E. ringens* larvae by Rojas de Mendiola (1974, 1980) and Ware et al. (1981).

As sardine and anchoveta have widely overlapping distribution areas off Peru, the results will be discussed with respect to food competition and to environmental changes such as caused by El Niño events.

Materials and Methods

Larvae were sampled during day and night at 45 stations along the Peruvian coast (18°04'S to 3°23'S) during February and March 1982 by vertical hauls (50-0 m) of a Hensen net (0.33 m^2 mouth area; 300 µm mesh size). The larvae were preserved in ethanol (70%) and later analyzed at the Instituto del Mar del Peru (IMARPE) with respect to (i) standard length, gut length, mouth width, (ii) eye pigmentation, (iii) mouth function and (iv) diet composition.

The mouth of the preserved larvae was assumed to be functional either when it was found open, or when it could straightforwardly be teased open. Fully pigmented eyes were considered functional.

Diet organisms were removed from the gut, identified, counted and grouped into 37 size classes of 10 µm intervals by measuring the short axis of the food particles, the important parameter limiting food ingestion.

Diet composition was described by reporting the percent frequency of occurrence (F(%)) of the diet items by taxa, stage and/or size class and the percentage of the total number of diet items (N(%)). As an index of the relative importance of each diet item the product of F% and N% (Laroche 1982; Govoni et al. 1983) has been used.

The calorific content of various items was estimated from the equation

$$\log_{10}\text{cal.} = -9.416 + 3.026\log_{10}\text{width} \qquad ...1)$$

(width in µm; r = 0.95) derived from data in Theilacker and Dorsey (1980) for phyto- and zooplankton species, including different size classes of nauplii and copepodites.

Equation (1) was used to estimate (i) the importance of phytoplankton in the gut compared to zooplankton and (ii) to estimate optimum prey widths, defined as the size class in a group of food organisms representing the fraction with the highest calorific value in the gut of each larva.

Results and Discussion

Size of First Feeding Larvae

As shown in Table 1, the minimum size for anchoveta with food in the gut was 3.02 mm and for sardine 4.07 mm. These findings agree with the available data on mouth and eye function in Fig. 1 which show curves obtained by grouping 1,077 anchoveta larvae ranging from 2 to 5 mm and 106 sardine larvae ranging from 3.5 to 5 mm into six size classes of 0.5 mm width. For both species, there is a close linkage between eye and mouth functions: larvae with completely pigmented eyes also had an open mouth. This development starts for anchoveta at around 2.7 mm, and is completed at a length of ca. 4 mm. In sardine, this development starts below 4 mm and is completed with 5 mm.

Table 1. Characteristics of samples used for the present study.
Tabla 1. Características de las muestras utilizadas para el presente estudio.

Characteristics	Anchoveta	Sardine
No. of samples[a]	33	22
No. of larvae	297	355
Size range (mm)	2.97-15.1	3.96-17.1
Mean size (mm)	4.97	7.99
S.D. of mean (mm)	1.94	2.89
No. of larvae with food in their guts	82	75
Size range (mm)	3.02-8.60	4.07-16.00
Mean size (mm)	4.08	6.07
S.D. of mean (mm)	1.23	2.00

[a]Number of samples with both anchoveta and sardines = 10.

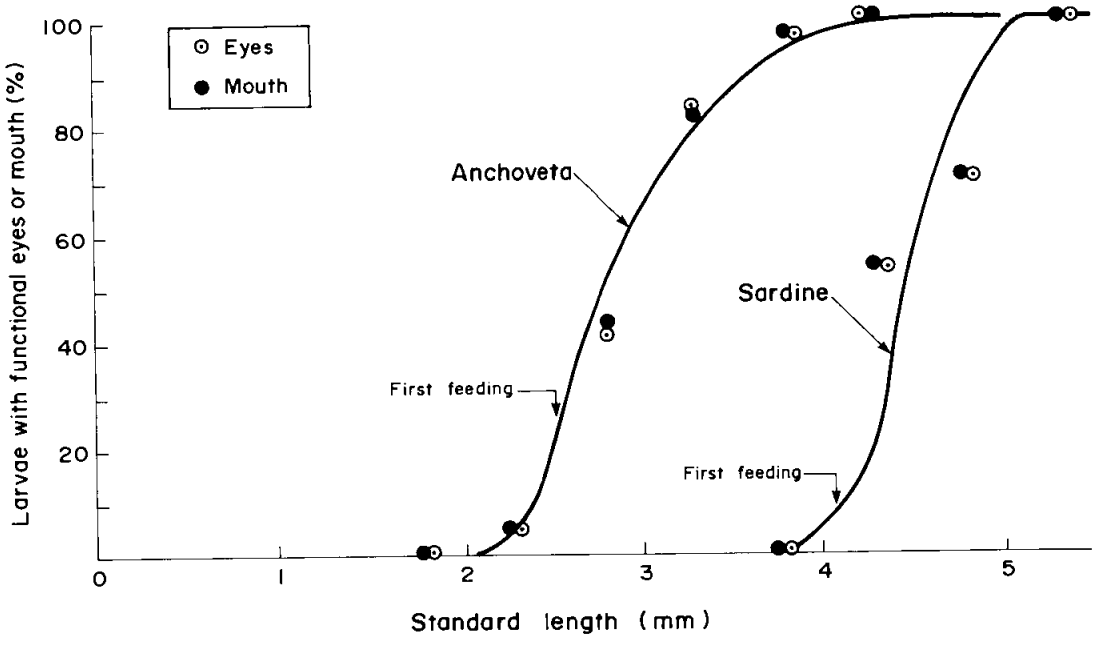

Fig. 1. Relationship between mouth and eye functionality and body length in 8 anchoveta and sardine larvae. Note close match between mouth and eye functionality.

Fig. 1. Relación entre la boca y la funcionalidad del ojo y longitud del cuerpo en 8 larvas de anchoveta y sardina. Notar la similitud de los valores entre la boca y la funcionalidad del ojo.

Diel Feeding Activity

The diel feeding cycle of anchoveta and sardine larvae is shown on Fig. 2. Grouping the available data (points) in four-hour intervals and computing means led to the solid line for anchoveta and the dotted one for sardine. The lines suggest nocturnal feeding by anchoveta (as in adults, see Pauly et al., this vol.) and a more diurnal feeding behavior in sardine. However, the available data points are widely scattered and more data are needed to decide whether or not species-specific differences do occur.

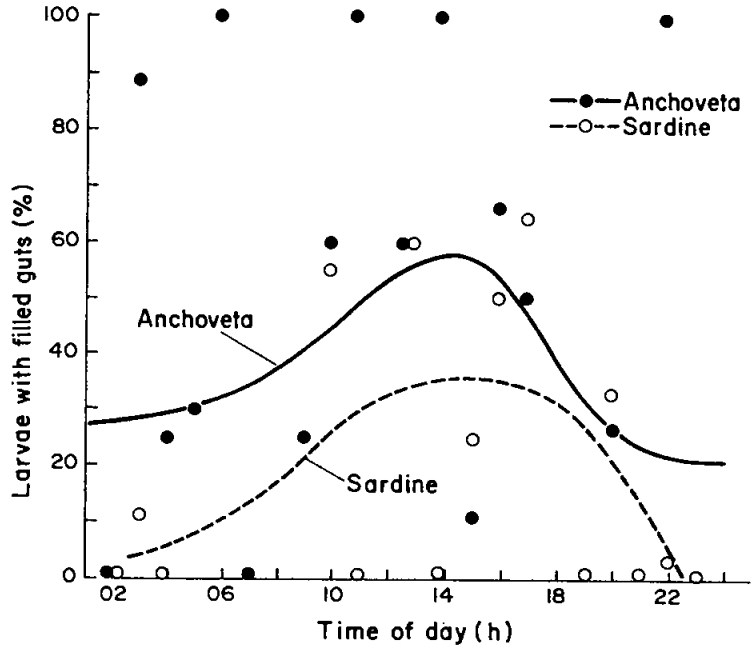

Fig. 2. Data on the diel feeding activity of anchoveta and sardine larvae. Dots: observations; lines: fitted by eye to 4-hourly means. Note suggestion of nocturnal feeding in anchoveta and of diurnal feeding in sardine larvae.

Fig. 2. Datos sobre la actividad de la dieta alimentaria de las larvas de anchoveta y sardina. Líneas punteadas: observaciones; líneas: ajustadas al ojo para promedios de cada 4 horas. Notar la sugestión de una alimentación nocturna y de una alimentación diurna en las larvas de anchoveta y sardina, respectivamente.

Diet Composition

Table 2 lists the diet organisms and their frequencies as estimated by gut analysis. The highest values for the relative importance of a diet item (N(%) x F(%)) correspond, in the case of anchoveta, to copepod nauplii (45-135 µm), to phytoflagellates (5-15 µm) and to copepod eggs (45-75 µm). In the case of sardine, the highest values of N(%) x F(%) pertain to nauplii (45-135 µm), copepod eggs (47-75 µm) and adult copepods (115-345 µm).

Related to the total number of diet groups analyzed, the fraction of copepods (including their eggs) is higher in sardine (92.2%) than in anchoveta larvae (46.2%). In contrast, we found algae in 53% of the cases in anchoveta and in only 6% in sardine.

Feeding Strategies

The clear differences presented above in the diet composition of both species are caused mainly by the different feeding behavior of the first-feeding larvae. Of the anchoveta larvae between 3.0 and 3.5 mm, 77% feed exclusively on phytoplankton, mainly flagellates with a

Table 2. Diet composition of anchoveta and sardine larvae. See Table 1 for details on samples; F(%) and N(%) refer to relative frequency and relative occurrence of an item, respectively. (See text).
Tabla 2. Composición de la dieta de las larvas de anchoveta y sardina. Ver tabla 1 para detalles de las muestras; F(%) y N (%) indican la frecuencia y la ocurrencia relativa de un item,respectivamente (ver texto).

Food items	Width range (µm)	*Engraulis ringens* F (%)	*Engraulis ringens* N (%)	*Sardinops sagax* F (%)	*Sardinops sagax* N (%)
Diatoms					
Actinocyclus sp.	45-55	1.22	0.24	1.33	0.35
Rhizosolenia delicatula	10-20	1.22	0.48	0.00	0.00
Roperia tessellata	40-70	1.22	0.24	0.00	0.00
Thalassiosira subtilis	15-25	4.88	1.43	0.00	0.00
Dinoflagellate					
Exuviaella marina	15-35	7.32	4.76	4.00	0.35
Gymnodinium splendens	40-45	3.66	0.95	0.00	0.00
Gymnodinium sp.	15-35	4.88	2.38	1.33	0.35
Prorocentrum gracile	15-20	2.44	0.48	2.67	1.39
Prorocentrum micans	25-30	3.66	0.71	2.67	1.30
Pyrocystis lunula	50-60	3.66	0.71	0.00	0.00
cyst of dinoflagellate	-	1.22	0.24	0.00	0.00
Small flagellates					
Phytoflagellate (round)	5-15	9.76	10.48	0.00	0.00
Phytoflagellates (stretched)	-	2.44	0.71	0.00	0.00
Spores	-	1.22	0.95	0.00	0.00
Flagellate cysts	-	0.95	0.00	0.00	0.00
Monades	5-15	4.88	1.90	2.67	3.47
Coccolithophorids					
Emiliania huxleyi	5-15	1.22	0.24	0.00	0.00
Ciliates					
Codonellopsis contracta	-	2.44	0.95	0.00	0.00
Epiplocycloides reticulata	45-65	3.66	0.72	1.33	0.35
Helicostomella subulata	-	1.22	0.24	0.00	0.00
Tintinopsis levigata	-	1.22	0.48	0.00	0.00
Copepods (mainly calanoids)					
Eggs	45-75	15.8	5.24	13.3	4.87
Nauplii	45-135	58.6	18.8	105.0	52.0
Nauplii fragments	-	3.66	1.43	1.33	0.69
Copepodits	105-215	0.00	0.00	2.66	0.70
Copepodit fragments	-	0.00	0.00	1.33	0.69
Adults (entire)	115-345	0.00	0.00	7.99	2.78
Ostracods		1.22	0.24	0.00	0.00
Crustacean eggs		0.00	0.00	1.33	0.35
Unidentifiable remains		17.1	5.71	2.67	0.69

mean width of 29.6 µm ± 25.3, whilst the first feeding larvae of sardine (4.0-4.5 mm) had all ingested nauplii, with a mean width of 72.1 µm ± 16.6 (Table 3).

With increasing length, anchoveta larvae gradually shift towards a zooplankton diet. The shift from phyto- to zooplankton starts at a standard length of ca. 4 mm. In contrast to this, sardine larvae of all size classes are strongly specialized and have an almost pure zooplankton diet; the average for the "mixed" and phytoplankton fraction is less than 10%.

In only 10 of the 45 hauls did the two species co-occur, with a total of 161 anchoveta and 175 sardine larvae. Co-occurrence occurred from 5°15' to 15°00'. Analysis of these data is difficult due to the low number of larvae with food in their guts (25% in anchoveta, 29% in sardine). Nevertheless, a comparison of their diet composition showed the same tendency (Table 3): almost exclusive feeding on zooplankton by sardine larvae whilst about 50% of the anchoveta diet is mixed food and pure phytoplankton:

anchoveta (4-8 mm)	:	pure zooplankton	=	47.6
		mixed diet	=	42.9
		pure phytoplankton	=	9.5
sardine (4-8 mm)	:	pure zooplankton	=	93.0
		mixed diet	=	4.6
		pure phytoplankton	=	2.3

The mean total calorific gut content for different larval size classes, for samples collected 5° and 20°'S, mainly around 13° (Table 4), was calculated using equation (1) to identify possible differences in feeding efficiency. The results suggest no differences for larvae >5 mm but

Table 3. Diet characteristics of different size classes of anchoveta (*Engraulis ringens*) and sardine (*Sardinops sagax*)[a]
Tabla 3. Características de la dieta de las diferentes clases de tamaños de anchoveta (Engraulis ringens) *y sardina* (Sardinops sagax).

	Anchoveta						Sardine					
Size class (mm)	n	Pure phytoplankton	Pure zooplankton	Mixed diet	Mean width (µm)	Mean cal. contents of phytoplankton	n	Pure phytoplankton	Pure zooplankton	Mixed diet	Mean width (µm)	Mean cal. contents of phytoplankton
3.0-3.4	22	77.3	13.6	9.1	29.6	79.5	-	no feeding				
3.5-3.9	29	29.2	37.5	33.3	53.2	29.2	-					
4.0-4.4	11	20.0	40.0	40.0	67.8	13.2	7	16.6	83.4	0.0	72.1	16.6
4.5-4.9	12	0.0	63.6	36.4	85.1	0.3	11	18.2	81.8	0.0	75.6	10.0
4.0-5.4	0	-	-	-	-	-	23	0.0	87.5	12.5	84.1	0.0
≥5.5	8	0.0	66.7	33.3	62.6	0.5	31	3.2	90.3	6.5	83.9	0.0

[a]All values (except n and widths) expressed as percentages.

Table 4. Mean energy contents (in cal.) of the gut contents of larval anchoveta and sardine.
Tabla 4. Promedio del contenido de energía (en calorías) del contenido intestinal de larvas de anchoveta y sardina.

Standard length (mm)	*Engraulis ringens* n	cal.	s.d.	*Sardinops sagax* n.	cal.	s.d.
3.0-3.9	21	0.00063	0.0011	-	no feeding	-
4.0-4.9	21	0.00283	0.0061	17	0.00057	0.00085
5.0-6.9	8	0.00170	0.0019	40	0.00150	0.00270
7.0-8.9	0	-	-	10	0.00310	0.00280

differences of a factor of 5 for larvae in the 4-5 mm size class. These differences are most probably caused by the low feeding success of first-feeding sardine larvae.

To quantify the importance of phytoplankton as food resource from a bio-energetic viewpoint, equation (1) has been used to estimate the total calorific content of the phytoplankton fraction in the gut of each larva as a percentage of total calorific content (=100%). These values were averaged for the individuals of each size class (Table 4) and plotted (Fig. 3).

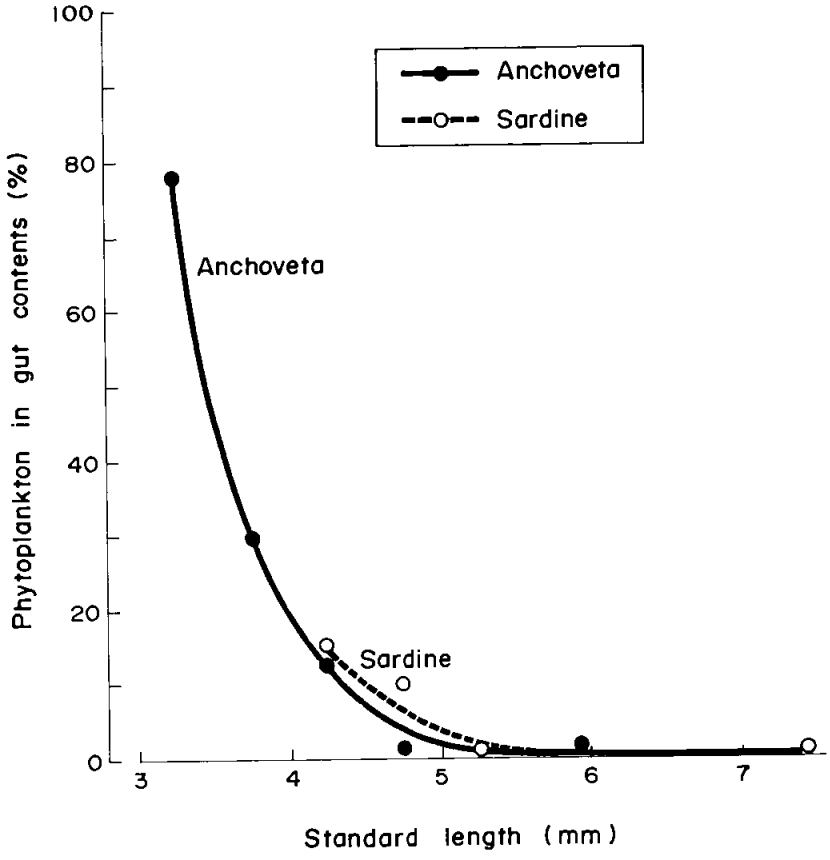

Fig. 3. Contribution of phytoplankton (in % of the gut contents, in cal.) in the diet of larval anchoveta and sardine.

Fig. 3. Contribución de fitoplacton (en % del contenido intestinal, en calorías) en la dieta de las larvas de anchoveta y sardina.

First feeding larvae of anchoveta mainly use phytoplankton (80%) as an energy resource. Phytoplankton, however, becomes negligible when the anchoveta larvae are larger than ca. 4.5 mm. For sardine, phytoplankton is of little importance (16%) for the youngest larvae and tends towards zero in larvae larger than 5 mm.

Regression and Correlation Analyses

The results of the regression and correlation analyses of morphological and functional characteristics are given in Table 5.

The relationships standard length/gut length and standard length/mouth width are significantly different between species: an anchoveta of 10 mm has a shorter gut (5.99 *vs.* 7.03 mm) but a wider mouth (0.65 *vs.* 0.60 mm) than a sardine larva of the same standard length.

For the relationships length/minimum, prey width, length/maximum prey width and length/optimum prey width, positive correlations were found for both species. These were associated, however, with low values of the correlation coefficient (r). Therefore, species-specific differences cannot be derived using the available data set. An exception seems to be the

Table 5. Results of regression and correlation analyses on larval anchoveta and sardine.[a]
Tabla 5. Resultados de los análisis de regresión y correlación sobre las larvas de anchoveta y sardina.

Relationship	Species	n	Size range (mm)	Correlation coefficient	Equation[b]	Confidence limits (95%) Intercept		Slope	
Length/length of the gut	anchoveta	297	2.97-15.1	0.95	Y = -0.0879 + 0.6075X	-0.065	-0.111	0.63	0.59
	sardine	358	3.96-17.1	0.99	Y = -0.3316 + 0.7361X	-0.311	-0.331	0.74	0.73
Length/mouth width	anchoveta	297	2.97-15.1	0.96	Y = 0.0628 + 0.0585X	0.065	0.061	0.061	0.056
	sardine	358	3.96-17.1	0.96	Y = -0.0249 + 0.0631X	-0.023	-0.027	0.065	0.061
Length/minimum prey width	anchoveta	82	3.02-8.64	0.23	Y = -4.819 + 35.75 lnX	28.88	-38.52	69.45	2.05
	sardine	76	4.07-16.0	0.38	Y = 137.38 $e^{-0.1154X}$	4.99	4.86	-0.05	-0.18
Length/maximum prey width	anchoveta	82	3.02-8.64	0.44	Y = -59.58 + 97.89 lnX	-14.86	-104.3	142.6	53.2
	sardine	76	4.07-16.0	0.33	Y = 52.09 + 7.135X	56.88	47.29	11.92	2.34
Length/optimum prey width	anchoveta	82	3.02-8.64	0.41	Y = -53.75 + 88.15 lnX	-9.98	-97.48	131.9	44.4
	sardine	76	4.07-16.0	0.08	-	-	-	-	-

[a]Only the last relationship (sardine larval length *vs.* optimum prey width) was not significant (at 95% level).
[b]Four types of equations were tested in each case (linear, exponential, logarithmic and power function); those reported here gave the best fit.

length/minimum prey width relationship. For anchoveta, the minimum size of the ingested food particles increases with increasing larval length, while for sardines, there is a weak negative relationship.

Fig. 4 presents the results of Table 5 to allow comparison of the specific difference on the interrelationships between larval length, mouth width and particle size.

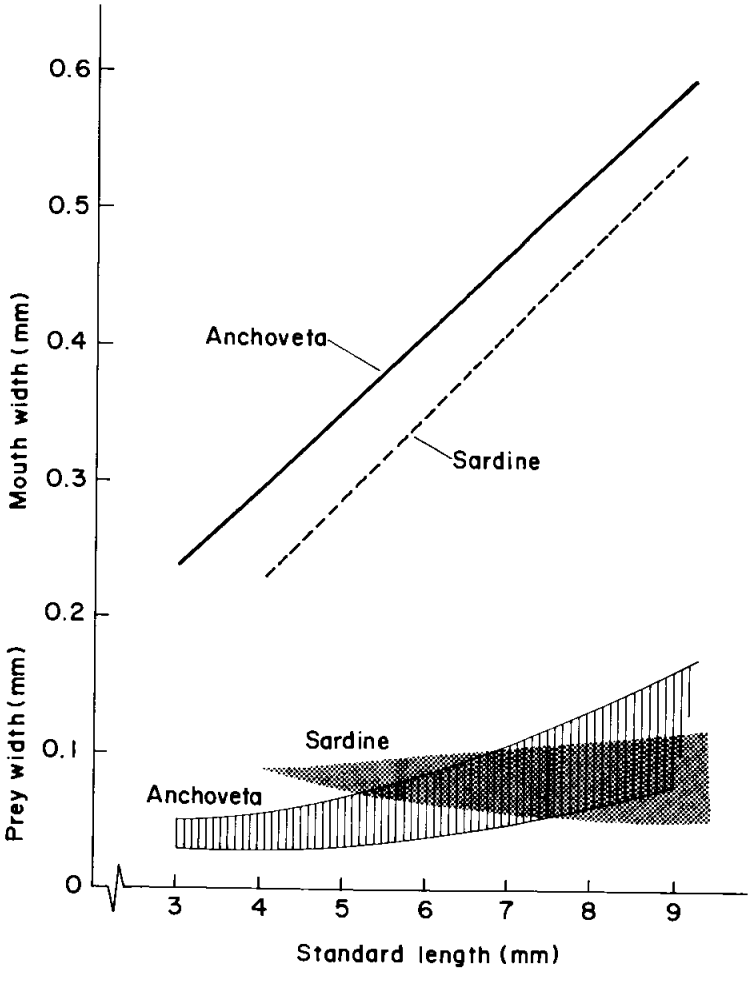

Fig. 4. Differences in mouth and prey width in larval anchoveta and sardine.
Fig. 4. Diferencias en el ancho de la boca y de la presa en larvas de anchoveta y sardina.

Discussion

Overall, the analysis of the available gut content data is hindered by the relatively low number of larvae with food in the gut. With respect to the daytime hauls, this seems to be more a question of sampling technique than of larval feeding behavior. Stress often induces defecation in fish larvae and probably a vertical haul from a depth of 50 m is sufficient to trigger off the defecation process. Therefore a gentler treatment such as using MOCNESS surface tows (Govoni et al. 1983) would be a more adequate technique.

Comparably low number of larvae with food in their guts were reported for *Engraulis mordax, Sardinops sagax* and *Limanda ferruginea* (Arthur 1976; Smith et al. 1978).

The most important result based on the data sampled in February/March 1982 is undoubtedly that anchoveta larvae in their first feeding period are almost exclusively phytophagous whilst the first feeding sardine larvae are mainly zoophagous.

Additional data from a cruise conducted in September 1982 show a similar tendency with respect to the anchovy phytoplankton diet for larvae smaller than 4 mm (n=30): 37% pure phytoplankton, 33% mixed diet, 30% pure zooplankton.

This food niche separation of the early larval stages corresponds to field data about distribution and environmental conditions. Rojas de Mendiola and Ochoa (1980) reported a strong correlation between phytoplankton abundance and the spawning centers of adult *Engraulis ringens*. Similar findings were reported by Walsh et al. (1980).

In contrast to anchoveta, sardine spawn relatively far offshore (35-70 km off the Peruvian coast, see Santander and de Castillo 1977) where zooplankton is more abundant than inshore (Walsh et al. 1980).

Even where both species co-occurred for a given size class, a higher percentage of anchoveta larvae had a pure phytoplankton or a mixed diet in the guts than did sardine larvae.

Because there is almost no overlap of the food niches of first-feeding anchoveta and sardine larvae, their survival rates will be different in periods of low phytoplankton availability, such as during El Niño events (Guillen and Rondan 1974; Guillen 1983) or when there is a southward displacement of the spawning stock to less productive areas (Walsh 1978; Walsh et al. 1980). Spawning in the sardine appears to occur earlier during El Niño years (Walsh et al. 1980). However, even if spawning in both species were to occur at the same time, sardine larvae would have a higher chance of survival during the initial phase of an El Niño event because of the time lag between reduced primary production and decreased zooplankton biomass. But with respect to the El Niño event of 1982-1983, which was probably the strongest since the beginning of this century, larvae of both species did not appear to have any chance of survival when hatched during the peak of this event (January-March 1983): compared with values based on normal years (Rojas de Mendiola 1981; Rojas de Mendiola et al. 1983), total planktonic biomass decreased by an average factor of 15 along all of the Peruvian coast and the temperature in the upper 70 m reached values between 26 and 30°C (Villavicencio and Muck 1985). Using a larval feeding and growth model (P. Muck, unpublished data) for *E. ringens* and *S. sagax,* Villavicencio and Muck (1985) estimated survival to be zero for both larvae during the peak of the 1982-1983 El Niño event.

Walsh et al. (1980) state that the high larval mortality of anchoveta, caused by the poor food conditions during the El Niño of 1965, 1972 and 1976, together with overfishing of the adult population, were the main reasons for the collapse of the Peruvian anchoveta stock and the partial replacement of anchoveta by sardine.

Niche separation for first feeding larvae is not directly related to difference in mouth width. Zoophagous sardine larvae of 4 mm feed on items with a mean particle width of 0.07 mm and have a mouth width of 0.23 mm. Phytophagous anchoveta larvae of 3 mm, on the other hand, which feed on items with a mean particle width of 0.03 mm have a mouth width of 0.24 mm.

The fact that sardine larvae have a longer gut than anchoveta of the same size does not appear to be of much ecological relevance because the gut diameter of sardine is smaller than that of anchoveta and thus the entire gut volume is more or less the same (B. Rojas de Mendiola, pers. obs.).

Fig. 4 suggests a second food niche separation for larvae larger than 9 mm. However, the correlation coefficients associated with the regression equations are low and the wide confidence limits for the regression coefficients (Table 5) prevent firm conclusions to be drawn.

With increasing length of anchoveta larvae, their mean maximum prey width and mean minimum prey width increase. This is also the case with the relationship length/optimum prey width, defined as the size of the group of diet organisms with the highest calorific value (see above). These findings correspond to those of optimal foraging theory (Eggers 1976), which implies a switch to larger food particles with increasing body size. This also agrees with the findings of Rojas de Mendiola (1981) on *E. ringens* and with data on other marine fish larvae (*Sardinops sagax* and *Engraulis mordax*, Arthur 1976; *Sardinops sagax*, Herrera and Balbontin 1983; *Leiostomus xanthurus* and *Micropogonias undulatus*, Govoni et al. 1983). Hunter (1977) found similarly that, when larval Californian anchovy *E. mordax* are fed exclusively with dinoflagellate *Gymnodinium splendens* (a mean width of 50 µm), growth becomes asymptotic at about 6 mm. Vlymen (1977) predicted similar results based on a feeding/growth model of Californian anchovy.

Using the formula for the length/minimum prey width relationship (Table 5) identical results are obtained: a 6 mm, growing anchoveta larvae consumes organisms not smaller than 60 µm (mean minimum particle size).

The relationship length/minimum prey width for sardine shows a weak downward trend, similar to what has been reported in the literature for larvae of *Brevoortia patronus* (Govoni et al. 1983), *Trachurus japonicus* and *Scomber* spp. (Yokota et al. 1961).

Thus overall, our results show a good agreement with those of other researchers working on various clupeoid and other species of pelagic fishes.

References

Arthur, D.K. 1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax, Engraulis mordax* and *Trachurus symmetricus*. U.S. Fish. Bull. 74: 517-530.

Blaxter, J.H.S. and M.E. Staines 1971. Food searching potential in marine fish larvae, p. 467-485. *In* D.J. Cirsp (ed.) Fourth European Marine Biology Symposium. Cambridge University Press, Cambridge.

Braum, E. 1967. The survival of fish larvae with reference to their feeding behavior and the food supply, p. 113-131. *In* S.D. Gerking (ed.) The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

Eggers, D.M. 1976. Theoretical effect of schooling by planctivorous fish predators on rate of prey consumption. J. Fish. Res. Board Can. 33: 1964-1971.

Govoni, J.J., D.E. Hoss and A.J. Chester. 1983. Comparative feeding of three species of larval fishes in the Northern Gulf of Mexico: *Brevoortia patronus, Leiostomus xanthurus*, and *Micropogonias undulatus*. Mar. Ecol. Prog. Ser. 13: 189-199.

Guillen, O. 1983. Condiciones oceanográficas y sus fluctuaciones en el Pacífico Sur Oriental, p. 607-658. *In* G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species of Neritic Fish Resources, 18-29 April 1983, San José, Costa Rica. FAO Fish. Rep. No. 291, Vol. 3, Rome.

Guillén, O. and R. Rondán. 1974. Avances del Proyecto de Productividad de las Aguas Costeras frente al Perú. IMARPE, Serie de Informes Especiales, IM-148.

Herrera, G. and F. Balbontín. 1983. Tasa de evacuación intestinal e incidencia de alimentación en larvas de *Sardinops sagax musica* (Pisces, Clupeiformes). Rev. Biol. Mar, Valparaiso 19(2): 113-132.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. CIEM 20: 1-228.

Houde, E.D. 1974. Effects of temperature and delayed feeding on growth and survival of larvae of three species of subtropical marine fishes. Mar. Biol. 26: 271-285.

Houde, E.D. 1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28: 395-411.

Hunter, J.R. 1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. U.S. Fish. Bull. 70: 821-838.

Hunter, J.R. 1977. Behavior and survival of northern anchovy *Engraulis mordax* larvae. U.S. Fish. Bull. 74: 81-88.

Laroche, J.L. 1982. Trophic patterns among larvae of fish species of sculpins (Family: Cottidae) in a Maine estuary. U.S. Fish. Bull. 80: 827-840.

Lasker, R., H.M. Feder, G.H. Theilacker and R.C. May 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. 5: 345-353.

May, R.C. 1974. Larval mortality in marine fishes and the critical period concept, p. 1-19. *In* J.H.S. Blaxter (ed.) The early life history of fish. Springer-Verlag, New York.

Rojas de Mendiola, B. 1974. Food of the larval anchovy *Engraulis ringens* J., p. 277. *In* J.H.S. Blaxter (ed.) The early life history of fish. Springer-Verlag, New York.

Rojas de Mendiola, B. 1980. Summaries of the studies about food and feeding habits of the anchovy (*Engraulis ringens* J.). IOC Workshop Report No. 28: 221-223.

Rojas de Mendiola, B. 1981. Seasonal phytoplankton distribution along the Peruvian coast, p. 348-356. *In* F. Richards (ed.) Coastal upwelling. Coastal and Estuarine Sciences 1. American Geophysical Union, Washington, DC.

Rojas de Mendiola, B. and O. Gómez. 1980. Food, survival and time of inactivity of larval anchovy (*Engraulis ringens* J.). IOC Workshop Report No. 28: 241-254.

Rojas de Mendiola, B. and N. Ochoa. 1980. Phytoplankton and spawning of anchoveta. IOC Workshop Report No. 28: 241-254.

Rojas de Mendiola, B., O. Gómez and N. Ochoa 1983. Efectos del fenómeno "El Niño" sobre el fitoplancton. IX Congreso Latinamericano de Zoología, Arequipa, Perú, 9-15 de Octubre 1983.

Rosenthal, H. and G. Hempel. 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.), p. 344-364. *In* J.H.S. Steele (ed.) Marine Food Chains, Oliver and Boyd, Edinburgh.

Santander, H. and O.S. de Castillo. 1977. Ichthyoplankton from the Peruvian coast, p. 105-123. *In* S.Z. Quasim (ed.) Proceedings of the Symposium on Warm Water Zooplankton, National Institute of Oceanography, India.

Smith, W.G., J.D. Sibunka and A. Wells. 1978. Diet movements of larval yellowtail flounder, *Limanda ferruginea*, determined from discrete depth sampling. U.S. Fish. Bull. 76: 167-178.

Theilacker, G. and K. Dorsey. 1980. Larval fish diversity, a summary of laboratory and field research, p. 105-143. *In* Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes. IOC Workshop Report No. 28.

Villavicencio, Z. and P. Muck. 1985. La importancia del cambio de la temperatura y de la biomasa planctónica para la producción y mortalidad de anchoveta (*Engraulis ringens* J.) y sardina (*Sardinops sagax* H.), p. 119-218. *In* W. Amtz, A. Landa and J. Tarazona (eds.) El Niño: su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao, Volumen Extraordinario.

Vlymen, W.J. 1977. A mathematical model of the relationship between larval anchovy (*Engraulis mordax*) growth, prey microdistribution, and larval behavior. Environ. Biol. Fish. 2: 211-233.

Walsh, J.J. 1978. The biological consequences of interaction of the climatic, El Niño, and event scales of variability in the Eastern Tropical Pacific. Rapp. P.-V. Réun CIEM 173: 182-192.

Walsh, J.J., T.E. Whitledge, W.E. Esaias, R.L. Smith, S.A. Huntsman, H. Santander and B. Rojas de Mendiola. 1980. The spawning habitat of the Peruvian anchovy, *Engraulis ringens*. Deep-Sea Res. 27A: 1-27.

Ware, D.M., B. Rojas de Mendiola and D.S. Newhouse. 1981. Behaviour of first-feeding Peruvian anchoveta larvae, *Engraulis ringens* J. Rapp. P.-V. Réun CIEM 178: 467-484.

Yokota, T., M. Toriyama, F. Kanai and S. Nomura. 1961. Studies on the feeding habit of fishes. Rep. Nankai Reg. Fish. Res. Lab. 14. 234 p. (In Japanese, English summary)

Stomach Contents of Anchoveta (*Engraulis ringens*), 1953-1974

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Abstract

A brief review of past research on the food and feeding habits of the Peruvian anchoveta (*Engraulis ringens*) is presented, with emphasis on studies published by the author and her collaborators. The methods used in these studies are recalled and an appended database is introduced, consisting of 3,682 records of individual anchoveta stomach contents, sampled from November 1953 to August 1974 and providing full details as to sampling location, time and hour, size, sex, maturity stages and other ancillary variables.

Resumen

Se presenta una breve revisión de las investigaciones realizadas sobre el alimento y hábitos alimenticios de la anchoveta peruana (*Engraulis ringens*) dando énfasis a los estudios publicados por el autor y sus colaboradores. Se mencionan nuevamente los métodos utilizados en estos estudios y se anexa una base de datos que provee información individual sobre el análisis del contenido estomacal de 3,682 anchovetas muestreadas desde Noviembre de 1953 a Agosto de 1974, e incluye además datos en detalles sobre localidad de muestreo, fecha, hora de colección, sexo, madurez sexual, longitud de las anchovetas, peso y otras variables.

Introduction

The Peruvian anchoveta *Engraulis ringen* (Jenyns) supported for many years the largest single-species fishery of the world, and its population biomass estimates ranged between 20 and 30 million tonnes (Longhurst 1971).

It is unarguably the high phyto- and zooplankton production of the Peruvian upwelling system which made such stock sizes possible. Besides, being extremely fecund, anchoveta are able to switch easily from phyto- to zooplankton, and from filtering to particulate feeding. This ability to switch between trophic levels in relation to environmental conditions is certainly one of the reasons for the persistence of this species in its highly variable environment. Schaefer (1965) correctly pointed out, however, that the high abundance of anchoveta off Peru is primarily a result of its predominantly phytophagous habits.

The feeding adaptations of anchoveta cannot totally prevent it from being negatively affected by environmental fluctuations. In fact, as noted by Frost (1974) the fishes of pelagic ecosystems tend to be strongly affected by fluctuations of the lower elements of the food web. Changes of species and size composition of their food organisms not only have a strong impact on the survival and individual and population growth of pelagic fishes, but also induce change in the geographic location of the stocks themselves.

Outside of the spawning season, the Peruvian anchoveta is generally concentrated at an average distance of 75 km from the coast, which is where phytoplankton concentrations are

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highest (Rojas de Mendiola 1981). Spawning occurs closer to the coast, in colder waters (Santander 1981).

Rojas de Mendiola and Gómez (1981) stressed that certain phytoplankton species are of great importance for anchoveta, i.e.,that this herbivore does not feed on whatever happens to be in the water. Rather, anchoveta largely select the phytoplankton species they consume. Conversely, different kinds of phytoplankton affect the development and growth of anchoveta differently.

Thus, for example in November 1975, in conjunction with the first stage of the El Niño event of 1976, a change occurred in the composition of the phytoplankton along the northern coast of Peru, which resulted in very high abundance of the dinoflagellate *Gymnodinium splendens*, normally not a food item of adult anchoveta (but see Muck et al., this vol., with regard to larval anchoveta). In May and June 1976, *G. splendens* had produced widespread blooms. Tsukayama and Alvarez (1981), unsurprisingly, reported a decline of the growth rate of anchoveta during the 1976 spring seasons: specimens of 15 months of age had reached only 12.5 cm and weights almost 30% less than normal. They attributed this to a scarcity of appropriate food items and/or to a reduction of their quality.

The behavior of anchoveta varies widely between day and night. Johannesson and Vilchez (1981) demonstrated how schools, formed in daytime, dissolve at night and how the fish move into deeper water. Mathisen (this vol.) related such daily migration to the feeding behavior of anchoveta.

It is thus obvious that food and feeding are among the most important factors affecting and/or regulating fish populations. Consequently, different purposes can be achieved from the analysis of fish stomach samples: they can be used to obtain general information on a food chain, on competition between species, on seasonal habitat changes, etc. Also geographical differences of feeding can be studied, and related to differences of growth rate, abundance, migration patterns, etc. Thus, in fishes, food and feeding habits studies can contribute to elucidating the causes of variations of stock abundances in space and time.

The first information on the food and feeding habits of anchoveta to become available were published by Vogt (1940), Sears (1941) in Peru, and Schneider (1943), Mann (1954) and de Buen (1958) in Chile.

This author began her studies of the food and feeding habits of the Peruvian anchoveta in the early 1950s (Rojas 1953), and the bulk of her further studies were reported in Rojas de Mendiola (1959, 1966, 1969, 1971, 1973, 1974, 1979, 1981), Rojas de Mendiola and Gómez (1981), Rojas de Mendiola and Ochoa (1973, 1981), Rojas de Mendiola et al. (1969), Ware et al. (1981) and Muck et al. (this vol.). The key points that emerged from these studies are as follows:

- the food and feeding habits of anchoveta change with length in relation to changing physiological requirements. Anchoveta larvae ingest round diatoms which do not form chains, and dinoflagellate such as *Gymnodinium splendens* (see Muck et al., this vol.). Postlarval anchoveta feed on zooplankton and prefer copepod eggs and nauplii. Juvenile anchoveta are largely zooplanktivorous, while the adults - at least off central and northern Peru - are almost exclusively phytoplanktivorous;
- with regard to adult food preference, distinct latitudinal differences are apparent. Anchoveta from the south of Peru and the north of Chile feed almost exclusively on zooplankton while those of the north are phytoplanktivorous. These latitudinal differences are matched by related differences in branchiospine number, length and spacing and relative gut length (see Palomares et al., 1987), as well as by different vertebral counts. This suggests the existence of at least two different stocks along the southeastern Pacific coast;
- changes in environmental conditions such as the El Niño events of 1972-1973 greatly alter the distribution patterns of the two anchoveta stocks. Thus, the reduction of suitable phytoplankton in the north of Peru led to the almost total disappearance of anchoveta in that area, and the few that were encountered had empty stomachs, or had ingested euphausids. In the south of Peru, on the other hand, anchoveta were found which had relatively long guts, a large number of gill rakers and their stomachs full of phytoplankton, suggesting that a north-south migration had taken place;

- during such environmental changes, cannibalism appears to increase, wherein both eggs and larvae are ingested in larger amounts than during other periods (for example, a single anchoveta of 16 cm had ingested at least one hundred eighty 15-mm larvae).

The overwhelming majority of the contributions which led to these generalizations were, however, descriptive studies, which do not provide the type of quantitative information needed, e.g., for modelling purposes.

This paper makes available to a wider scientific community the bulk of the raw data, covering the years 1953 to 1974, upon which earlier studies were based. Together with the data of Alamo (this vol.), covering the years 1974 to 1982, these data can be used to answer questions such as:

i) have the quantity and the quality of the food of the Peruvian anchoveta changed in the last decades?
ii) if such changes occurred, can they be related to changes of (a) individual, (b) population growth rates and (c) the maturation and reproduction of anchoveta?
iii) what is the extent of food size selection by anchoveta; e.g., does anchoveta consume the larger or the smaller representatives of the phyto- and zooplankton?
iv) if anchoveta become particulate feeders and concentrate on zooplankton when appropriate phytoplankton is scarce, does it imply a greater consumption of anchoveta eggs and larvae and does this impact on subsequent recruitment?
v) are there one or several populations of anchoveta, and if the latter applies, are they distinguishable by their food and feeding habits?

It is likely that answers to at least some of these questions, and of other related questions that may be formulated, will be obtained from detailed analysis of the data presented below.

Materials and Methods

Sources of Samples

The material presented here stems from different sources and were collected from 19 November 1953 to 8 August 1974. The anchoveta samples of 1953 and early 1954 were obtained on board Danish vessels especially contracted by the "Compañia Administratora del Guano", which needed basic information on anchoveta, the major food item of the guano birds (see Tovar 1987 and Muck and Pauly 1987 for an account of their biology). From mid-1954 to 1958, the principal source of samples was the reduction (i.e., fish meal) plants, especially those in the Chimbote area (see Castillo and Mendo 1987 for an account of anchoveta meal production). From 1960 to 1975, samples were obtained from a number of sources, notably scientific and "EUREKA" surveys organized by the Instituto de Investigáción de Recursos Marinos (IREMAR) and its successor, the Instituto del Mar del Perú (IMARPE). Some samples were also obtained during this period by foreign scientific vessels operating in Peruvian waters.

Analytical Procedures (General)

The anchoveta samples generally consisted of about 100 specimens, taken randomly from the catch. They were immediately put into a plastic bag, into which a 20% formalin-seawater solution was poured such as to entirely cover the anchoveta sample and to stop all further digestion process. A label with details on the sample was then put into each bag. This label included the following information: date and hour of sampling, location (or fishing area, see Fig. 1), depth (if more than 16 fathoms) and sea surface temperature (in ^{o}C). Whenever possible, a plankton sample was also taken, using a net with a 75 µm mesh size.

Upon working up those samples, it emerged after about one year that within-sample differences of stomach content weight and composition were rather small. It was therefore decided to take at random subsamples of 20 specimens from the original samples of 100 anchoveta.

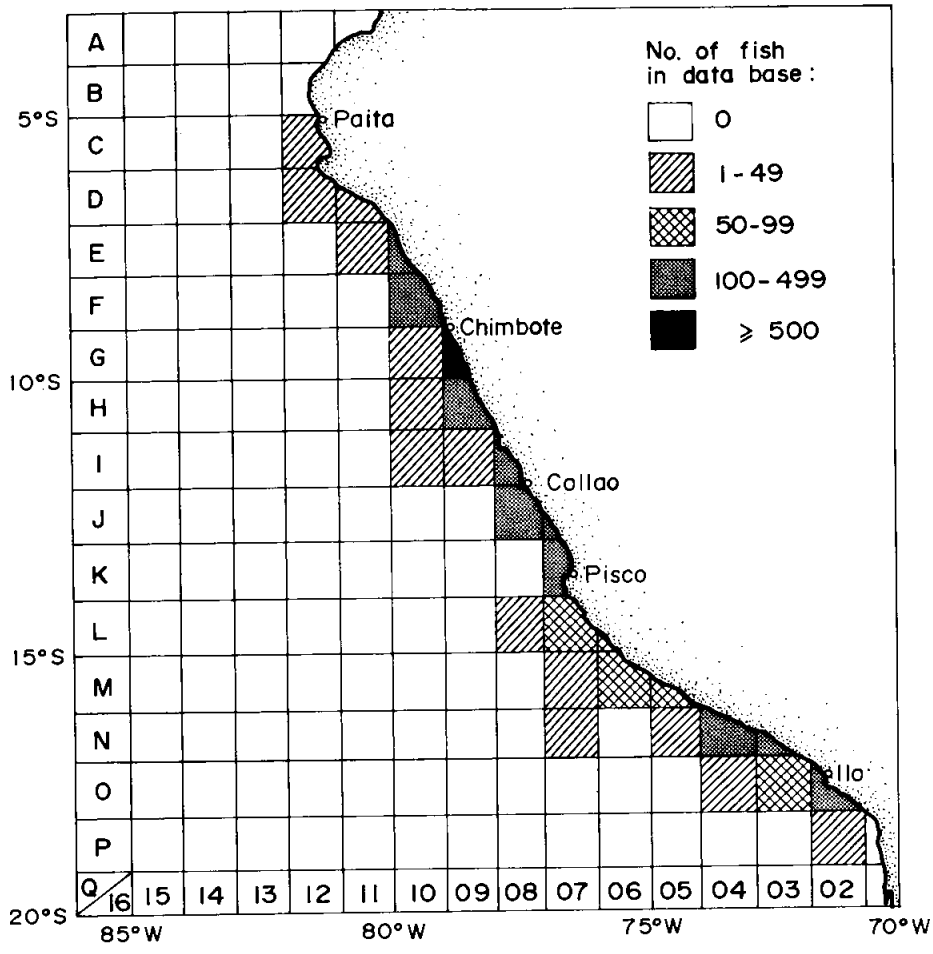

Fig. 1. Sampling location and density of data included in database described in text. Letters and numbers refer to the code used by the author to locate samples along the Peruvian coast.
Fig. 1. Lugar de muestreo y densidad de los datos incluidos en la base de datos que se describe en el texto. Las letras y los números indican el código usado por el autor para localizar los muestreos a lo largo de la costa peruana.

In the laboratory, the following information were recorded for each intact individual anchoveta:

i) total and/or standard length (in mm)
ii) total wet weight (in g).

The body cavity was then opened and the following were recorded:

iii) sex and sexual maturity
iv) stomach fullness and stomach contents.

Details on the various procedures of scales used for items (iii) and (iv) are given below.

Recording of Reproduction-Related Information

The scale in Table 1, adapted from Clark (1954) and Einarsson et al. (1966), was used to describe the various maturation stages of the sampled anchoveta.

Table 1. Maturity scale for anchoveta, adapted from Clark (1954) and Einarsson et al. (1966).[a]
Tabla 1. Escala de madurez para la anchoveta, adaptada de Clark (1954) y Einarsson et al. (1966).

Stage	Definition
I	Immature <8 cm TL
II	Immature or recuperating ≥8 cm TL
III	Maturing; prespawning phase
IVb	Mature; spawning phase
Vc	Partially spent
VIc	Spent; postspawning

[a]Editors' note: this scale was derived at a time when anchoveta and other clupeoids were assumed to spawn only once or twice during a spawning season. The recent finding that anchoveta and other clupeoids may spawn once a week during the spawning season (see Lasker 1985) does not detract from the utility of the older scale as a descriptive tool (see other contributions in this vol.).

[b]Maturity stage IV is used at IMARPE to separate the adult from the juvenile stock (see also Pauly and Soriano 1987).

[c]Color differences are used to differentiate stages V and VI.

Recording of Food and Feeding-Related Information

The digestive tract of each anchoveta was removed, and gently extended. Its length was then measured (in mm, from the pylorus to the anus).

Then, the stomachs (gastric and pyloric parts) were separated from the rest of the gut, and weighted (to the nearest mg). Their degree of fullness was then determined according to the scale in Table 2.

Table 2. Scale used for quantifying the fullness of anchoveta stomachs.
Tabla 2. Escala utilizada para cuantificar la llenura de los estómagos de anchoveta.

Fullness	Original definition	Percent fullness[a]
full ("*lleno*" or "*repleto*")	Stomach is full and distended	100
almost full ("*semilleno*" or "*mesolleno*")	Stomach is more than 70% full	60
almost empty ("*semivacio*" or "*poco*")	Food fills up to 30% of stomach	40
empty ("*vacio*")	Stomach is empty	0

[a]See Pauly et al. (this vol.) for details on the derivation of this new scale, which was also used for the contents of the pyloric parts of the stomachs (see text).

The stomachs were then cut open, their contents separated from the stomach walls and added to flasks partly filled with 10% formalin solution. The empty stomachs were weighed and the weight of the stomach contents determined by subtraction. The state of digestion of the stomach contents was then assessed, using the scale in Table 3.

Table 3. Scale used for quantifying the state of digestion of anchoveta food organisms.
Tabla 3. Escala usada para cuantificar el estado de digestión de los organismos en el contenido estomacal de las anchovetas.

State	Definition	Corresponding percentage[a]
whole ("*entero*")	organisms intact	100
almost whole ("*casi entero*")	organisms almost intact	70
halfdigested ("*semidigerido*" or "*semientero*")	organisms broken into parts but still easily identifiable	50
almost digested ("*casi digerido*")	only parts of organisms are identifiable	25
digested ("*digerido*")	food contents consists of a paste and/or organisms are totally unidentifiable	0

[a]Editors' note: assumed values, used to allow some quantitative analysis of what originally were qualitative data.

Until 1958, stomach contents were routinely identified and reported at the species level. For phytoplankton, all identification and counts were based on an aliquot, drawn from the thoroughly mixed material of each stomach sample. For zooplankton, the entire samples were counted, with each still identifiable head providing a count of one. All identifications were performed with a compound microscope. This type of detailed analysis was replaced, starting in 1959 and in the early 1960s by a less detailed analysis, i.e., all identifications were still performed at the species level, but without counting the single cells of aliquots or the individual zooplankton in the whole sample. Rather, a qualitative scale was used, as follows:

+++ **very abundant**
++ **abundant**
+ **present**

Fish eggs and fish larvae were always counted; the identification of the anchoveta eggs was facilitated by their rather unique elliptical shape.

Finally, the whole stomach sample was put into a Petri dish, and the overall ratio of phyto- to zooplankton was assessed subjectively, using a stereomicroscope.

Tabulation and Computerization of Results

Tabulation of the information described above occurred in three major phases:

i) initial tabulation on raw data sheet (by the author and her associates), including counts or relative abundance of all taxa identified as food items. This process occurred from 1953 to 1974 and formed the basis for the author's various publications on anchoveta food and feeding habits, listed above;

ii) retabulation in 1987 by the author of a large fraction of the data in (i) reduced as follows:
   a) only 1/5 of all fish from each sample were taken (at random), such as to reduce the number of fish collected at the same place, date and hour;
   b) only the 4 or 5 most abundant food items reported from each stomach were included (the overall list of items still includes over 259 entries, see Pauly et al., this vol.)

iii) creation, in 1988, at ICLARM, of a computerized database including the data in (ii) and those of Alamo (this vol.). This part of the work was performed by Ms. Susan "Tuttay" Luna working under the supervision of Dr. D. Pauly and using the DBase III Plus program implemented on an IBM XT-compatible microcomputer. Finally, Ms. Astrid Jarre performed quality and logic checks on the entries.

Results and Discussion

The database reported upon here includes data on 3,682 specimens of anchoveta, sampled from 11 November 1953 to 8 August 1974. Fig. 1 illustrates the spatial distribution of these 3,682 specimens along the Peruvian coast, as well as the code used to record the sampling locations.

Further details on the contents and organization of this database, which also includes the anchoveta stomach content data of Alamo (this vol.) may be found in Appendix I of this volume.

A very preliminary analysis of some aspects of this database is presented in Pauly et al. (this vol.). Readers are welcome to probe further.

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The author would like to take this opportunity to thank her collaborators, notably former coauthors for their cooperation over several decades of work on the food of the Peruvian anchoveta. Sincere gratitude also goes to GTZ/PROCOPA for support of the work leading to this contribution, to Dr. D. Pauly for his translation and editing of the original Spanish-language draft and to Ms. S. Luna and Ms. A. Jarre for their assistance with the computerized version of the database presented here.

References

Castillo, S. and J. Mendo 1987. Estimation of unregistered Peruvian anchoveta (*Engraulis ringens*) in official catch statistics, 1951 to 1982, p. 109-116. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Clark, F.N. 1954. Biología de la anchoveta. Bol. Cient. Cia. Admin. Guano 1(1): 98-132.

de Buen, F. 1958. Peces de la superfamilia Clupeoidea en aguas de Chile. Rev. Biol. Mar (Valparaiso) 8(1/3): 83-110.

Einarsson, H., F. Flores and J. Miñano. 1966. El ciclo de madurez de la anchoveta peruana (*Engraulis ringens* J.), p. 128-135. *In* I Seminario Latinoamericano sobre el Océano Pacífico Oriental. Univ. Nacional Mayor, San Marcos, Lima, Perú.

Frost, B.W. 1974. Feeding processes at lower trophic levels in pelagic communities, p. 59-77. *In* C.B. Miller (ed.) The biology of the Oceanic Pacific. Proceedings of the 33rd Annual Biology Colloquium. Oregon State University Press, Oregon.

Johannesson, K. and R. Vilchez 1981. Notes on hydroacoustic observations of changes in distribution and abundance of some common pelagic fish species in the coastal waters off Peru, with special emphasis on anchoveta, p. 287-323. *In* G.D. Sharp (ed.) Workshop on the Effects of Environmental Variations on the Survival of Larval Pelagic Fishes. IOC Workshop Report No. 28. UNESCO, Paris.

Lasker, R., Editor. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS 36. 99 p.

Longhurst, A.R. 1971. The clupeoid resources of tropical seas. Oceanogr. Mar. Biol. Ann. Rev. 9:349-385.

Mann, G.F. 1954. La vida de los peces en aguas chilenas. Universidad de Chile, Valparaiso.

Muck, P. and D. Pauly 1987. Monthly anchoveta consumption of guano birds off Peru, 153 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Palomares, M.L., P. Muck, J. Mendo, E. Chúman de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982, p. 117-141. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and M. Soriano 1987. Monthly spawning stock and egg production of Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982, p. 167-178. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Rojas, B. 1953. Estudios preliminares del contenido estomacal de las anchovetas. Bol. Cient. Cia. Admin. Guano 1(1): 32-42.

Rojas de Mendiola, B. 1959. Breve informe sobre los hábitos alimenticios de la anchoveta (*Engraulis ringens* J.) en los años 1954-1958. Informe presentado a la Cia. Admin. del Guano el 30 de Abril de 1959. (Unpublished MS).

Rojas de Mendiola, B. 1966. Relación entre la cosecha estable del fitoplancton, el desove y la alimentación de la anchoveta (*Engraulis ringens* J.), p. 60-69. *In* I Seminario Latinoamericano sobre el Oceano Pacífico Oriental. Univ. Nacional Mayor, San Marcos, Lima, Perú.

Rojas de Mendiola, B. 1969. The food of the Peruvian anchovy. J. Cons. CIEM 32(3): 433-434.

Rojas de Mendiola, B. 1971. Some observations on the feeding of the Peruvian anchovy (*Engraulis ringens* J.) in two regions of the Peruvian coast, p. 417-440. In J. Costlow (ed.) Fertility of the sea. Vol. 2. Gordon and Breach Science Publ., New York.

Rojas de Mendiola, B. 1973. El alimento de la anchoveta (*Engraulis ringens* J.) en un área de afloramiento (Sán Juan). Informe Inst. Mar Perú-Callao (49): 1-15.

Rojas de Mendiola, B. 1974. Food of the larval anchoveta *Engraulis ringens* J., p. 277-285. *In* J.H. Blaxter (ed.) The early life history of fishes. Springer Verlag, Berlin.

Rojas de Mendiola, B. 1979. Red tide along the Peruvian coast, p. 183-190. *In* D.L. Tayler and H.H. Seliger (eds.) Toxic dinoflagellate blooms. Elsevier-North Holland, New York.

Rojas de Mendiola, B. 1981. Summary of the studies about food and feeding habits of the anchoveta (*Engraulis ringens* J.), p. 221-231. *In* G.D. Sharp (ed.) Workshop on the Effects of Environmental Variations on the Survival of Larval Pelagic Fishes. IOC Workshop Report No. 28. UNESCO, Paris.

Rojas de Mendiola, B. and N. Ochoa 1973. Observations on the food and feeding habits of the anchovy *Engraulis ringens* Jenyns made during cruise 6908-09, p 457-461. *In* R. Fraser (ed.) Oceanography of the South Pacific. New Zealand Commission for UNESCO, Wellington, NZ.

Rojas de Mendiola, B. and N. Ochoa 1981. Fitoplancton y desove de la anchoveta (*Engraulis ringens* J.), p. 241-253. *In* G.D. Sharp (ed.) Workshop on the Effects of Environmental Variations on the Survival of Larval Pelagic Fishes. IOC Workshop Report No. 28, UNESCO, Paris.

Rojas de Mendiola, B., N. Ochoa, R. Calienes and O. Gómez. 1969. Contenido estomacal de anchoveta en cuatro areas de la costa Peruana. Inf. Inst. Mar Perú-Callao 27. 30 p.

Rojas de Mendiola, B. and O. Gómez. 1981. Primera alimentación, sobrevivencia y tiempo de actividad de la larvas de anchoveta (*Engraulis ringens* J.), p. 72-79. *In* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosystema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao, Volumen Extraordinario.

Santander, H. 1981. Fluctuaciones del desove de anchoveta y algunos factores relacionados, p. 255-274. *In* G.D. Sharp (ed.) Workshop on the Effects of Environmental Variations on the Survival of Larval Pelagic Fishes. IOC Workshop Report No. 28. UNESCO, Paris.

Schaefer, M.B. 1965. The potential harvest from the sea. Trans. Am. Fish. Soc. 94:123-128.

Schneider, O. 1943. Catálogo de los peces marinos del litoral de Concepción y Arauco. Museo de Concepción, Chile.

Sears, M. 1941. ¿Qué es el plancton y por qué debemos estudiarlo? Bol. Cient. Cia. Admin. Guano 17.

Tovar, H., V. Guillen and M. Nakama. 1987. Monthly population size of three guano bird species off Peru, 1955 to 1982, p. 208-218. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Tsukayama, I. and M. Alvarez 1981. Fluctuaciones en el stock de anchoveta desovantes durante los ciclos reproductivos de primavera 1964-1978, p. 233-240. *In* G.D. Sharp (ed.) Workshop on the Effects of Environmental Variations on the Survival of Larval Pelagic Fishes. IOC Workshop Report No. 28. UNESCO, Paris.

Vogt, W. 1940. Una depresión ecológica de la costa Peruana. Bol. Cient. Cia. Admin. Guano 16(10).

Ware, D.M., B. Rojas de Mendiola and D.S. Newhouse. 1981. Behavior of first-feeding Peruvian anchoveta *Engraulis ringens* J. Rapp. P.V. Réun. CIEM 147: 467-474.

Stomach Contents of Anchoveta (*Engraulis ringens*), 1974-1982

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ALAMO, A. 1989. Stomach contents of anchoveta (*Engraulis ringens*), 1974-1982, p. 105-108. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

A database on anchoveta (*Engraulis ringens*) stomach contents covering the period from 3 September 1974 to 18 October 1982 is presented which complements a similar database initiated in 1953 by B. Rojas de Mendiola. Most of the available 6,053 individual records include information on sampling location and time (data and hour), length, weight, gonad weight and maturity stage, as well as on food and feeding (stomach contents in weight and by taxa). Some ancillary information and a brief review of the sampling methods are provided.

Resumen

Se presenta la base de datos sobre contenidos estomacales de anchoveta (*Engraulis ringens*) que abarca el periódo del 3 de Septiembre de 1974 al 18 de Octubre de 1982 como complemento a la base de datos iniciados en 1953 por B. Rojas de Mendiola. La mayoría de los 6,053 registros individuales incluyen información sobre área y tiempo del muestreo (fecha y hora), longitud, peso, peso de gonada y estadío de madurez, asi como alimento (peso de contenido estomacal por grupo taxonómico). Se incluye una breve información complementaria y una breve revision sobre los métodos de muestreo.

Introduction

The large fluctuations of abundance of Peruvian marine fish stock have prompted a series of investigations aimed at explaining these changes in terms of the peculiarities of the Peruvian upwelling system.

Food and feeding habits studies form a significant part of these investigations. Rojas de Mendiola (this vol.) gives a brief review of such work with regard to the anchoveta (*Engraulis ringens*).

These previous studies and that of Alamo (1981) indicate that anchoveta is a planktivore which relies, as shown on Fig. 1, on both phytoplankton (e.g., diatoms) and zooplankton (e.g., copepods) and that its diet varies with size, maturity stage, area, season, water temperature, etc. Particularly important are the facts that anchoveta also consume fish eggs and larvae - including its own - and that such cannibalism (and predation with reference to the other species) can be assumed to have a strong impact on stock sizes (Santander et al. 1983).

Detailed analysis of the database accumulated so far, however, cannot proceed without the data being computerized and should not proceed without reference to the related database of Rojas de Mendiola (this vol.).

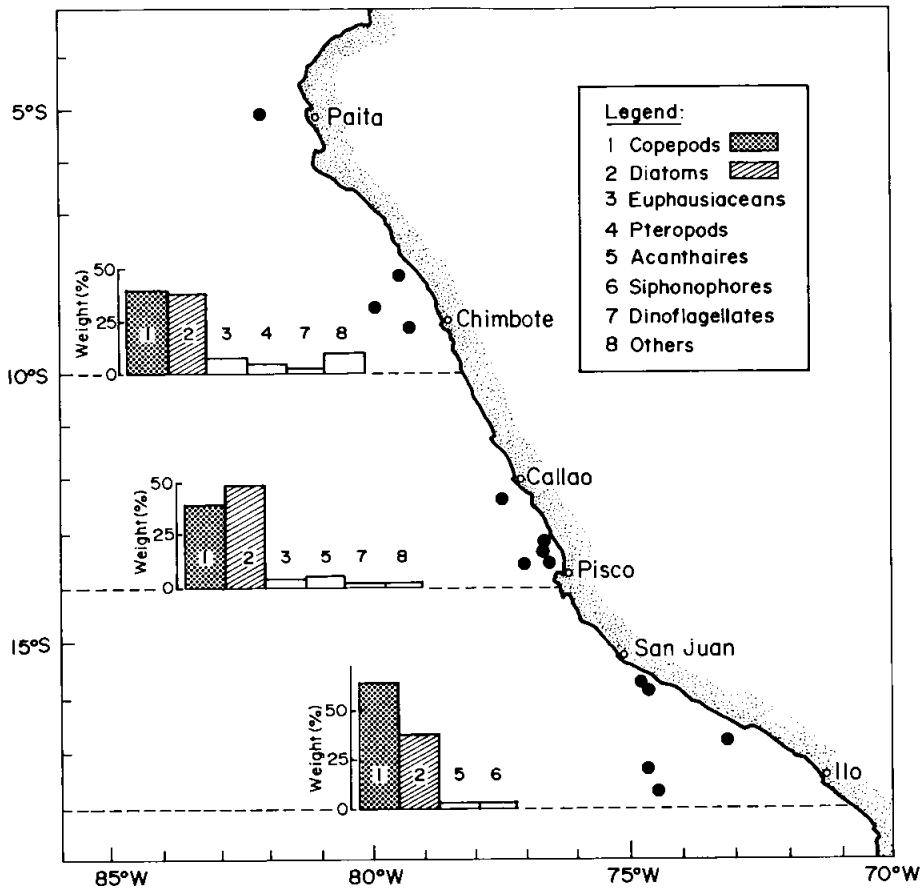

Fig. 1. Food composition of 500 anchoveta sampled in September 1982, during the 1982-1983 El Niño event. (Black dots represent sampling stations; redrawn from Sánchez de Benites et al. 1985).

Fig. 1. Composición del alimento de 500 anchovetas muestreadas en Septiembre de 1982, durante el evento El Niño 1982-1983 (los puntos negros representan las estaciones muestreadas; redibujado de Sánchez de Benites et al. 1985).

Materials and Methods

Sampling Procedures

The data presented here were collected from 3 September 1974 to 18 October 1982, and consist of records for 6,053 specimens of juvenile and adult anchoveta caught off Peru between 4 and 18°S.

All fish samples were preserved in 10% formalin and the sampling data and hour were recorded. Sampling locations were reported as 1° Marsden squares (during computerization, the Marsden square numbers were replaced by the longitude and latitude corresponding to the center of each square, see Fig. 2), and the sea surface temperature noted.

Overall, sampling procedures resembled those of Rojas de Mendiola (this vol.).

Analytical Procedures

In the laboratory the specimens of each anchoveta sample were analyzed individually, and the following information noted:

i) total length (in cm),
ii) total wet weight (in g),
iii) sex and maturity stage,
iv) amount of visceral fat,
v) stomach content weight (in g),

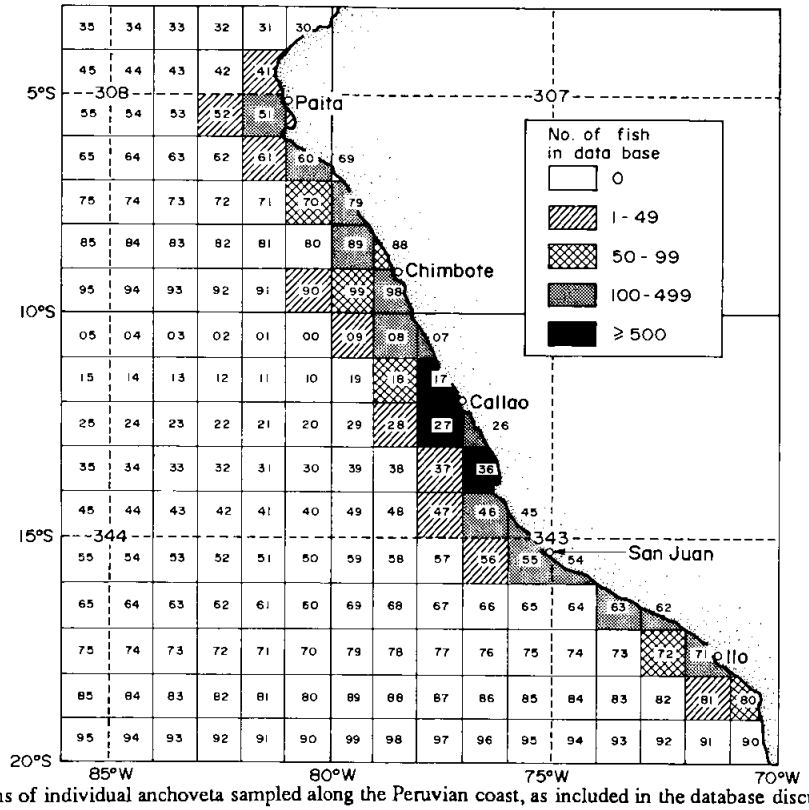

Fig. 2. Distributions of individual anchoveta sampled along the Peruvian coast, as included in the database discussed here. The numbers refer to Marsden squares, used for initial coding of the origin of anchoveta samples. [Note that all fish caught within a given square were attributed the longitude and latitude of the center of that square (for example, square #307/99 = 9°30'S and 79°30'W)].

Fig. 2. Distribución de anchovetas muestreadas a lo largo de la costa peruana, incluidas en la base de datos discutidos en este trabajo. Los números se refieren a cuadrados Marsden usados en las muestras originales de anchoveta. [Notar que, todos los peces capturados dentro de un cuadrado fueron atribuidos a la longitud y latitud del centro del cuadrado (ejemplo, cuadrado #307/99 = 9°30'S y 79°30'W)].

vi) stomach fullness,
vii) state of digestion, and
viii) relative abundance of food items.

The scale used to assess maturity stages was the same as that of Rojas de Mendiola (this vol.); Table 1 was used to assess the amount of visceral fat present in each anchoveta.

The anchoveta stomach contents were separated into their phytoplanktonic and zooplanktonic components by means of a 130 m filter. The identification of zooplankton organisms was performed with a grooved "Bogorov" counting tray (Newell and Newell 1963) and a stereomicroscope.

The phytoplankters were identified from a drop of the stomach content sample using a microscope; their relative abundance was expressed through the following scale:

+ + + very abundant
+ + abundant
+ present

The fullness of anchoveta stomachs and the state of digestion of the various food items were assessed using scales presented in Rojas de Mendiola (this vol.).

Results and Discussion

This contribution serves as a background for a database and not as a presentation and analysis of available information.

An example of the type of analysis that could be conducted with this database is the strong association of various taxa occurring in anchoveta stomach contents with different water temperature ranges.

Table 1. Scale used for rapid visual assessment of the amount of visceral fat in anchoveta.[a]
Tabla 1. Escala usada para la evaluación visual rápida de la grasa visceral en anchoveta.

Stage	Definition
0	no fat is visible along digestive tract
1	only a thin thread of fat is visible along intestine
2	visceral fat is abundant but does not entirely surround intestine
3	intestine is entirely surrounded by fat

[a]Editors' note: this scale corresponds to that developed by Johan Hjort for herring (see Suworow 1959, p. 427 and Nikolsky 1963, p. 211). A Spanish version is given in Tresierra and Culquichicón (1982).

Thus, diatoms are generally associated with low temperatures, and this often involves the genera *Asterionella, Chaetoceros, Coscinodiscus, Rhizosolenia, Thalassionema* and *Thalassiosira*, among others.

Conversely, dinoflagellates tend to be associated with high temperatures and this often involves the genera *Ceratium* and *Peridinium*.

Other groups - particularly zooplankters such as *Calanus, Eucalanus, Oncea, Centrophages* or Euphausids are common at various temperature regimes, while anchoveta eggs occur mainly in spawning areas during the spawning seasons, and thus can help defining these in the absence of other information.

Details on the contents and organization of the database presented here, and which can be used to answer such questions are provided in Appendix I of this volume.

A very preliminary analysis of some aspects of this database is presented in Pauly et al. (this vol.). Readers are welcome to probe further.

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References

Alamo, A. 1981. Estudio sobre la alimentación de la anchoveta peruana *Engraulis ringens* J. durante los años 1976 y 1977. Bol. Inst. Mar. Perú-Callao. Volumen Extraordinario/ICANE: 258-263.

Newell, G.E. and R.C. Newell. 1963. Marine plankton: a practical guide. Hutchinson Educational, London. 207 p.

Nikolsky, G.V. 1963. The ecology of fishes. Academic Press, London. 352 p.

Sañchez de Benitez, G., A. Alamo and H. Fuentes. 1985 Alteraciones en la dieta alimentaria de algunos peces comerciales por efecto del fenómeno "El Niño", p. 135-142. *In* W. Amtz, A. Landa and J. Tarazona (eds.) "El Niño" su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario.

Santander, H., J. Alheit, A.D. MacCall and A. Alamo. 1983. Egg mortality of the Peruvian anchovy (*Engraulis ringens*) caused by cannibalism and predation by sardine (*Sardinops sagax*), p. 1011-1025. *In* G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291. Vol. 3.

Suworow, J.K. 1959. Allgemeine Fischkunde. VEB Deutscher Verlag der Wissenschaften, Berlin. 581 p.

Tresierra, A. and B.P.Z. Culquichicón. 1982. Manual Práctico de biología pesquera. Univ. Nac. Trujillo, Trujillo, Perú. 142 p.

On the Quantity and Types of Food Ingested by Peruvian Anchoveta, 1953-1982*

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Abstract

This contribution presents the results of a first analysis of a computerized database on the food and feeding habits of the Peruvian anchoveta *(Engraulis ringens)* for the years 1953 to 1982, besides serving as (partial) documentation for the same database, which documents, on an unaggregated basis, nearly 10,000 anchoveta stomach contents and ancillary information. Detailed phylogenic "trees" were graphed whose "branches" represent different food items and whose frequency of occurrence is reported. The diel periodicity of mean stomach contents in over 5,000 anchoveta was used to estimate their food consumption. Feeding starts near noon and is continuous until near midnight. A ration of 0.45 g · day^{-1} (mixed phyto- and zooplankton) was estimated from anchoveta with a mean live weight of 20.4 g. This implies, given a mean total mortality of Z = 4.5 year^{-1}, a relative population consumption rate of 3.3%/day. The fraction of zooplankton in the mixed phyto- and zooplankton diet of anchoveta was found to increase with distance from the coast, southern latitude and temperature.

Resumen

En esta contribución se presentan los resultados de un primer análisis de la base de datos computarizada sobre el alimento y hábitos alimenticios de la anchoveta peruana (*Engraulis ringens*) para los años 1953 a 1982, los que además sirven como documentación (parcial) para la misma base de datos, cuyos documentos sobre una base desagregada, llegan casi a los 10,000 contenidos estomacales de anchoveta y adicional informacion. Se grafican "árboles" filogenéticos cuyas "ramas" representan los diferentes items alimentarios y cuya frecuencia de ocurrencia es reportada. La alimentación empieza cerca del medio dia y se continúa hasta cerca de la medianoche. Para estimar el consumo de alimento se utilizó la periodicidad diaria del contenido estomacal promedio de más de 5,000 anchovetas. Se estimó una ración de 0.45 g·dia^{-1} (mezcla de fito- y zooplancton) para anchovetas de un peso promedio de 20.4 g. Esto significa que, dado un promedio de mortalidad de la poblacion de Z = 4.5 año^{-1}, la tasa de consumo de la poblacion es de 3.3%/día. La fracción de zooplancton en una dieta mixta de fito- y zooplancton se incrementa con la distancia de la costa, con la latitud hacia el sur y con la temperatura.

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Introduction

This contribution presents a preliminary analysis of the food types and food consumption of the Peruvian anchoveta *(Engraulis ringens),* based on the data of Rojas de Mendiola (this vol.) and Alamo (this vol.), covering the years 1953 to 1982. No attempt will be made here to extract all information contained in the now computerized Rojas/Alamo database. Rather we aim at providing a framework for future, more detailed studies on the feeding habits of anchoveta in relation to fluctuations of the Peruvian upwelling system.

This contribution consists of three parts:

i) presentation and partial reduction of the taxonomic diversity of anchoveta food items;

ii) testing of some extant hypotheses on the spatial and temporal variations of the zooplankton fraction (ZF), i.e., the ratio zooplankton/(zooplankton + phytoplankton) in anchoveta stomach contents; and

iii) estimation of the daily ration of an "average" anchoveta and of the relative food consumption of the entire population.

Part (i) serves three purposes: (a) to illustrate the wide range and the frequency of occurrence of food items recorded from anchoveta stomachs, (b) to identify the taxonomic affinities of these food items and (c) to assign these food items to a small number of taxonomically homogeneous groups, such as needed for future quantitative analyses.

The hypotheses involved in Part (ii) are: (a) that anchoveta in the north of Peru have lower ZF values than those in the south, (b) that anchoveta sampled inshore should have a lower ZF than anchoveta sampled offshore (Vinogradov 1981), (c) that high sea surface temperatures (SST) are associated with higher ZF and (d) that anchoveta in the 1950s and 1960s had higher ZF than in the following decades (Palomares et al. 1987).

Finally, we shall present in Part (iii) the first rigorous attempt to estimate the daily ration of anchoveta based on stomach content data. Our aim here is to allow comparison with and a calibration of ration estimates based on metabolic considerations (Villavicencio 1981; Tsukayama and Sanchez 1981; Palomares et al. 1987), and eventually, to allow quantitative modelling of the transfer of primary production off Peru (Chávez et al., this vol.; Mendo et al., this vol.) to higher trophic levels.

For general orientation, we present a photo of an anchoveta (Fig. 1.) and, in Figs. 2, 3 and Table 1, some key anatomical features of anchoveta that are related to food capture and processing.

Fig. 1. Thawed, 13-cm specimen of anchoveta *Engraulis ringens* (Photo: Mark Prein).
Fig. 1. Anchoveta de 13 cm, especimen descongelado (Foto: Mark Prein).

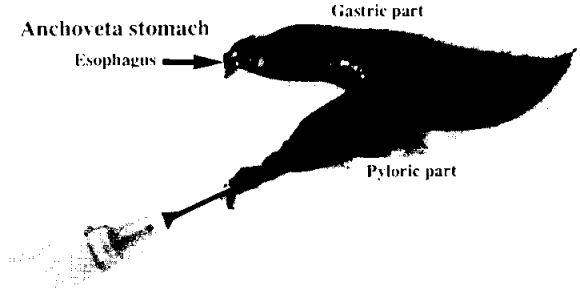

Fig. 2. Stomach of an anchoveta, slightly distended through injection of water. Note gastric and pyloric parts of the stomach (Photo: Mark Prein).
Fig. 2. Estómago de anchoveta ligeramente distendido después de inyectársele agua. Nótese la parte gástrica y pilorica del estómago. (Foto: Mark Prein).

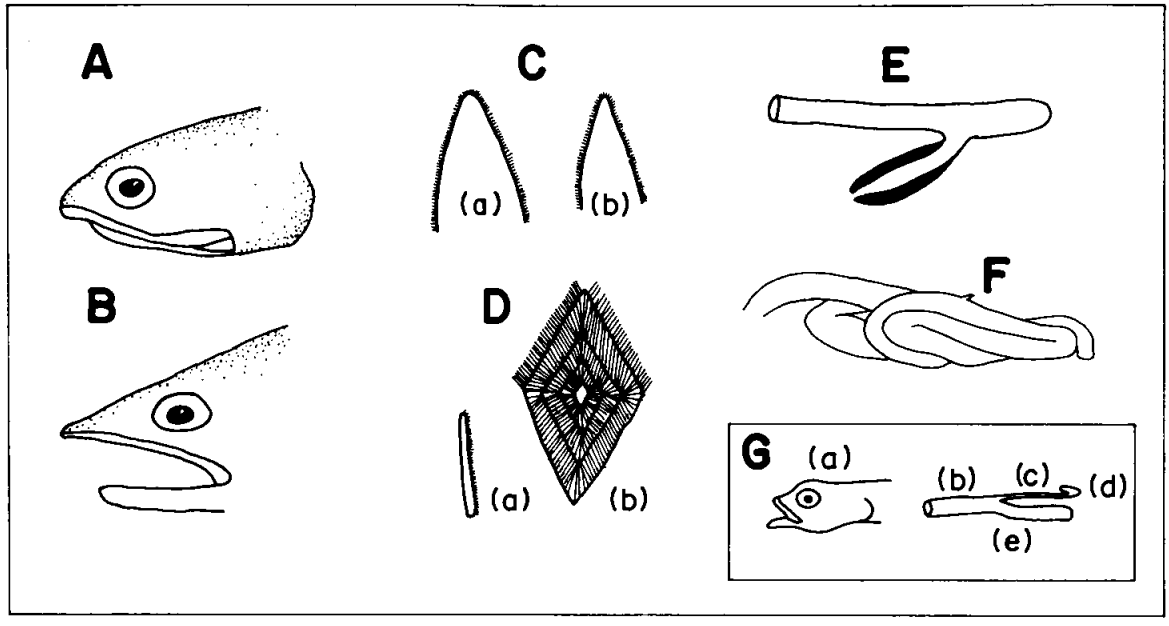

Fig. 3. Anatomical features of anchoveta related to its food and feeding habits: (A) The inferior mouth of anchoveta. (B) The same, open. (C) Villiform teeth (a) superior maxilla, (b) inferior maxilla. (D) Gill rakers (a) a single, enlarged gill raker, (b) the filtering apparatus. (E) The stomach and the thick-walled pylorus (see also Fig. 2). (F) The intestine. (G) Larval organs (a) head,(b) foregut,(c) ductus pneumaticus, (d) caudal part of gas bladder, (e) stomach. (Adapted from Vegas-Velez 1981; Harder 1957, 1960)
Fig. 3. Características anatómicas de la anchoveta relacionadas con su alimento y hábitos alimenticios: A. Boca de la anchoveta; B. la misma abierta; C. Dientes de apariencia vellosica a) maxila superior, b) maxila inferior; D. Branquispinas a) una sola branquispina ampliada, b) aparato filtrador; E. Estómago y las paredes gruesas del piloro (ver también Fig. 2); F. Intestino; G. Especimen larval a) cabeza, b) conducto alimentario, c) tubo neumático, d) parte caudal de la vejiga natatoria, e) estómago. (Adaptado de Vegas-Vélez 1981 ; Harder 1957, 1960).

Table 1. Selected information on the intestinal tract of anchoveta *Engraulis ringens*.[a]
Tabla 1. Información seleccionada sobre el tracto digestivo de la anchoveta Engraulis ringens.

Item	Measurement	Mean value	Mean in % of S.L.
Standard length	from tip of snout to end of hypural bone	108	100
Height	maximum height of fish between dorsal and ventral edge of body	20.0	18.5
Width	maximum width of fish	12.5	11.6
Visceral cavity	length of visceral cavity	43.2	40.0
"Branchial gut"	from tip of snout to begin of esophagus	30.5	28.2
"Foregut"	from begin of esophagus to begin of stomach (bulge)	16.5	15.3
Stomach	from begin of stomach to pylorus	12.0	11.1
Intestine	from pylorus to anus	125	116
All digestive tract	from tip of snout to anus	184	170

[a]Adapted from Harder (1960), based on three specimens collected near Guañape, Peru, in 1954, by staff of the Inter-American Tropical Tuna Commission; all lengths are in mm.

Materials and Methods

The data used for Part (i) of this contribution are the raw data sheets of Rojas de Mendiola (this vol.) and Alamo (this vol.), which include, for each anchoveta sampled, up to six of the most abundant food items. Each of these food items was listed, and the total number of occurrences was recorded (no distinction was made between the periods covered by the data of Rojas de Mendiola, this vol., and those of Alamo, this vol.). Then, the taxonomic affinities of each item were identified, using standard references (e.g., Bougis 1976; Mann 1978 or Barnes 1980) and phylogenetic "trees" were constructed which included only organisms recorded as anchoveta food item. Finally, fifteen groups of food items were defined, whose boundaries represent compromises between taxonomic homogeneity and the need for a roughly similar number of occurrences within each group.

Part (ii) is based on analysis of the ZF values in the Rojas/Alamo database. Fig. 4 presents the geographic distribution of entries in this database, as well as definitions for:

(a) the northern, central and southern sections of the Peruvian coast (all locations north of 9°59'S, 10°00' - 13°59'S and all locations south of 14°00'S, respectively), and

(b) the inshore, intermediate and offshore parts of the coastal strip inhabited by anchoveta.

With regard to hypotheses (c) and (d) above, the three temperature ranges selected are <17, ≥17 to ≤19.9 and ≥20°C, while the three periods considered are 1953 to 1974, 1975 to 1978 and 1979 to 1985. The cutoff points used for hypotheses (a) to (d) were selected such as to allow enough entries to be represented in each of the three groups used for the comparisons, and also such as to be consistent with an earlier subdivision (that between northern, central and southern anchoveta stock and/or substock, pertaining to hypothesis (a)). All analyses involving ZF values were performed after application of an arcsine transform, which has the effect of normalizing percentage values (Sokal and Rohlf 1981; Sachs 1984), a fact which we confirmed for the data at hand. Differences in mean transformed ZF values were tested for significance using t-tests (Sachs 1984).

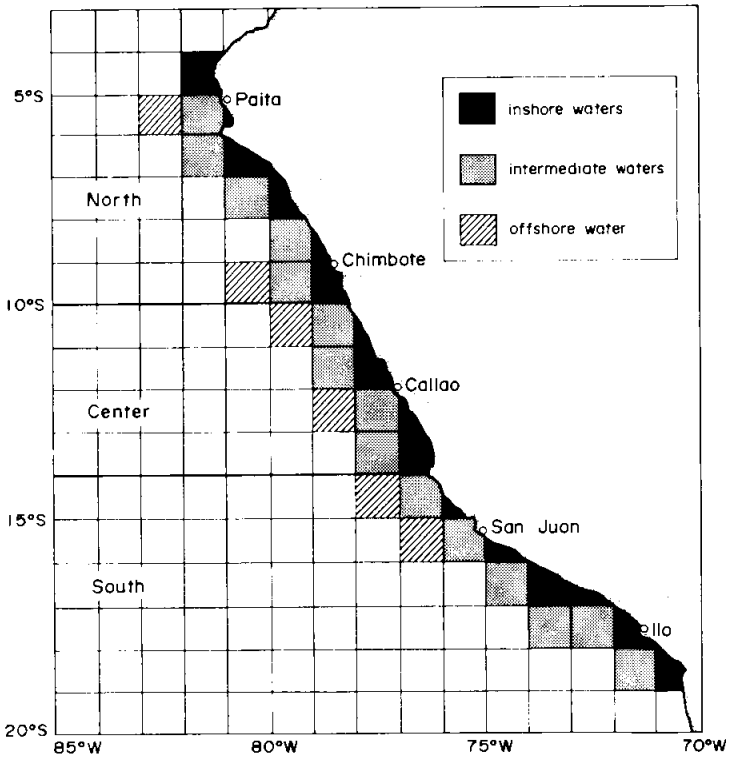

Fig. 4. Definition of the southern, central and northern zone of the Peruvian coast, and of inshore, intermediate and offshore waters as used in this contribution. All shaded squares contain anchoveta samples (see text).

Fig. 4. Delimitacion de las zonas Sur, Centro y Norte de la costa peruana; y de las aguas costeras, intermedias y afuera de la costa, como se presentan en esta contribución. De todos los cuadros sombreados se obtuvieron muestras de anchoveta (ver texto).

Part (iii) of this contribution was performed in a number of steps best presented jointly, then discussed separately in more detail:

(1) Establishment of a quantitative relationship between degrees of fullness and relative stomach content weight in those anchoveta for which both types of entries were available;

(2) Estimation of relative stomach content weight using the relationship above in all anchoveta for which only the degree of fullness was available, and transformation of absolute weight of stomach content into relative weight of stomach content in all anchoveta for which both stomach content weight and body weight were available;

(3) Computation of mean relative weight of stomach content of anchoveta caught in different parts of a 24-hour cycle; and

(4) Application of the model of Sainsbury (1986) for estimation of daily ration from the data in (3).

The scale expressing degree of stomach fullness used by Rojas de Mendiola (this vol.) and Alamo (this vol.) has four steps: "empty", "half empty", "half full" and "full". Two of these are straightforwardly reexpressed as % values: "empty" = 0% and "full" = 100%. Rojas de Mendiola's definition of "half empty" differs from that of "half full", however, and these two categories could therefore not be set equal to each other and to 50%.

We have, therefore, used an iterative approach, i.e., identified the % value for "half empty" (and hence also the % value of "half full" = 100 - half empty) which maximized the correlation between (transformed) relative stomach weight and degree of fullness. Also, we have estimated the parameter b in the relationship:

$$\sqrt{\frac{(\text{stomach content weight}) * 100}{\text{body weight}}} = b*(\%\ \text{fullness}) \qquad \text{... 1)}$$

where the square root transformation was used to normalize the variance (the corresponding linear regression had an intercept not significantly different from zero, hence the reduced form of equation (1)).

Once the optimal % values for "half empty" and "half full" and the corresponding version of equation (1) were identified, relative stomach content weights ($S_{(R)}$) were derived for all anchoveta for which only fullness values had been available and a file was created which also included $S_{(R)}$ values computed directly from weight of stomach content/body weight data pairs.

To describe a diurnal cycle of mean stomach content weights, the available $S_{(R)}$ values were then grouped into 16 classes of 1.5 h each, i.e., 00h01' - 01h30' (mid-point 00h45'), 01h31' - 03h00' (mid-point 02h15'), etc. These groupings appear optimal given the relatively low number of nighttime observations, and the need to use an appropriate number of classes, i.e., between about 12 and 20 (Sokal and Rohlf 1981).

In view of the non-normal distribution of the $S_{(R)}$ values within each temporal class, we abstained from using the arithmetic mean as a measure of central tendency. Rather, we used

$$\bar{X} \approx 0.33\ (D_1 + \tilde{X} + D_9) \qquad \text{... 2)}$$

where D_1 and D_9 are the 1st and the 9th deciles, respectively, and $\tilde{X}$ the median, i.e., the 5th decile (Sachs 1984). The corresponding estimate of standard deviation is

$$\text{s.d.} \approx 0.39\ (D_9 - D_1) \qquad \text{... 3)}$$

Standard errors (s.e.) were computed from

$$\text{s.e.} = \text{s.d.} * \sqrt{n} \qquad \text{... 4)}$$

The model used here for the estimation of food consumption (i.e., daily ration, or R_d) from the diurnal dynamics of stomach contents is the simpler of two models presented by Sainsbury (1986).

The model assumes that the 24-hour diurnal cycle can be split into two phases:

(a) a feeding phase, during which feeding occurs at a constant *rate,* while a constant *fraction* (c) of the stomach content is (simultaneously) being evacuated, and
(b) a nonfeeding phase, during which only stomach evacuation takes place.

If, for a 24-hour cycle
τ is the "physiological time," measured from the beginning of feeding period (in hour),
S_τ the mean weight of the stomach content at time τ,
α the feeding rate (in $g \cdot hour^{-1}$),
c the evacuation rate (in $hour^{-1}$),
T_m the duration (in hour) of the feeding period, and
S_r the residual stomach content at the beginning of feeding period,

then the mean weight of stomach content can be calculated as

$$S_\tau = \frac{\alpha}{c} + \frac{(cS_r - \alpha)}{c} e^{-c\tau} \qquad \text{... 5a)}$$

during feeding time when $O < \tau < T_m$, and

$$S_\tau = \left[\frac{\alpha}{c} + \frac{(cS_r - \alpha)}{c} e^{-cT_m} \right] e^{-c(\tau - T_m)} \qquad \text{... 5b)}$$

during nonfeeding time when $T_m < \tau < 24$ hours,

wherein

$$S_r = \frac{\alpha(e^{-c(24h-T_m)} - e^{-c*24h})}{c(1-e^{-c*24h})} \qquad \text{... 5c)}$$

The daily ration of food consumed is calculated as $R_d = \alpha T_m$.

Fitting of equation (5) to our data was performed after smoothing the data over three time intervals, using a BASIC program implemented on an MS-DOS computer[a], and representing a modified version of a FORTRAN listing kindly supplied by Dr. K. Sainsbury (CSIRO, Hobart, Australia, pers. comm.)

Estimation of the gross food conversion efficiency of anchoveta (K_1 = growth increment/food ingested, see Ivlev 1966) was based on the equation

$$K_1 = (dw/dt)/R_d \qquad \text{... 6)}$$

with growth increment (= growth rate) obtained from

$$dw/dt = 3KW\,((W_\infty/W)^{1/3} - 1) \qquad \text{... 7)}$$

[a] Available from the first author.

i.e., from the first derivative of the von Bertalanffy Growth Function (VBGF). The VBGF has, for growth in weight the form

$$W_t = W_\infty (1-e^{-K(t-t_0)})^3 \qquad \text{... 8)}$$

where W_t is the weight at age t
W_∞ the asymptotic weight
K a growth constant, and
t_o the "age" at weight zero.

The estimate of K_1 was then used to estimate the parameter β in the equation:

$$K_1 = 1 - (W/W_\infty)^\beta \qquad \text{... 9)}$$

through

$$\beta = \log_{10} (1 - K_1)/\log_{10} (W/W_\infty) \qquad \text{... 10)}$$

Using β and K, food consumption (Q) per unit biomass (B) of an age-structured population (Q/B) can be estimated using a simplified version of the model of Pauly (1986), of the form

$$Q/B = \frac{\int_o^\infty \frac{(dw/dt)\, e^{-Z(t-t_o)}}{K_{1(t)}}\, dt}{\int_o^\infty W_t\, e^{-Z(t-t_o)}\, dt} \qquad \text{... 11)}$$

where $K_{1(t)}$ is the gross conversion efficiency as a function of fish age (obtained by combining equations (8) and (9)), Z is the exponential rate of total mortality in the population studied, and
W_t is obtained from equation (8).

Transfer efficiency (E_t) was obtained, finally, from $E_t = Z * (B/Q)$, i.e., by multiplying the inverse of the relative food consumption by the production biomass ratio (because Z = P/B under steady-state conditions, see Allen 1971).

Results and Discussion

Figs. 5 and 6 present taxonomic "trees" of anchoveta food items listed in the raw data sheets of B. Rojas de Mendiola and A. Alamo, along with number of occurrences. Figs. 7 to 9 provide details on three important "branches" of these trees, the Protozoa (with emphasis on the dinoflagellates), the Chrysophyta (i.e., the diatoms), and the crustaceans (with emphasis on the copepods). Altogether 259 different food items were identified, from nearly 10,000 individual anchoveta, and this number would have been far greater had it not been for the fact that only the 5-6 most abundant food items were recorded from each stomach examined.

An approach is presented in Table 2 to arrange these food items into 15 more or less homogeneous groups with roughly comparable numbers of occurrences (ratio of smallest to largest = 1:27, i.e., 1.43 log units). Of these 15 groups, 14 are used for the food type fields (I-V) in the computerized database of Rojas de Mendiola (this vol.) and Alamo (this vol.). (The 15th group, i.e., anchoveta eggs, is listed separately, see below.) Table 3 gives details on the "miscellaneous items" of Table 2.

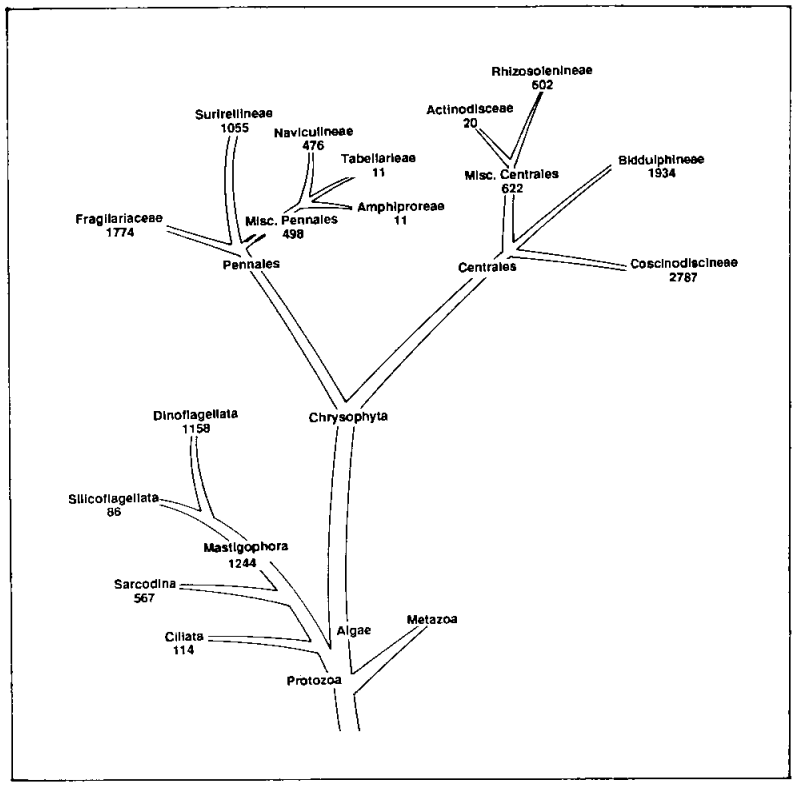

Fig. 5. Taxonomic "tree" for single cell organisms ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences; see also Fig. 6).

Fig. 5. Diagrama taxonómico (posición genealógica) de los organismos unicelulares ingeridos por la anchoveta, 1953 a 1982. (Los números indican la ocurrencia; ver también Fig. 6).

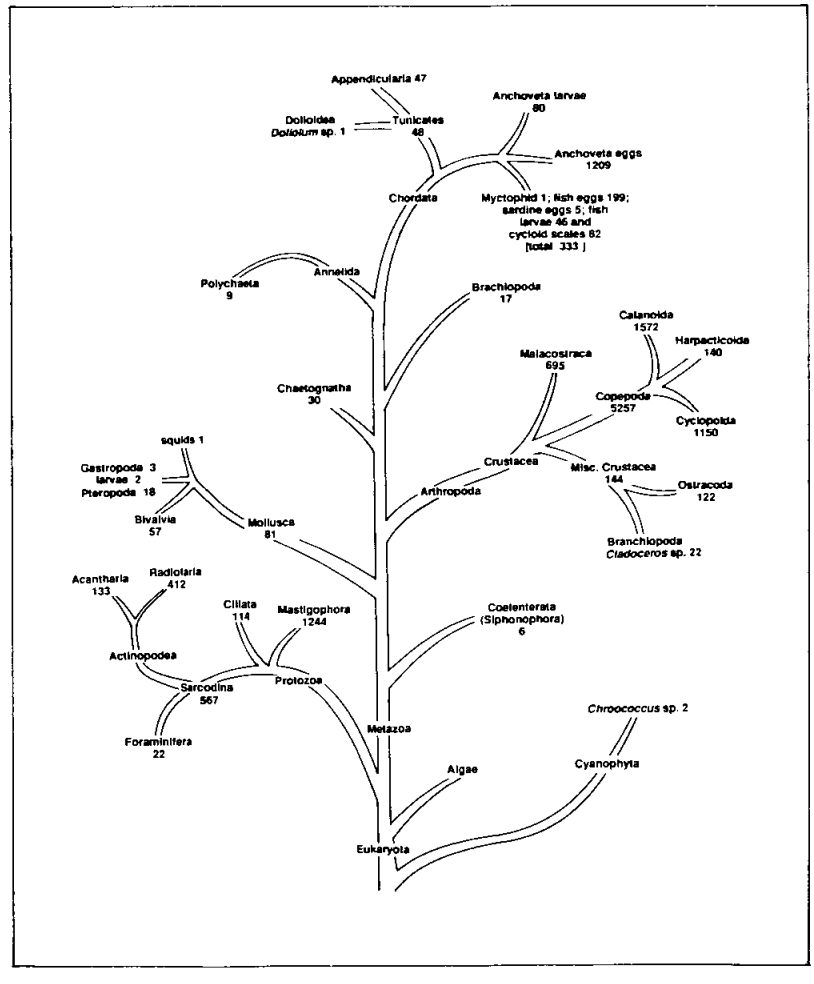

Fig. 6. Taxonomic "tree" emphasizing metazoan organisms ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences; see also Fig. 5).

Fig. 6. Diagrama taxonómico que resalta los metazoos ingeridos por la anchoveta, 1953 a 1982 (los números indican la ocurrencia, ver también Fig. 5).

Table 4 and Fig. 10 present the results of the tests of four different hypotheses relating to changes in the zooplankton fraction (ZF) in the diet of anchoveta.

These results suggest (a) that anchoveta in the northern/central part of Peru rely on zooplankton less than do their counterparts on the south of Peru, (b) that mean ZF significantly

Table 2. Taxonomic and other grouping used to describe the food of Peruvian anchoveta.
Tabla 2. Grupos taxonómicos usados para describir el alimento de la anchoveta peruana.

Group number	Taxa included	Details in	No. of occurrences[a]
1	Miscellaneous items	Table 3	485
Phytoplankton			
2	Fragilariaceae	Fig. 8	1,643
3	Surirellineae	Fig. 8	1,044
4	Misc. Pennales	Fig. 8	473
5	Coscinodiscineae	Fig. 8	3,487
6	Biddulphineae	Fig. 8	1,646
7	Misc. Centrales	Fig. 8	608
8	Mastigophora	Fig. 7	621
Zooplankton			
9	Sarcodina + Ciliata	Fig. 7	1,069
10	Misc. invertebrates[b]	Fig. 6	149
11	Malacostraca	Fig. 9	688
12	Copepoda	Fig. 9	3,998
13	Misc. crustaceans[c]	Fig. 9	285
14	Misc. chordata[d]	Fig. 6	442
15	Anchoveta eggs[e]	Fig. 6	-[e]

[a]These numbers do not match those in Figs. 6-9 because for those, the component taxa of all groups (1-15) were counted separately, as recorded on the raw data sheets of B. Rojas de Mendiola and of A. Alamo, while for this table, only group occurrences in the computerized database were counted.

[b]Including Coelenterates, Chaetognaths, Polychaetes, Mollusks and Brachiopods.

[c]Including Ostracoda and Branchiopoda.

[d]Including tunicates, small fish, anchoveta and other fish larvae, fish scales and non-anchoveta fish eggs.

[e]Not included as food item 15 in the Rojas/Alamo database; listed separately as "no. of eggs per stomach".

Table 3. Reported occurrences in anchoveta stomachs of items not attributable to any definite taxon.[a]
Tabla 3. Relación de las ocurrencias en los estómagos de anchoveta de ítems no atribuibles a un definido grupo taxonómico.

Item	Occurrences (in %)
Invertebrate eggs	24.1
Invertebrates	1.7
mucus	3.5
Unidentified material	12.8
Organic material	0.6
Plankton	1.5
Phytoplankton[b]	29.5
Zooplankton	17.5
Algae	1.7
Detritus	5.0
Fibers	0.4
Chromatophores	1.7
Total number of occurrences	485

[a]These items are listed as "miscellaneous items" in Table 2.

[b]Including 2 occurrences of Cyanophyta.

Fig. 7. Protozoan taxa ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences; see also Fig. 5).

Fig. 7. Protozoos ingeridos por la anchoveta peruana, 1953 a 1982 (los números indican la ocurrencia; ver tambien Fig. 5).

increases with offshore distance, (c) that more zooplankton is consumed when SST is high and (d) that the mean ZF values were different in the three sampling periods considered here.

Interpretation of these results is straightforward in the case of (a), (b) and (d). In the case of hypothesis (b), we have indeed a rather stunning confirmation of the process described by Vinogradov (1981) wherein a plume of upwelled water enriches itself with zooplankton as it moves "downstream" (i.e., offshore, in the case of a coastal upwelling).

Fig. 11 shows the relationship between the linearity of equation (1), expressed by means of its coefficient of determination, and different values for reexpression (in %) of "half empty" and "half full". As might be seen, 40% for half empty and 60% for half full best linearizes equation (1), given the data at hand. Fig. 12 shows the resulting plot of transformed stomach contents and fullness index.

Fig. 13 and Table 5 summarize the results of the application of Sainsbury's model I (i.e., equations 5a, 5b and 5c) to the stomach content/fullness data in the Rojas de Mendiola/Alamo database.

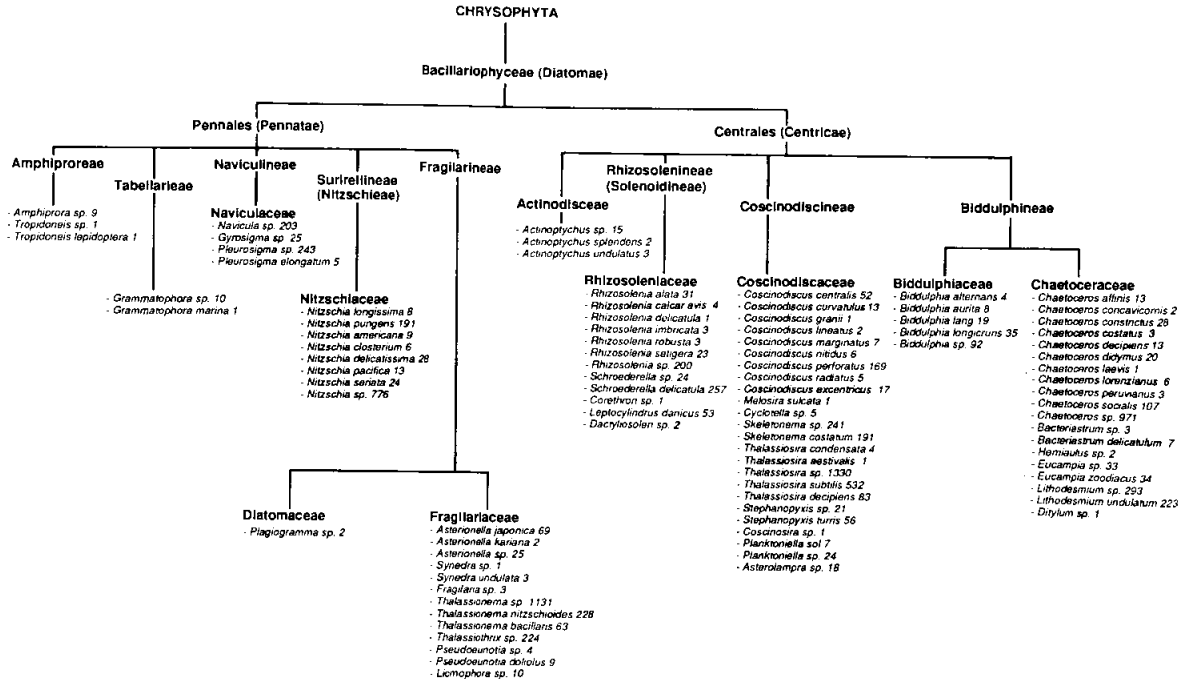

Fig. 8. Diatom species ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences, see also Fig. 5.).
Fig. 8. Especies de diatomeas ingeridas por la anchoveta peruana, 1953 a 1982 (los números indican la ocurrencia, ver también Fig. 5).

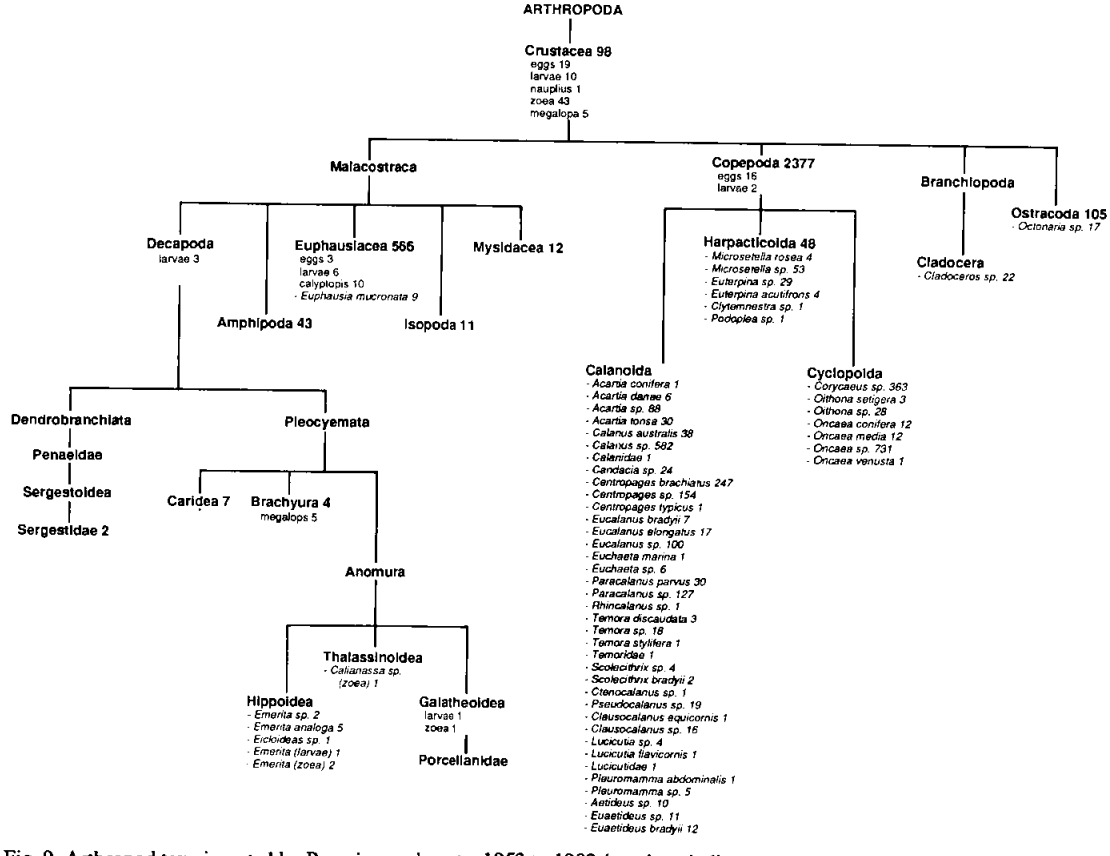

Fig. 9. Arthropod taxa ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences, see also Fig. 6).
Fig. 9. Artropodos ingeridos por la anchoveta peruana, 1953 a 1982 (los números indican la ocurrencia, ver también Fig. 6).

Table 4. Results of test of comparison of the mean zooplankton fractions in Fig. 10 (see also text).
Tabla 4. Resultados del test de comparación de los promedios de las fracciones de zooplancton de la Fig. 10 (ver también texto).

Items tested			t	Degrees of freedom	Significant? ($\alpha < 0.05$)
North/South					
<10°S	*vs.*	10-13°59'S	12.66	4,063	yes
<10°S	*vs.*	14°S	9.27	3,924	yes
10-13°59'S	*vs.*	14°S	3.32	4,487	yes
Temperature					
<17°C	*vs.*	17-19.9°C	1.56	5,296	no
<17°C	*vs.*	≥20°C	7.24	3,644	yes
17-19.9°C	*vs.*	≥20°C	8.29	3,676	yes
Time					
<1975	*vs.*	1975-1978	5.99	4,613	yes
<1975	*vs.*	1979	3.04	3,842	yes
1975-1978	*vs.*	1979	9.33	4,022	yes
Distance from shore					
Inshore	*vs.*	intermediate	4.84	6,158	yes
Inshore	*vs.*	offshore	11.32	120	yes
Intermediate	*vs.*	offshore	9.36	133	yes

Information on stomach contents and exact sampling time were available for 5,245 individual anchoveta (mean wet weight 20.4 g); their mean sampling year was 1977 and their mean stomach content (as obtained by direct weighting or through conversion) are plotted as a function of time in Fig. 13, and further statistics are given on Table 5.

Sainsbury's model fitted these data extremely well (mean sum of squared residuals = 0.008), and this led to the following parameter estimates (all converted from relative to absolute stomach content):

a = 0.0340 g·hour^{-1}, i.e., an ingestion rate of 0.034 g·hour^{-1} during the feeding period

T_f = 10.92 hours, i.e., anchoveta starts feeding at 10:55 a.m.

T_m = 12.81 hours, i.e., the feeding period is of 12.81 hours and lasts until 11:45 p.m.

and c = 0.1518 hours^{-1}, i.e., anchoveta evacuate 15.2% of their stomach content per hour.

This leads to a daily ration estimate of $R_d = 0.448$ (g · day^{-1}), and hence a relative daily food consumption (% BWD) of 2.2%.

The mean growth rate, for anchoveta of 20.4 g live weight was computed based on W_∞ = 61 g, K = 1.05 year^{-1} and $t_0 = 0$ (i.e., using estimates of L_∞, K and t_0 for 1977 in Palomares et al. 1987, and based on the conversion of L_∞ = 21 cm to W_∞ using a mean condition factor of 0.661 based on the mean of the 12 monthly values given for 1977 in Tsukayama and Palomares 1987).

The resulting growth rate was dw/dt = 0.0772 g · day^{-1} and hence

$$K_1 = 0.0772/0.448 = 0.2075$$

which leads, given equation (10) to $\beta = 0.173$.

These parameter estimates, led, when used in conjunction with Z = 4.5 year^{-1} (Pauly and Palomares, this vol.) and equation (11) to an estimate of Q/B = 3.30% (daily), i.e., the anchoveta population would consume 12.1 times its own weight per year (at a mean SST of 17.1°C).

These results correspond well with previous estimates obtained from metabolic studies. Palomares et al. (1987), based on Villavicencio (1981) and Villavicencio and Muck (1983a, 1983b, 1985), had estimated ration of adult anchoveta (in % BWD) to range between 3.50% ("1950" conditions) and 2.6% ("1980" conditions), thus bracketing our estimate of 3.30%/day.

Table 5. Data for the estimation of ration and feeding periodicity in anchoveta. (Source: Rojas/Alamo database, see text).
Tabla 5. Datos para la estimación de la ración alimenticia y periodicidad de alimentación de la anchoveta (fuente de informacion: base de datos de Rojas/Alamo, ver texto).

Time (hours)	n	Relative stomach content (% body weight)	Standard error (% body weight)	Observed stomach content[a,b] (g)	Estimated stomach content[b] (g)
0.75	50	1.32	0.133	0.191	0.1696
2.25	95	0.46	0.038	0.135	0.1351
3.75	76	0.21	0.018	0.074	0.1076
5.25	170	0.43	0.034	0.063	0.0857
6.75	484	0.29	0.013	0.068	0.0682
8.25	832	0.28	0.010	0.067	0.0543
9.75	773	0.41	0.015	0.074	0.0433
11.25	694	0.40	0.014	0.067	0.0516
12.75	379	0.17	0.003	0.051	0.0867
14.25	369	0.17	0.005	0.099	0.1146
15.75	373	1.11	0.054	0.177	0.1369
17.25	353	0.88	0.041	0.181	0.1546
18.75	216	0.68	0.025	0.173	0.1687
20.25	241	0.99	0.056	0.152	0.1799
21.75	53	0.57	0.076	0.177	0.1889
23.25	87	1.04	0.101	0.199	0.1960
Total	1,948			Mean 0.12175	

[a]Refers to an average body weight of 20.37 g calculated from 1,948 individual anchoveta and to a running average over three time intervals.
[b]See Fig. 13.

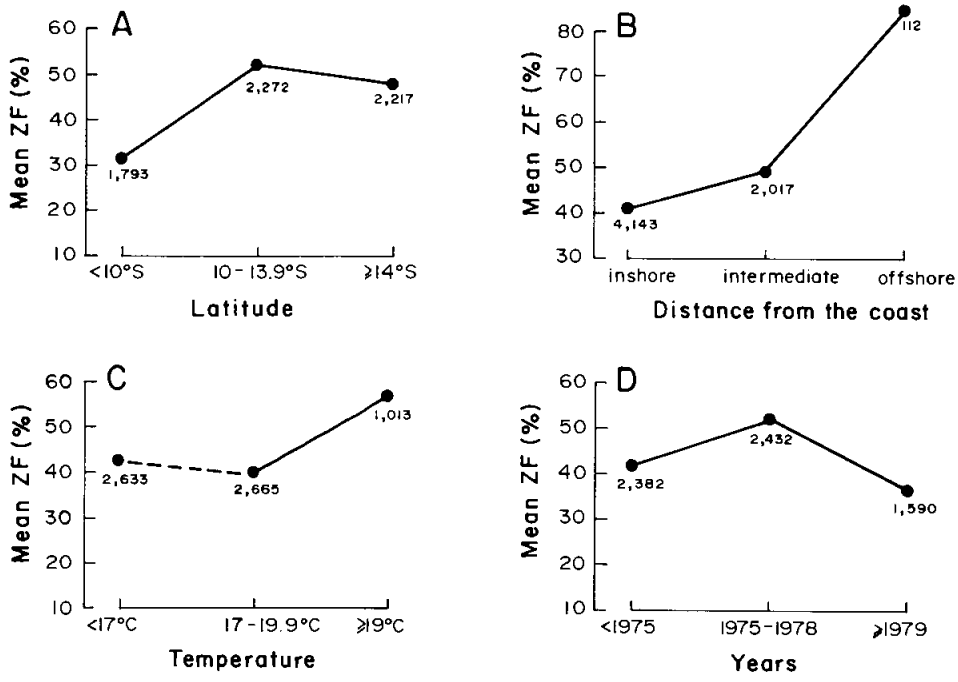

Fig. 10. Trends in zooplankton fraction (ZF) of anchoveta diet off Peru. The solid lines illustrate significant changes ($P < 0.05$), while the dotted line links means that are not significantly different; the number of observations are given under each mean.
Fig. 10. Tendencias de la fraccion de zooplanton (ZF) en la dieta de la anchoveta en la costa peruana. La línea sólida muestra cambios significantes ($P < 0.05$), mientras que la linea entrecortada une promedios que no son significativamente diferentes; el número de observaciones se anotan debajo del promedio.

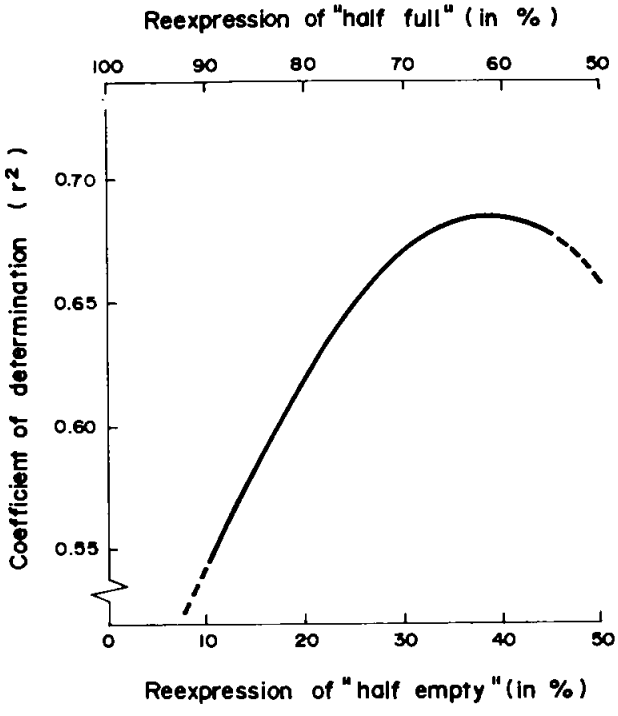

Fig. 11. Relationship between linearity of equation (1) - as expressed by the coefficient of determination - and different % values for the quantitative reexpression of "half empty" and "half full" as fullness indices of anchoveta stomach (see text and Rojas de Mendiola, this vol.).

Fig. 11. Relación entre la linearilidad de la ecuación (1) - expresada por el coeficiente de determinación - y los diferentes valores porcentuales para la reexpresión cuantitativa de "semivacío" y "semilleno", como índice de llenura del estómago (contenido estomacal) de anchoveta (ver texto y Rojas de Mendiola, este vol.).

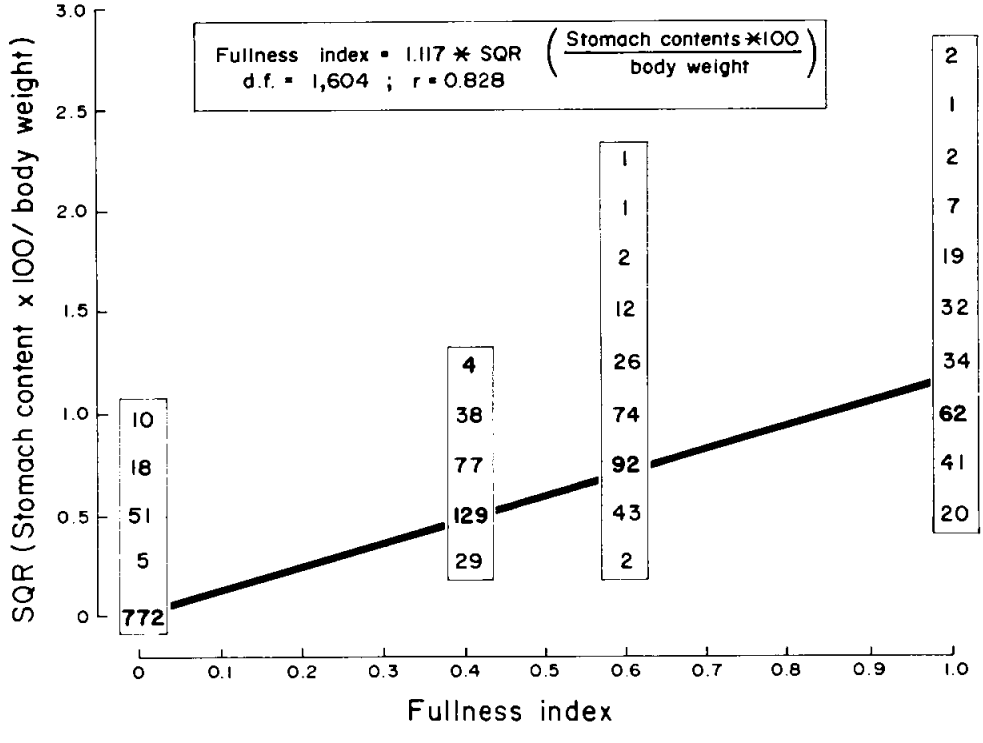

Fig. 12. Relationship between transformed stomach contents and their fullness index in 1,604 anchoveta for which pairs of values were available. Note linearity of relationship achieved by reexpression of "half empty" as 0.4 and "half full" as 0.6 (see text and Rojas de Mendiola, this vol.).

Fig. 12. Relación entre los contenidos estomacales transformados y su índice de llenura en 1,604 anchovetas en las que estuvieron disponibles pares de valores. Notese la linearilidad de la relacion obtenida para la reexpresión de "semivacío" como 0.4 y para "semilleno" como 0.6 (ver texto y Rojas de Mendiola, este vol.).

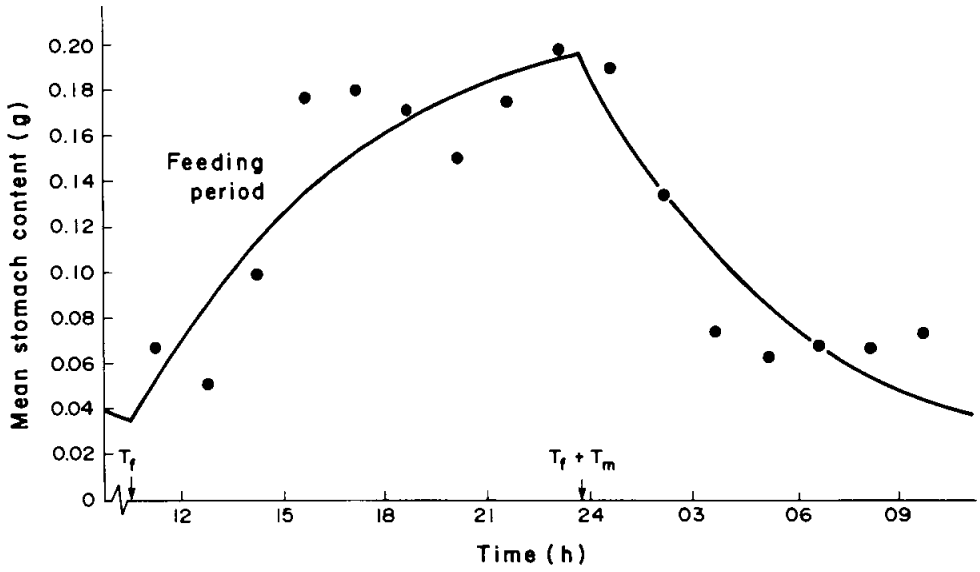

Fig. 13. Dynamics of stomach contents in Peruvian anchoveta, 1953 to 1982 (n = 5,245). Note marked diurnal feeding cycle, with shape consistent with Sainsbury's (1986) feeding model (see also Table 5 and text).
Fig. 13. Dinámica (cambios) del contenido estomacal de la anchoveta peruana, 1953 a 1982 (n = 5245). Notese un marcado ciclo diurno de alimentación, compatible con el modelo de alimentación de Sainsbury (1986) (ver también Tabla 5 y texto).

Tsukayama and Sanchez (1981), based on Villavicencio (1981), and on experiments in which they fed fish flesh to anchoveta, estimated a daily consumption of 4% BWD for anchoveta of 10 g.

Cushing (1978) suggested that "the daily ration as percentage of body weight for a fish as small as the anchoveta is likely to be nearer 5% than 1%. If the mean length were 12.5 cm, a reasonable daily ration would be equal to 0.66 ml, which is 10 times the weight of algae in the guts".

Equations (6) to (11), applied to Cushing's estimate of ration for 12.5 cm anchoveta (i.e., of 13 g), and assuming 1 ml = 1 g, the same growth and mortality as used above, leads to Q/B = 6.34%/day. This is markedly higher than our estimate of 3.30%, and also higher than the estimate of 2.6 to 3.5% reported in Palomares et al. (1987). However, these lower estimates are based on mixed zoo- and phytoplankton diet (mean ZF for data used to estimate R_d = 49.6%, see Villavicencio and Muck (1983a, 1983b, 1985)). If one assumed, with Brett and Groves (1979), that zooplankton provides about four times more net energy than the pure phytoplankton diet considered by Cushing (1978), one can estimate as Q/B = 3.95%/day value, had he considered an equal proportion of zoo- and phytoplankton in the diet of anchoveta. This is close enough to our estimate, considering that it actually was a "guesstimate".

Our value of E_t = 0.373 is, on the other hand, higher than the previously estimated "growth efficiency of 0.093 ("1950") to 0.239 ("1980", see Palomares et al. 1987), and also higher than the range of 0.10-0.20 used by Chavez et al. (this vol.). However, this high value is in line with Muck (this vol.) who suggests that anchoveta has a higher growth (i.e., trophic) efficiency than sardine, for which values of up to 0.185 have been proposed (Lasker 1973).

References

Allen, K.R. 1971. Relation between production and biomass. J. Fish. Res. Board Can. 28:1573-1581.
Barnes, R.D. 1980. Invertebrate zoology. Holt-Saunders, Philadelphia.
Bougis, P., Editor. 1976. Marine plankton ecology. Elsevier North Holland, Amsterdam.
Brett, J.R. and T.D. Groves. 1979. Physiological energetics, p. 279-352. *In* W.S. Hoar, D.J. Randall and J.R. Brett (eds.) Fish physiology. Vol. III. Bioenergetics and growth. Academic Press, New York.
Cushing, D.H. 1978. Upper trophic levels in upwelling areas, p. 101-110. *In* R. Boje and M. Tomczak (eds.) Upwelling ecosystems. Springer Verlag, Berlin.

Harder, W. 1957. Die Darmlänge bei Clupeoiden von Fundorten verschiedener geographischer Breite. Ann. Biol. 33(3/4):171-178.

Harder, W. 1960. Verleichende Untersuchungen zur Morphologie des Darmes bei Clupeoidea. Z. Wiss. Zool. 163(1/2):65-167.

Ivlev, V.S. 1966. The biological productivity of waters. J. Fish. Res. Board, Can. 23(11):1727-1759. (W.E. Ricker, transl.)

Lasker, R. 1973. Utilization of zooplankton by a Pacific sardine population in the California current, p. 265-284. *In* J.H. Steele (ed.) Marine food chains. Oliver & Boyd, Edinburgh.

Mann, A. 1978. Report on the diatoms of the Albatross voyage in the Pacific Ocean, 1888-1904. Lubrecht and Cramer, New York.

Palomares, M.L., P. Muck, J. Mendo, E. Chúman de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1982, p. 109-141. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. U.S. Fish. Bull. 84(4):827-840.

Sachs, L. 1984. Angewandte Statistik: Anwendung statistischer Methoden. Springer Verlag, Berlin.

Sainsbury, K.J. 1986. Estimation of food consumption from field observation of fish feeding cycles. J. Fish Biol. 29:23-36.

Sokal, R.L. and F.J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. Second Edition. W.H. Freeman and Company, San Francisco.

Tsukayama, I. and D. Palomares. 1987. Monthly catch and catch composition of Peruvian anchoveta *(Engraulis ringens)* (northern-central stock, (4-14°S), 1953 to 1982, p. 89-108. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Tsukayama, I. and G. Sánchez. 1981. Estimado de consumo de alimento en anchovetas adultas. Bol. Inst. Mar Perú-Callao (ICANE) Volumen Extraordinario, p. 254-263.

Vegas-Vélez, M. 1981. Los filtradores en la cadena alimenticia del mar Peruano. Boletín de Lima 13:1-8.

Villavicencio, Z. 1981. Investigación preliminar de lo requerimientos energéticos de anchoveta adulta (metabolismo estandar y actividad). Bol. Inst. Mar Perú-Callao (ICANE) Volumen Extraordinario, p. 193-205.

Villavicencio, Z. and P. Muck. 1983a. Costos metabolicos de *Engraulis ringens* y *Sardinops sagax* en relación al peso, temperatura y nivel de actividad. Bol. Inst. Mar Perú-Callao 7(3):49-68.

Villavicencio, Z. and P. Muck. 1983b. La ración de mantenimiento y la eficiencia de crecimiento de *Engraulis ringens* y *Sardinops sagax* como una medida de su potencia ecológica. Bol. Inst. Mar Perú-Callao 7(4):69-108.

Villavicencio, Z. and P. Muck. 1985. La importancia del cambio de la temperatura y de la biomasa planctónica para la producción y mortalidad de anchoveta (*Engraulis ringens*) y sardina *(Sardinops sagax)*, p. 119-218. *In* W. Amtz, A. Landa, J. Tarazona (eds.) El Niño: su impacto en la fauna marina. Bol. Inst. Mar. Perú-Callao, Volumen Extraordinario.

Vinogradov, M.E. 1981. Ecosystem of equatorial upwellings, p. 69-93. *In* A.R. Longhurst (ed.) Analysis of marine ecosystem. Academic Press, London.

Dynamics of the Fat Content of Peruvian Anchoveta *(Engraulis ringens)*

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TSUKAYAMA, I. 1989. Dynamics of the fat content of Peruvian anchoveta *(Engraulis ringens)*, p. 125-131. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Monthly mean fat content data of adult Peruvian anchoveta (*Engraulis ringens*) sampled off Chimbote and Callao, Peru during 1964 to 1986 are presented. The observed seasonal and inter-year fluctuations of fat content are related to the condition factor of anchoveta and to sea surface temperatures.

Resumen

Se presentan datos mensuales del contenido de grasa en ejemplares adultos de la anchoveta peruana (*Engraulis ringens*) de las localidades de Chimbote y Callao, Perú, durante 1964-1986. Se analizan las variaciones estacionales e interanuales en relación con las variaciones de la temperatura superficial del mar y el factor de condición.

Introduction

Numerous monthly time series, covering both oceanographic and biological factors were presented in the volume edited by Pauly and Tsukayama (1987) as part of a multidisciplinary effort to identify the factors which determine the recruitment of the Peruvian anchoveta *(Engraulis ringens)*.

The opportunity is taken here to add to this database a time series of monthly fat content data, representing one of the factors likely to impact on reproduction, and hence on recruitment (Pauly 1987).

The literature on bioenergetics makes abundantly clear that somatic growth, gonad maturation and reproduction occur only when the energy intake of fish exceeds their maintenance requirements (Hoar 1969; Philipps 1969; Brett 1979; Ware 1980). In adult fish, however, when maturity is attained, growth is reduced, and the bulk of the energy intake is used to build a fat reserve, which is subsequently used to form gametes. These processes are strongly influenced by environmental conditions, notably positive temperature anomalies, which increase routine metabolism. This is illustrated here by the results of studies on adult *Engraulis ringens* which show that at 15°C the maintenance ration is 2.3% body weights per day (%BWD), but increases to 5% BWD at 23°C (Tsukayama and Sánchez 1981; Villavicencio and Muck 1985).

Thus, studies of fat content dynamics, and more precisely, a model to predict the fat content of anchoveta from environmental and other data would be useful to unravel the population dynamics of anchoveta. The present contribution is an attempt to derive such predictive model.

Materials and Methods

The fat content data used for the present contribution stem from four sources:

i) the report of Lam (1968) for the years 1968 to 1972,
ii) from field stations ("*Laboratorios Costeros*") of IMARPE for the years 1968 to 1976,
iii) from the archives of the state fishing enterprise PESCAPERU and from various EUREKA cruises for the years 1977 to 1986.
iv) some of the data of Alamo (this vol.) on visceral fat stages of anchoveta for the years 1974 to 1982 were also analyzed, with emphasis on their relationship to the percentage fat content data which form the bulk of the present contribution.

The time series reconstructed from the data in (i) to (iii) has some noticeable gaps. Some of these could have been filled by pooling the data from Chimbote (9°05'S) and Callao (12°00'S), but this was not done, due to clear differences in the fat content of anchoveta from these two sampling sites (see below).

The fat content data presented here refer to either of three size groups:

i) anchoveta of 12 to 14 cm TL
ii) anchoveta ≥ 14 cm TL
iii) "average" adult anchoveta, i.e., the mean of the values in (i) and (ii).

The available fat content data, averaged on a monthly basis were plotted against time and other variables with which they could be expected to correlate. Following a suggestion of D. Pauly (pers. comm.) a multivariate model was also derived for prediction of fat content given the condition factor (c.f.) of anchoveta (c.f. = $W \cdot 100/L^3$; TL in cm, weight in g), SST anomaly (in °C) a dummy variable (loc.) expressing the sampling location (Callao = 0, Chimbote = 1), and 11 additional dummy variables expressing the month of the year (only 11 such variables are needed, i.e., when all are set at zero, the 12th month is implied).

This model had the form:

$$\%\ \text{fat cont.} = a + b1(\text{c.f.}) + b2\ (\text{temp.anom.}) + b3\ (\text{loc.}) + b_{4\text{-}15}\ (\text{month}) \qquad ...1)$$

and was fitted using the multiple regression option of the Lotus 1-2-3 spreadsheet program.

Of the data of Alamo (this vol.) only 1,381 individual records were used (23% of the total file), pertaining to anchoveta > 12 cm LT ("adult anchoveta") and stemming from 8°00' to 9°59'S ("Chimbote") and 11°00' to 12°59'S ("Callao").

The mean monthly SST data used here for Chimbote and Callao are reproduced here as Tables 1 and 2. The c.f. data stem from Tsukayama and Palomares (1987); only actual values were used, i.e., values estimated from SST were not included in the analyses.

Results and Discussion

Tables 3 and 4 present the available monthly time series of fat content of adult anchoveta for Chimbote and Callao, respectively. A subset of these data, pertaining to the years 1964-1976 only, is presented as Figs. 1 and 2 in the form of averaged seasonal patterns. As might be seen from these figures, anchoveta caught off Chimbote have a higher fat content than those caught off Callao, particularly from April to June.

Fig. 3 depicts the seasonal trend of fat content of anchoveta expressed by the data of Alamo (this vol.). As might be seen, this trend is roughly similar to those in Figs. 1 and 2.

The basic similarity between the data in Tables 3 and 4 and those of Alamo (this vol.) is also illustrated by Fig. 4, which allowed derivation of the empirical relationship

$$\log_{10}(\%\text{fat content}) = 1.28 + 2.21 \log_{10}(\text{c.f.}) \qquad ...2)$$

Fig. 5 illustrates the positive relationship between the condition factor of anchoveta and its fat content. This relationship is also expressed by

$$\log_{10}(\%\ \text{fat content}) = 1.28 + 2.21 \log_{10}(\text{c.f.}) \qquad ...3)$$

which, with $r = 0.426$ and d.f. 206, is significant ($P < 0.01$).

Table 1. Mean monthly sea surface temperature off Chimbote, Peru (9°05'S, 78°31'W); °Celsius. (Data courtesy of Dr. P. Lagos).
Tabla 1. Promedios mensuales de temperatura superficial del mar frente a Chimbote, Peru (9°05'S, 78°31'W); °Celsius. (Datos cortesía de Dr. P. Lagos).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1956	20.2	20.6	22.0	19.7	18.8	18.8	17.9	17.7	17.1	17.4	18.3	18.2
1957	18.8	23.2	23.8	23.0	23.5	21.9	21.8	20.2	19.1	19.4	19.6	22.2
1958	24.0	21.2	23.9	22.1	19.6	19.2	19.3	17.7	18.5	19.1	19.5	19.5
1959	23.0	23.1	21.5	21.1	19.1	19.7	18.0	17.9	18.6	20.8	19.6	24.0
1960	20.7	22.2	21.0	19.8	18.7	17.5	17.3	17.7	17.6	18.0	18.4	19.3
1961	19.9	21.8	21.0	20.5	19.4	18.8	17.0	17.6	17.3	17.4	17.9	18.7
1962	19.8	21.7	21.0	20.2	20.0	17.9	17.1	17.1	17.5	17.1	17.9	18.1
1963	18.6	19.1	20.1	19.3	18.9	18.2	17.8	17.5	18.2	18.5	18.5	19.8
1964	20.1	21.3	21.8	19.3	17.5	16.6	16.6	16.9	17.3	17.6	17.7	17.7
1965	18.8	20.5	20.5	21.1	21.0	20.5	20.7	18.8	18.6	18.6	18.9	19.5
1966	21.5	22.5	22.0	21.5	20.0	18.0	17.0	16.0	15.0	16.4	18.0	20.1
1967	21.8	23.6	21.6	18.2	17.1	14.3	15.6	14.6	16.0	14.8	15.6	17.6
1968	18.6	18.6	20.3	19.0	17.2	15.4	14.8	14.7	16.0	16.6	15.8	17.0
1969	18.8	18.5	19.6	20.1	21.0	20.3	17.9	18.0	18.1	17.8	16.2	17.2
1970	19.8	21.9	22.2	22.0	21.9	20.6	19.4	19.0	19.2	19.3	19.5	19.4
1971	19.3	19.4	20.3	21.7	21.5	21.0	21.3	21.6	20.4	18.8	18.1	18.7
1972	19.4	19.6	20.1	21.6	21.7	22.1	22.2	21.1	19.5	19.6	19.5	20.7
1973	24.6	24.7	22.2	19.0	18.4	17.0	16.1	15.9	17.0	16.6	19.2	17.9
1974	19.3	20.2	20.5	20.9	20.2	20.2	18.5	17.9	17.1	17.5	18.6	18.8
1975	20.5	21.0	24.2	21.2	21.1	18.7	17.6	17.0	16.8	17.0	17.3	18.8
1976	19.2	21.7	23.5	21.3	21.0	20.3	19.5	19.9	19.1	19.4	20.1	22.7
1977	23.3	23.4	23.5	21.9	20.8	18.6	18.7	18.1	18.6	19.0	19.3	18.5
1978	19.9	22.1	22.5	20.8	19.0	17.4	17.9	17.4	17.7	18.1	19.4	19.4
1979	22.4	21.3	21.5	21.6	19.9	18.1	18.8	18.8	18.7	19.1	19.9	20.9
1980	21.4	21.7	22.3	21.5	20.9	20.3	19.8	18.6	18.6	19.1	19.7	20.9
1981	21.1	22.3	20.8	21.3	21.3	19.3	18.1	18.4	18.1	19.0	19.3	19.3
1982	19.4	19.6	20.0	20.4	19.4	19.7	19.2	19.0	19.9	20.8	23.4	26.1
1983	28.5	28.2	-	-	-	-	-	-	-	-	-	-
Means	20.81	21.61	21.62	20.74	19.96	18.90	18.37	17.97	17.99	18.25	18.71	19.67

Table 2. Mean monthly sea surface temperature off Callao, Peru (12°00'S, 77°07'W); °Celsius. (Data courtesy of Dr. P. Lagos).
Tabla 2. Promedios mensuales de temperatura superficial del mar frente a Callao, Perú (12°00'S, 77°07'W); °Celsius. (Datos cortesía de Dr. P. Lagos).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1956	17.0	17.5	18.2	18.0	16.7	16.5	16.1	15.8	15.4	14.9	15.2	15.5
1957	15.9	19.1	20.2	20.0	20.4	19.9	19.0	17.5	16.5	16.6	16.1	18.4
1958	19.9	21.0	20.0	18.9	18.1	17.0	17.1	15.9	15.5	15.4	16.4	15.7
1959	15.8	18.4	18.8	18.1	17.7	16.5	16.0	15.5	15.2	15.2	15.7	15.6
1960	16.7	17.2	17.6	16.9	16.2	16.1	15.6	15.6	15.4	15.1	15.2	15.8
1961	16.2	17.6	17.9	17.1	17.2	15.9	15.6	15.7	15.5	15.4	15.1	15.3
1962	16.8	17.8	16.5	16.1	15.7	16.3	16.0	15.6	15.5	15.4	15.2	15.7
1963	15.6	15.3	18.1	17.3	17.1	17.3	16.9	16.5	16.2	15.6	15.9	15.8
1964	17.3	18.2	17.3	16.7	15.8	14.7	13.5	14.7	14.6	14.3	14.5	14.9
1965	15.4	16.5	19.9	19.6	18.6	18.6	17.8	18.0	16.4	15.9	16.6	17.4
1966	17.9	18.1	17.6	16.5	16.1	15.9	15.6	15.1	14.8	14.9	14.8	14.4
1967	15.6	15.5	17.0	17.0	17.0	15.5	15.3	14.0	14.3	14.0	14.1	14.6
1968	15.3	15.4	17.6	15.5	14.9	14.6	14.6	15.0	15.1	15.1	15.4	16.4
1969	17.8	19.4	20.5	19.0	20.8	18.2	16.7	17.6	16.7	16.9	18.0	17.7
1970	16.7	16.9	16.8	16.1	15.8	15.3	14.9	14.5	14.4	14.7	14.1	14.7
1971	15.5	16.3	15.1	16.0	16.3	15.8	15.6	15.5	15.3	14.8	14.8	15.3
1972	16.0	17.6	19.5	19.4	19.7	19.4	19.3	18.8	18.2	17.4	18.2	19.0
1973	21.1	20.5	19.0	16.6	16.2	15.1	15.2	14.4	14.4	14.4	14.4	14.8
1974	15.3	15.8	16.7	16.7	17.3	16.9	16.3	15.5	14.7	14.6	15.6	14.9
1975	15.3	15.6	18.6	17.6	16.6	15.1	15.2	14.6	14.3	13.8	14.7	14.9
1976	14.8	16.8	18.4	18.2	18.5	18.9	18.0	18.6	15.8	16.6	16.9	18.2
1977	17.8	18.3	18.1	18.7	18.3	16.5	16.4	16.0	15.6	15.2	16.0	16.4
1978	16.2	17.7	18.6	19.0	16.4	15.5	15.5	15.1	14.7	15.1	15.5	16.2
1979	17.0	17.7	19.4	17.9	17.6	16.2	16.1	16.1	15.8	15.4	15.7	17.2
1980	16.3	16.9	18.9	18.6	17.3	16.7	16.4	15.6	15.3	14.7	15.7	15.6
1981	15.5	16.6	15.7	16.9	17.6	16.7	15.7	15.4	14.1	14.9	15.4	15.5
1982	15.6	16.6	17.3	16.9	17.5	17.3	17.1	16.6	16.7	17.4	19.1	21.4
1983	23.7	23.8	24.0	24.2	23.8	24.0	19.7	-	-	-	-	-
Means	16.79	17.65	18.33	17.84	17.54	16.87	16.33	15.90	15.42	15.32	15.71	16.20

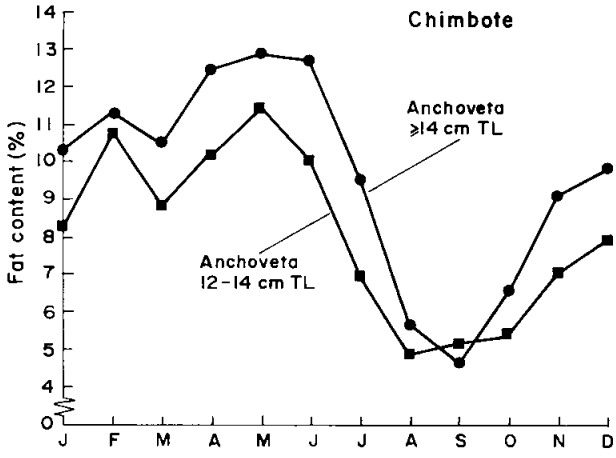

Fig. 1. Monthly changes of fat content of anchoveta off Chimbote, Peru (based on data for 1964-1976 in Table 3).
Fig. 1. Cambios mensuales en el contenido de grasa de anchoveta frente a Chimbote, Perú (basado en datos de 1964-1976 de la Tabla 3).

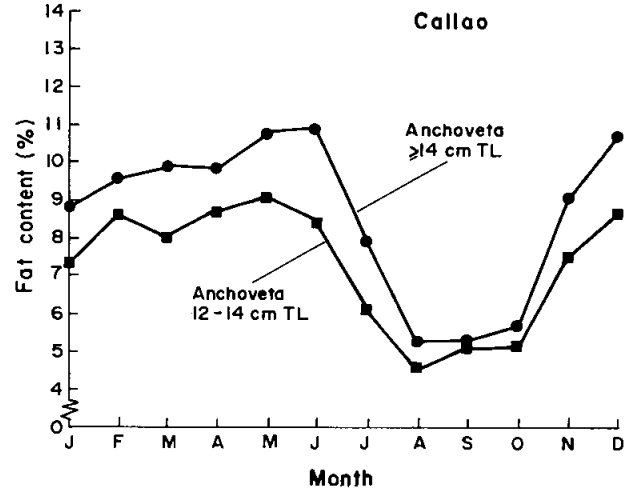

Fig. 2. Monthly changes of fat content of anchoveta off Callao, Peru (based on data for 1964-1976 in Table 4).
Fig. 2. Cambios mensuales en el contenido de grasa de anchoveta frente a Callao, Perú (basado en datos de 1964-1976 de la Tabla 4).

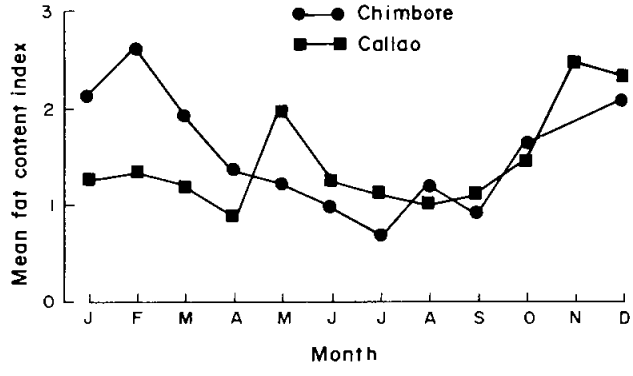

Fig. 3. Monthly changes of visceral fat index of Peruvian anchoveta based on data for 1974-1985 in Alamo (this vol.).
Fig. 3. Cambios mensuales del índice de grasa visceral de la anchoveta peruana (basado en datos de 1974-1985 de Alamo, este vol.)

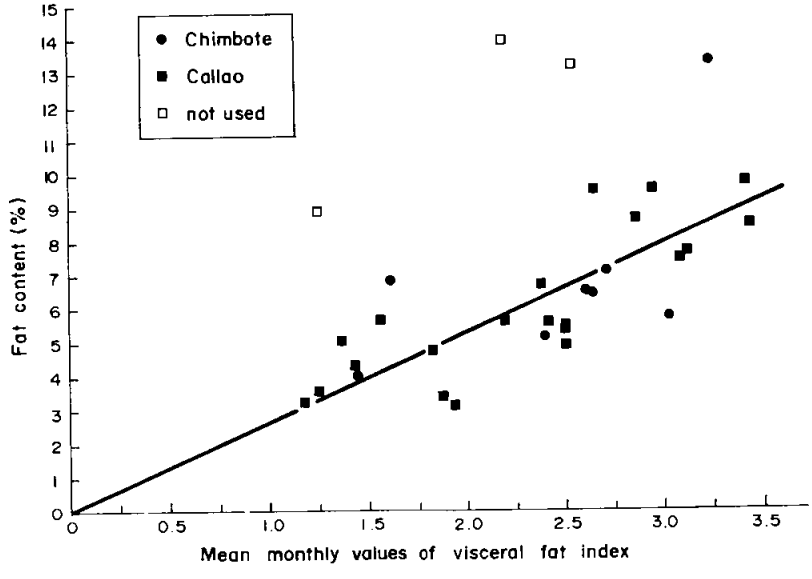

Fig. 4. Relationship between % fat content data in Tables 3 and 4 and mean monthly visceral fat index values extracted from data in Alamo (this vol.).
Fig. 4. Relación entre el % del contenido graso de las Tablas 3 y 4, y los promedios mensuales del índice de grasa visceral extraido de los datos de Alamo (este vol.).

Table 3. Monthly values of fat content (%) of Peruvian anchoveta (*Engraulis ringens*), Chimbote, 1964-1986; adult specimens with sizes ≥12 cm T.L.

Tabla 3. Valores mensuales del contenido de grasa (%) de la anchoveta peruana (Engraulis ringens), *Chimbote 1964-1986; ejemplares adultos con tallas ≥12 cm L.T.*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1964	6.55	6.10	6.34	14.23	15.53	13.13	13.27	9.99	4.40	6.38	8.81	10.13
1965	13.55	-	8.18	7.84	7.40	8.24	6.65	-	3.45	.94	4.98	5.68
1966	7.04	9.11	10.34	12.64	17.17	-	7.40	7.50	4.30	6.29	-	12.63
1967	13.23	-	7.15	9.20	10.84	12.65	7.64	5.86	5.10	8.65	9.70	12.72
1968	11.07	12.10	12.13	12.68	11.22	-	-	-	5.22	5.27	7.50	8.43
1969	12.80	-	9.52	11.88	11.94	-	-	-	-	3.20	6.90	9.30
1970	-	-	-	10.10	13.35	-	-	-	7.62	10.45	-	-
1971	-	-	10.75	9.05	8.80	7.10	-	-	8.20	9.40	16.60	18.80
1972	-	-	14.50	12.90	7.10	4.80	3.00	2.41	3.24	4.19	-	-
1973	5.53	-	-	-	-	-	-	4.98	6.32	-	7.74	-
1974	10.54	-	9.55	-	6.14	-	-	2.61	-	-	10.37	-
1975	-	11.88	-	8.58	10.52	-	-	4.00	5.16	8.60	-	-
1976	6.41	-	-	-	-	-	-	1.45	-	-	-	-
1977	-	-	-	5.71	-	-	-	-	-	-	-	-
1978	-	-	-	-	-	-	-	-	-	-	-	-
1979	-	-	7.11	-	-	-	-	-	-	2.82	4.73	-
1980	-	-	-	-	-	-	-	-	-	-	-	12.27
1981	-	-	-	5.74	4.17	4.58	-	-	-	6.50	9.13	10.80
1982	-	13.30	13.30	13.00	13.66	13.29	-	-	6.81	4.97	3.19	3.20
1983	2.60	2.70	-	-	-	-	-	-	-	-	-	-
1984	-	-	-	-	-	-	-	-	-	-	-	-
1985	-	-	-	-	-	-	-	8.40	7.60	7.10	7.20	7.60
1986	10.70	11.60	10.70	13.30	-	-	-	7.90	6.40	6.30	-	-

Table 4. Monthly values of fat content (%) of Peruvian anchoveta (*Engraulis ringens*), Callao, 1964-1983; adult specimens with sizes ≥12 cm T.L.

Tabla 4. Valores mensuales del contenido de grasa (%) de la anchoveta peruana (Engraulis ringens), *Callao 1964-1983; ejemplares adultos ≥12 cm L.T.*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1964	8.14	5.64	6.82	8.35	9.34	11.55	6.67	4.85	4.00	7.31	5.91	7.03
1965	4.67	8.14	7.79	8.03	7.59	7.48	6.54	3.92	3.08	4.95	6.73	7.98
1966	5.02	6.75	8.26	9.84	12.61	13.02	9.90	6.47	5.28	5.95	8.17	10.54
1967	7.05	6.54	7.67	8.15	9.68	8.93	7.39	8.40	4.64	6.14	8.09	10.89
1968	9.20	9.43	9.08	11.43	11.31	11.21	8.20	5.56	3.97	3.97	5.58	7.99
1969	4.25	7.62	8.81	10.48	11.79	7.60	6.52	4.92	3.93	4.14	7.21	10.87
1970	11.03	7.90	10.95	10.42	10.73	11.98	7.88	5.96	5.95	5.80	10.17	11.53
1971	8.93	9.46	9.85	9.32	9.53	9.75	7.40	5.16	6.02	7.15	12.38	14.05
1972	14.09	15.71	15.91	12.24	-	7.70	4.61	2.56	3.35	5.71	-	-
1973	5.59	4.43	6.91	8.51	-	-	-	6.52	5.95	-	8.57	-
1974	13.48	12.89	11.47	-	8.71	-	-	4.21	6.68	-	9.67	-
1975	-	16.86	12.07	11.41	11.98	-	-	5.99	9.49	-	-	-
1976	9.49	-	4.30	4.72	5.48	5.65	-	2.10	-	3.53	5.84	8.89
1977	-	-	-	-	8.30	-	3.23	-	3.29	5.05	-	-
1978	-	-	-	5.57	4.90	4.12	3.38	-	4.71	-	6.22	7.64
1979	-	-	8.46	8.65	-	-	-	-	3.10	-	-	-
1980	-	-	7.88	12.51[a]	4.42	4.30	-	-	5.60	-	-	-
1981	-	-	-	5.37	7.46	7.14	-	-	-	7.47	8.27	12.31
1982	-	13.21	13.92	13.76	7.30	12.32	-	-	9.71	2.33	3.06	3.87
1983	3.25	2.38	-	-	-	-	-	-	-	-	-	-

[a]Not used for Fig. 5.

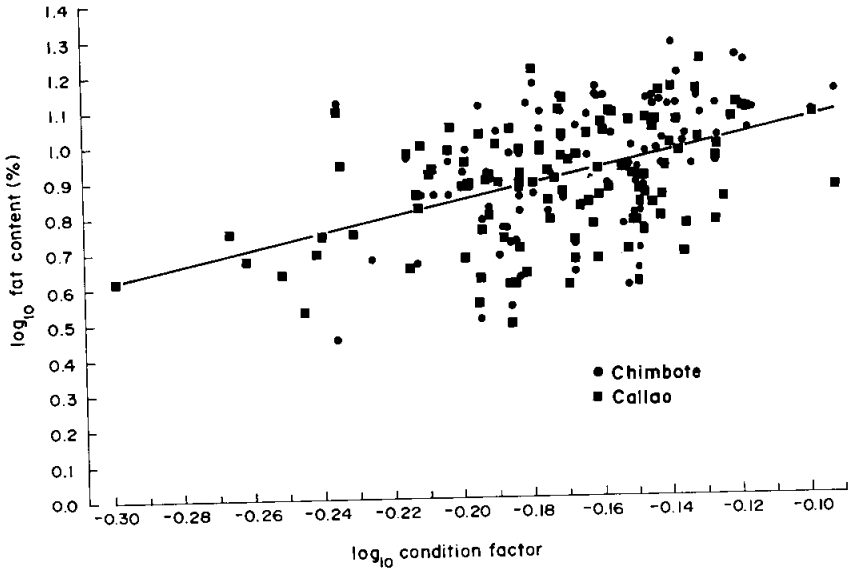

Fig. 5. Relationship between the condition factor of the Peruvian anchoveta and its fat content. Note wide scatter of data, due to inclusion of data from different months and from periods with high temperature anomalies.

Fig. 5. Relación entre el factor de condición de la anchoveta peruana y su contenido de grasa. Nótese la amplia dispersión de los datos debido a la inclusión de datos de diferentes meses y de períodos con altas anomalías de temperatura.

Table 5. Partial regression coefficients of equation (4) expressing the impact of time of the year (i.e., month) on the fat content of anchoveta (see also text and Fig. 6).

Tabla 5. Coeficientes de regresión parcial de la ecuación (4) expresando el impacto de la época del año (es decir, mes) en el contenido de grasa de la anchoveta (ver tambien texto y Fig. 6).

Month	Partial regression coefficient (b_i)	s.e. of b_i values
January	(0)	-
February	+0.987	0.892
March	+1.110	0.781
April	+1.346	0.753
May	+0.689	0.771
June	+0.712	0.841
July	-1.660	1.077
August	-3.155	1.340
September	-3.830	0.847
October	-3.360	0.841
November	-1.670	0.855
December	+0.774	0.824

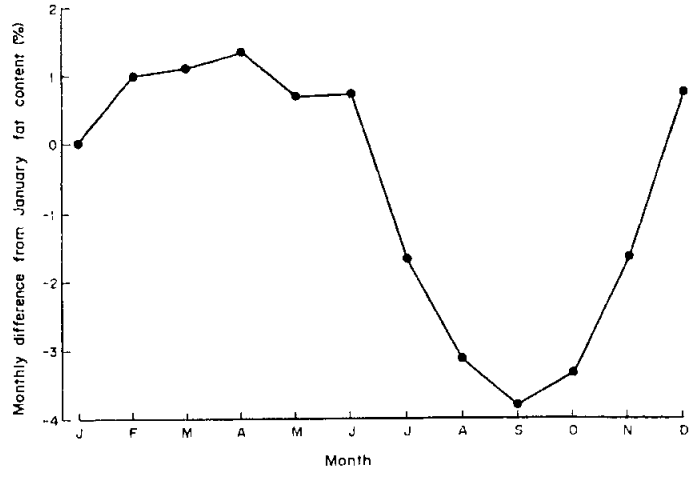

Fig. 6. Monthly change in fat content of Peruvian anchoveta, as expressed by the values of the monthly partial slopes (b_i) of equation (4). See also text and Table 5.

Fig. 6. Cambios mensuales en el contenido de grasa de la anchoveta peruana, expresada por los valores mensuales de la pendiente parcial (b_i) de la ecuacion (4). Ver tambien texto y Tabla 5.

However, the wide scatter of this plot suggests that prediction of fat contents from condition factors alone would be very unreliable.

More useful here is the relationship

$$\%\text{fat content} = 11.2 + 28.8\ (\text{c.f.}) - 0.24\ (\text{temp. anom.}) + 1.02\ (\text{loc.}) + b_i\ (\text{month}) \qquad ...4)$$

which has a multiple correlation coefficient R = 0.708 (d.f. = 187) and whose values of b_i are given in Table 5 and on Fig. 6 as well. These coefficients reproduce quite faithfully the seasonal oscillation of anchoveta fat content, and hence equation (4) can be expected to provide reasonable results when used for predictions.

References

Brett, J.R. 1979. Environmental factors and growth, p. 599-675. *In* W.S. Hoar, D.J. Randall and J.R. Brett (eds.) Fish physiology. Vol. 8. Academic Press, New York.

Hoar, W.S. 1969. Reproduction, p. 1-72. *In* W.S. Hoar and D.J. Randall (eds.) Fish physiology. Vol. 3. Academic Press, New York.

Lam, R. 1968. Estudio sobre la variación del contenido de grasa en la anchoveta peruana (*Engraulis ringens* J.). Informe Inst. Mar Perú-Callao 24, 29 p.

Pauly, D. 1987. Managing the Peruvian upwelling ecosystem: a synthesis, p. 324-342. *In* D. Pauly and I. Tsukayama (eds.) The peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama, editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Philipps, A.M. 1969. Nutrition, digestion, and energy utilization, p. 391-423. *In* W.S. Hoar and D.J. Randall (eds.) Fish physiology. Vol. 1. Academic Press, New York.

Tsukayama, I. and M.L. Palomares. 1987. Monthly catch and catch composition of Peruvian anchoveta *(Engraulis ringens)* (northern-central stock, 4-14°S), 1953 to 1982, p. 89-108. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Perú (IMARPE), Callao Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Tsukayama I. y G. Sánchez. 1981. Estimado de consumo de alimento en anchovetas adultas. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario ICANE:254-258.

Villavicencio, Z. y P. Muck. 1985. La importancia del cambio de la temperatura y de la biomasa planctónica para la producción y mortalidad de anchoveta (*Engraulis ringens*) y sardina (*Sardinops sagax*), p. 119-128. *In* W. Arntz, A. Landa and J. Tarazona (eds.) "El Niño, su impacto en la fauna marina. Inst. Mar Perú-Callao. Volumen Extraordinario.

Ware, D. 1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37(6):1012-1024.

Sexual Maturity of Peruvian Anchoveta *(Engraulis ringens)*, 1961-1987*

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Abstract

Time series of gonad maturity stages of Peruvian anchoveta *(Engraulis ringens)* are presented; they cover the period 1961-1987 and the area from 6 to 18°S. An increasing trend of mean gonad stage is demonstrated which is particularly strong for the stock south of 14°S. The seasonality of gonad maturation is discussed with reference to stage, anchoveta size (age) and sampling location.

Resumen

Se presentan las series temporales del estadío de madurez gonadal de la anchoveta peruana *(Engraulis ringens)* del área 6 a 18°S para el período 1961 a 1987. El estadío de madurez promedio muestra una tendencia a incrementarse particularmente en el stock al sur de 14°S. Se discute la estacionalidad de la madurez gonadal con referencia al estadío, tamaño (edad) de la anchoveta y al lugar de muestreo.

Introduction

The Peruvian anchoveta *(Engraulis ringens)*, constituted the base of the Peruvian fish meal and oil industry during the 1960s and 1970s. In view of this, the Instituto del Mar del Perú (IMARPE) and its predecessor, the Instituto de los Recursos Marinos, directed their research towards this resource, accumulating biological information on this species from the 1950s to date.

Part of this information has been analyzed and published in the book "The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change" (Pauly and Tsukayama 1987a).

The objective of the present work is to contribute to the biological data time series published in the above-mentioned book, by presenting and analyzing data on the sexual maturity of anchoveta sampled from different regions of the Peruvian coast.

*PROCOPA Contribution No. 93.

Materials and Methods

For this study, data on sexual maturity stages obtained through biological sampling of the landings of the industrial fishery have been used. The samples were grouped into three regions: north (06°-9°59'S), central (10°-13°59'S) and south (14°-18°30'S) (Fig. 1).

Sexual maturity stages were obtained by macroscopic observation of the gonads, according to Einarsson et al. (1966) who used a 6-stage scale (see also Rojas de Mendiola, this vol.):

Stage I Immature
Stage II Immature or recuperating
Stage III Maturing
Stage IV Mature
Stage V Spawning, and
Stage VI Spent; postspawning

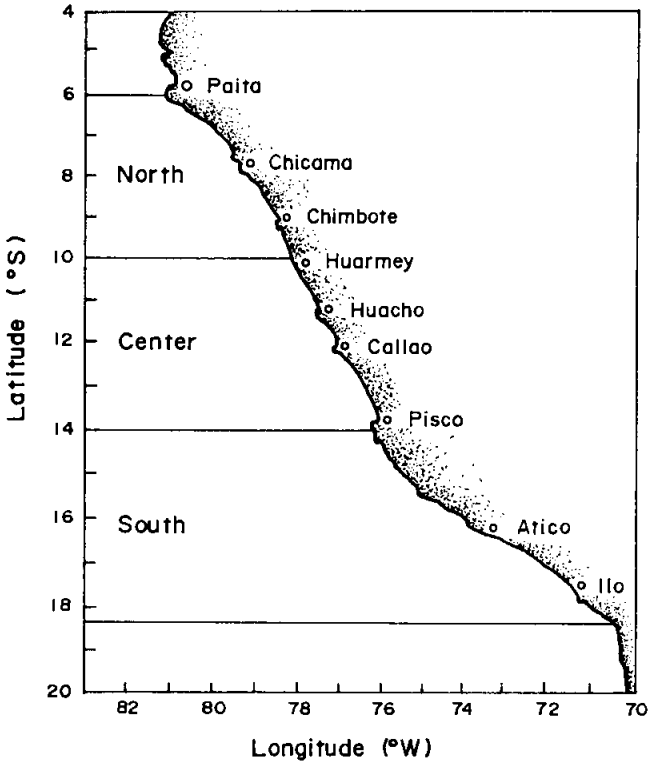

Fig. 1. Definition of northern, central and southern areas off the Peruvian coast, as used in this contribution.
Fig. 1. Delimitación de las áreas norte, centro y sur de la costa peruana usadas en ésta contribución.

Analysis and Data Processing

The frequencies (number of individuals) for each maturity stage per length and month were raised separately to the total catch of anchoveta from the northern/central region (6°-13°59'S) - the main distribution area for this species - and from the southern region, where a different stock occurs (IMARPE 1973; Pauly and Tsukayama 1987b). These raised data were used to obtain the monthly mean sexual stages by length class.

Unaggregated mean monthly maturity stages by length, sex and by region are presented for the 1961-1987 period in Pellón et al. (1988), and the data presented here represent a subset of those compiled in that paper. Particularly, we do not report here our results on a length-class basis.

Results and Discussion

Variation of the Mean Maturity Stages

Table 1 and Figs. 2 and 3 show the monthly mean values of sexual maturity in the northern/central and southern stocks of adult anchoveta (≥ 10.25 cm), for the 1961-1987 period. As might be seen, these values tend to increase through time, especially so in the south.

The highest mean maturity stages generally occurred, for both stocks, during the spring and summer months, when stages IV, V and VI predominate (see Table 1).

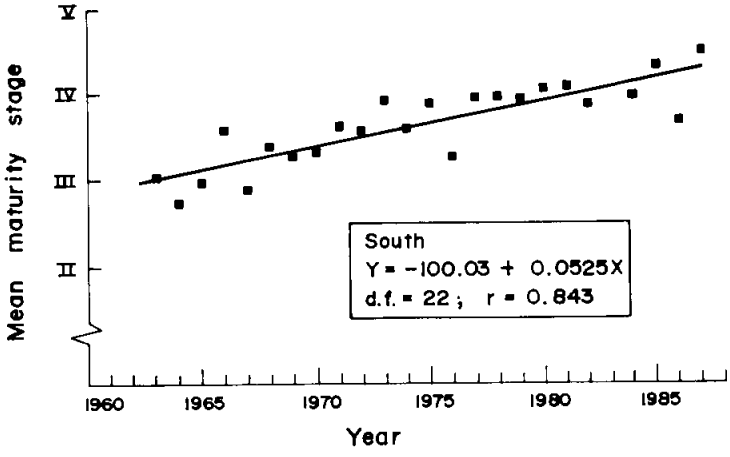

Fig. 2. Trend of mean annual maturity stage of anchoveta, 1961-1987 off northern/central Peru (based on data in Table 1 with missing months replaced by the appropriate monthly means before averaging).
Fig. 2. Tendencia del estadío de madurez promedio anual de la anchoveta del área norte/central del Perú para 1961-1987 (basado en datos de la tabla 1; para los meses sin datos se usaron el promedio mensual antes de promediar el valor anual).

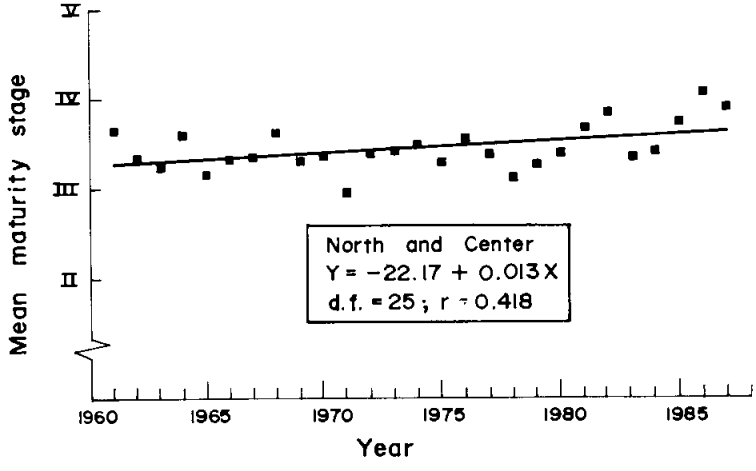

Fig. 3. Trend of mean annual maturity stage of anchoveta, 1963-1987 off southern Peru (based on data in Table 1 with missing months replaced by the appropriate monthly means before averaging).
Fig. 3. Tendencia del estadío de madurez promedio anual de la anchoveta del área sur del Perú para 1963-1987 (basado en dotos de la Tabla 1; para los meses sin datos se usaron el promedio mensual antes de promediar el valor anual).

Variation of the Maturity Stages

Both the northern/central and the southern stocks show a large fraction of individuals to be in stage I during the 1960s and 1970s. Additionally, low values were observed in the northern/central stock in 1961-1963 and from 1971 to 1987, except for 1976, and in the southern stock in 1968-1969 and from 1971 to 1987, except for 1981 (Table 2).

Table 3 gives the percent values of stages II + III. These oscillated markedly during 1963-1966, especially in the southern stock. The lowest values in this stock are obtained during 1963-1966 and 1979-1984, and the highest in 1967-1977 and from 1986 on; for the northern/central stock, the lowest values belong to the 1971-1967 period, which was followed by relatively high values from 1968 on. Both stocks generally have their highest values in the winter months.

Table 1. Mean monthly sexual maturity stage of adult female and male anchoveta (≥10.25 cm TL) in the northern/central and southern areas of Peru, 1961-1987.

Tabla 1. Valores mensuales promedios del estadio de madurez sexual para anchoveta, hembras y machos adultos (≥10.25 cm LT) del stock del norte/centro y sur del Perú, 1961-1987.

Year	January	February	March	April	May	June
1961	- / -	- / -	3.06/ -	3.52/ -	4.18/ -	3.36/ -
1962	3.98/ -	3.48/ -	3.45/ -	3.66/ -	3.39/ -	2.47/ -
1963	3.29/ -	3.71/ -	3.42/3.12	3.00/3.86	2.32/2.65	2.14/ -
1964	3.62/2.66	3.62/2.44	3.18/2.25	2.89/2.25	2.55/1.93	2.32/2.50
1965	3.35/ -	3.50/3.19	3.39/2.96	2.83/2.08	2.41/1.75	2.50/1.78
1966	3.34/3.00	3.43/2.91	3.39/3.59	2.57/3.77	1.65/3.44	- / -
1967	3.24/2.48	2.86/2.13	2.76/2.01	2.65/1.57	2.30/1.58	2.00/1.86
1968	3.79/3.02	4.05/2.15	4.30/2.15	2.66/1.84	2.25/2.08	
1969	3.50/3.37	- /3.55	3.30/2.22	2.81/1.78	2.38/1.79	- /1.93
1970	2.64/3.94	3.28/3.31	3.08/3.06	2.61/2.43	2.48/1.77	3.27/1.98
1971	- / -	- / -	2.35/3.17	2.05/2.81	2.26/3.06	2.33/ -
1972	- / -	- /3.14	2.71/3.09	2.72/ -	3.02/ -	3.64/ -
1973	- / -	- / -	3.42/2.82	3.71/2.72	- /3.93	- /4.73
1974	- /2.99	- /3.41	3.46/2.93	3.34/2.40	2.40/ -	- / -
1975	2.97/3.79	3.06/3.70	2.98/3.52	2.59/3.05	2.55/3.11	- / -
1976	3.77/2.64	3.27/2.66	2.93/2.57	3.86/2.42	3.65/2.38	3.16/2.67
1977	3.79/3.24	- /3.16	- /3.15	2.96/3.26	2.73/2.86	- /3.48
1978	- /4.03	- /3.70	- / -	2.60/ -	2.56/2.77	2.92/2.91
1979	- /3.76	- /3.51	2.51/3.71	2.64/2.36	- /2.51	- /3.99
1980	- /4.21	- /3.96	- /3.58	3.01/3.66	3.00/3.45	3.10/4.03
1981	- /3.13	- /3.78	- /3.67	3.54/4.52	3.57/3.69	4.27/4.42
1982	- /3.86	4.25/2.98	4.15/3.28	3.37/4.00	3.08/3.32	3.23/ -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	- / -	- /4.41	- / -	- /3.78	3.46/ -	2.91/4.07
1985	3.61/3.52	3.86/4.21	3.91/ -	- /2.65	- / -	3.27/4.93
1986	3.21/5.52	3.11/ -	3.20/3.27	3.07/2.54	3.33/2.43	3.72/3.21
1987	4.63/5.36	4.02/4.76	3.10/3.46	3.32/4.00	3.57/ -	3.64/4.72
Means	3.30/3.58	3.30/3.35	3.09/3.03	2.88/2.90	2.71/2.66	2.86/3.33

Year	July	August	September	October	November	December
1961	2.77/ -	2.88/ -	4.15/ -	3.72/ -	4.19/ -	5.26/ -
1962	2.38/ -	2.96/ -	3.53/ -	3.54/ -	3.27/ -	3.91/ -
1963	2.44/2.56	3.39/2.99	3.47/3.41	3.81/3.02	4.21/2.15	3.66/2.39
1964	3.09/2.59	3.71/3.78	4.80/3.80	5.10/3.84	4.90/2.74	3.38/2.00
1965	3.42/2.68	- / -	3.24/3.34	3.55/3.66	3.41/3.57	3.10/2.68
1966	- / -	- / -	4.12/4.46	4.12/3.89		4.23/2.38
1967	- / -	- / -	4.62/3.05	4.67/4.38	4.47/3.72	4.30/ -
1968	- /3.62	- /4.76	4.22/3.98	4.18/4.58	4.63/ -	4.24/4.97
1969	- /2.19	- / -	4.47/4.65	4.54/4.52	3.76/4.59	2.48/4.18
1970	- /2.26	- / -	4.16/4.44	4.31/4.14	3.86/4.09	4.33/4.09
1971	- / -	- / -	3.78/4.48	3.85/4.23	3.14/3.90	2.76/3.52
1972	- / -	- / -	- / -	- / -	- /3.42	3.84/3.79
1973	- /4.29	- / -	- / -	- / -	- /4.47	- /3.91
1974	- / -	- / -	- / -	4.65/4.15	4.70/4.99	- / -
1975	- / -	- / -	- / -	4.64/5.04	- /5.06	3.77/3.54
1976	2.99/ -	3.23/ -	- / -	- /4.20	4.01/3.69	3.60/3.34
1977	- /4.63	- /4.74	- /5.06	- /5.08	- /4.89	- /3.81
1978	3.03/4.89	2.00/ -	3.66/4.69	3.79/4.44	3.68/4.49	3.26/5.30
1979	- /3.89	- /4.73	- /5.24	- /4.79	- /4.42	- /4.28
1980	- / -	- / -	- /4.73	- /4.63	- /5.02	- /3.24
1981	- /3.99	- /4.67	- /4.93	- /4.55	4.79/4.09	3.84/3.57
1982	3.52/4.22	- /4.48	- / -	5.17/4.66	5.19/ -	- / -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	3.17/4.46	- / -	- / -	- /4.97	- / -	- / -
1985	3.94/4.67	4.57/5.71	4.95/4.85	4.80/5.28	3.29/5.26	2.83/4.94
1986	4.29/ -	5.30/3.20	5.18/4.74	5.37/4.59	4.40/3.74	4.36/3.86
1987	4.49/4.71	- /4.81	- /4.85	4.50/4.64	- /4.35	4.31/5.49
Means	3.04/3.71	3.12/4.39	3.89/4.39	4.12/4.42	3.88/4.13	3.57/3.76

Table 2. Relative frequency (%) of sexual maturity stage I of male and female anchoveta (6.25 - 19.25 cm TL) in the northern/central and southern areas of Peru, 1961-1987.

Tabla 2. Frecuencia relativa (%) del estadio de madurez sexual I para anchoveta machos y hembras (6.25 - 19.25 cm LT) en las áreas norte/centro y sur del Perú, 1961-1987.

Year	January	February	March	April	May	June
1961	- / -	- / -	24.2/ -	12.7/ -	20.8/ -	29.4/ -
1962	3.0/ -	15.8/ -	20.1/ -	8.9/ -	27.7/ -	27.9/ -
1963	11.4/ -	4.4/ -	21.1/19.2	33.2/ -	34.0/ -	42.5/ -
1964	29.5/84.2	45.7/71.7	52.6/65.1	47.8/60.1	41.8/43.6	37.6/16.8
1965	49.7/ -	40.4/61.9	30.0/69.7	33.4/13.5	39.1/51.5	38.2/76.7
1966	73.2/75.7	83.6/46.2	79.7/12.2	72.4/ 5.3	58.1/ 7.6	- / -
1967	50.6/68.1	71.6/76.6	58.3/19.6	44.7/ 1.8	69.8/21.5	58.2/10.7
1968	52.9/26.0	62.2/20.7	36.7/ -	39.3/16.4	45.8/12.2	- / -
1969	68.5/10.5	- / 8.0	50.9/ 6.7	16.2/36.9	12.4/39.0	- /11.2
1970	61.8/19.5	25.6/16.5	4.1/16.4	11.5/62.0	7.8/23.0	- / 8.0
1971	- / -	- / -	35.6/ 9.6	32.4/ 1.1	21.9/ 1.6	7.0/ -
1972	- / -	- /10.6	1.2/ 3.8	2.1/ -	6.3/ -	6.6/ -
1973	- / -	- / -	14.5/ -	1.6/ -	- / 0.9	- / -
1974	- / -	- / -	17.6/19.6	20.5/ -	6.6/ -	- / -
1975	13.5/ 8.6	6.7/ 2.1	4.4/ -	5.1/ 1.4	2.5/ 0.7	- / -
1976	23.6/ 3.4	39.2/14.1	56.8/ 3.4	74.9/ 5.4	47.8/ 3.4	52.6/ 0.5
1977	25.2/ 2.6	- / 0.2	- / 2.2	4.3/ 0.8	3.3/16.7	- / 4.1
1978	- /18.6	- / 2.4	- / -	35.2/ -	29.7/ -	14.5/ -
1979	- / 0.0	- / 0.5	6.3/ 0.4	10.0/ 1.1	- / 2.2	- / -
1980	- / 8.8	- /17.6	- /10.2	- / 1.4	0.1/ -	0.1/ -
1981	- /54.2	- /31.8	- /27.9	- /12.0	1.0/20.6	- / -
1982	- /14.8	- / 3.2	- / 0.4	- / -	0.1/ -	- / -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	- / -	- / -	- / -	- / -	- / -	- / -
1985	- /25.5	- / 8.8	- / -	- /30.8	- / -	1.3/ -
1986	- / -	- / -	- / -	- /15.0	- / -	- / -
1987	- / -	- / -	1.3/ -	- / -	0.7/ -	0.6/ -

Year	July	August	September	October	November	December
1961	6.5/ -	3.3/ -	- / -	8.2/ -	5.3/ -	- / -
1962	27.5/ -	4.5/ -	2.1/ -	7.9/ -	4.2/ -	0.2/ -
1963	14.1/16.1	12.3/ 5.6	4.2/ 2.4	1.6/ 1.7	8.4/18.8	34.4/72.1
1964	25.9/ 6.8	5.4/ 2.7	- / 7.8	- / 1.5	0.5/ 0.4	17.6/23.9
1965	26.7/69.5	- / -	7.1/70.6	0.8/63.6	8.1/64.0	31.0/89.0
1966	- / -	- / -	- / 0.2	0.9/ 0.8	- / -	- /32.0
1967	- / -	- / -	- / -	- / -	0.2/ -	0.4/ -
1968	- / -	- / -	0.8/ -	0.2/ -	- / -	11.2/18.8
1969	- / 6.5	- / -	- / -	- / 0.3	26.5/11.2	64.5/68.6
1970	- /21.5	- / -	0.2/ 0.3	- / 7.3	- /16.9	- /47.8
1971	- / -	- / -	- / -	0.1/ -	- /10.9	- / 5.1
1972	- / -	- / -	- / -	- / -	- /12.9	14.7/ 8.4
1973	- / -	- / -	- / -	- / -	- / -	- / -
1974	- / -	- / -	- / -	- / 0.1	- / -	- / -
1975	- / -	- / -	- / -	- / -	- / -	5.9/ 3.3
1976	38.4/ -	- / -	- / -	0.1/ -	- / 0.1	0.4/ 2.9
1977	- / -	- / -	- / -	- / -	- / -	- /18.3
1978	19.7/ -	- / -	1.1/ -	- / -	- / 0.0	0.0/ -
1979	- / 1.0	- / -	- / -	- / -	- / -	- / -
1980	- / -	- / -	- / -	- / -	- / -	- /45.5
1981	- / 0.1	- / -	- / -	- / -	- / -	- /32.9
1982	- / -	- / -	- / -	- / -	- / -	- / -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	- / -	- / -	- / -	- / -	- / -	- / -
1985	- / -	- / -	- / -	- / -	- / -	- / -
1986	- / -	- / -	- / -	- / -	- / -	- / -
1987	0.3/ -	- / -	- / -	- / -	- / -	- / -

Table 3. Relative frequency (%) of sexual maturity stages II and III of male and female anchoveta (6.25 - 19.25 cm TL) in the northern/central and southern areas of Peru, 1961-1987.

Tabla 3. Frecuencia relativa (%) del estadio de madurez sexual II y III para anchoveta machos y hembras (6.25 - 19.25 cm LT) en las áreas norte/centro y sur del Perú, 1961-1987.

Year	January	February	March	April	May	June
1961	- / -	- / -	40.3/ -	25.4/ -	22.2/ -	33.8/ -
1962	15.2/ -	23.0/ -	21.0/ -	34.1/ -	35.1/ -	61.4/ -
1963	36.6/ -	32.3/ -	25.1/40.9	35.5/56.4	47.3/81.2	51.4/ -
1964	15.7/11.0	26.6/24.9	30.3/28.5	36.4/31.3	48.9/48.0	49.9/65.2
1965	12.9/ -	13.7/27.5	14.0/24.0	42.2/78.6	41.1/48.1	45.1/22.8
1966	8.9/22.6	5.3/44.0	5.8/42.9	14.1/58.5	41.2/59.2	- / -
1967	11.7/27.9	18.0/21.7	25.5/80.4	43.4/98.0	27.1/78.5	37.2/88.8
1968	21.0/68.4	8.9/79.1	28.0/98.8	50.4/83.4	50.4/87.2	- / -
1969	11.0/49.7	- /58.4	42.7/85.7	75.9/63.1	84.9/61.0	- /88.3
1970	33.6/46.2	58.3/63.2	85.0/67.8	83.0/35.8	90.3/77.0	83.6/89.8
1971	- / -	- / -	60.5/75.9	66.9/96.5	78.1/76.7	92.0/ -
1972	- / -	- /79.2	89.1/90.1	91.6/ -	75.1/ -	56.1/ -
1973	- / -	- / -	55.7/97.0	45.5/95.4	- /71.6	- /46.8
1974	- /81.1	- /59.8	33.7/71.1	38.1/99.4	66.7/ -	- / -
1975	59.4/61.4	79.8/79.8	71.2/88.0	79.2/88.4	75.0/81.0	- / -
1976	43.3/92.9	9.4/83.9	33.1/92.0	20.9/91.6	46.4/95.3	42.8/97.9
1977	23.6/63.3	- /65.1	- /65.9	67.7/86.2	80.6/76.7	- /77.3
1978	- /63.2	- /69.6	- / -	61.5/ -	66.0/91.2	79.2/69.5
1979	- /26.8	- /33.0	82.3/34.9	78.7/78.0	- /77.7	- /43.8
1980	- /44.1	- /65.9	- /50.5	71.7/35.7	80.3/61.0	67.4/28.6
1981	- /39.8	- /48.3	- /50.7	49.9/42.4	51.3/59.1	26.3/31.9
1982	- /50.3	8.6/85.2	22.7/74.8	65.0/63.7	56.4/40.9	58.1/ -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	- / -	- /26.1	- / -	- /38.9	60.0/ -	95.0/17.4
1985	46.3/40.1	46.0/51.1	65.8/ -	- /55.5	- / -	90.6/ 2.3
1986	91.3/ 2.2	97.7/ -	96.3/65.5	97.0/81.2	82.0/90.5	53.2/84.6
1987	13.8/11.0	40.0/21.7	67.1/58.1	66.8/49.4	42.3/ -	10.9/23.1

Year	July	August	September	October	November	December
1961	67.6/ -	63.1/ -	32.0/ -	13.0/ -	9.2/ -	6.7/ -
1962	63.4/ -	64.2/ -	40.9/ -	37.0/ -	35.7/ -	27.5/ -
1963	77.4/46.0	45.8/41.6	45.3/20.1	37.6/58.4	14.4/69.9	5.9/19.1
1964	41.3/57.9	23.3/11.2	0.9/12.2	2.4/21.6	8.6/77.1	17.8/71.1
1965	52.4/16.0	- / -	81.8/17.8	59.0/22.8	44.1/16.4	30.4/10.1
1966	- / -	- / -	29.1/18.4	29.5/46.9	- / -	18.4/60.6
1967	- / -	- / -	0.4/84.6	8.8/24.7	16.6/62.5	27.1/ -
1968	- /69.4	- /14.1	15.9/47.3	7.6/24.8	8.3/ -	6.1/ 5.7
1969	- /93.2	- / -	20.1/ 7.1	19.7/14.7	0.7/20.7	26.9/15.7
1970	- /78.5	- / -	7.8/24.5	12.3/25.1	50.2/24.9	31.8/16.5
1971	- / -	- / -	47.0/33.6	43.7/71.1	81.4/48.5	92.8/72.6
1972	- / -	- / -	- / -	- / -	- /46.8	22.9/45.1
1973	- /32.0	- / -	- / -	- / -	- /28.9	- /42.3
1974	- / -	- / -	- / -	5.5/44.6	21.9/19.0	- / -
1975	- / -	- / -	- / -	5.4/22.2	- /16.6	41.2/47.2
1976	49.4/ -	- / -	- / -	18.6/48.7	27.0/54.0	38.6/47.3
1977	- /18.7	- /24.0	- / 3.3	- / 4.9	- / 9.7	- /51.5
1978	63.1/ 9.5	- / -	18.3/ 6.1	6.3/41.1	59.2/30.1	85.5/10.3
1979	- /31.9	- /20.7	- / 1.1	- /12.1	- / 6.1	- / 5.6
1980	- / -	- / -	- / 6.9	- / 1.6	- / 8.3	- /51.5
1981	- /19.2	- / 3.4	- / 4.5	- /15.4	1.9/36.0	9.9/46.2
1982	60.9/15.6	- / -	- / -	1.1/12.1	- / -	- / -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	68.2/ 6.7	- / -	- / -	- / 3.1	- / -	- / -
1985	28.6/12.7	4.4/ -	1.7/ 3.7	10.1/ 7.0	85.3/ 8.4	96.4/ 8.0
1986	12.8/ -	- /88.8	0.3/20.8	2.4/ 9.3	20.0/35.2	29.5/44.9
1987	7.3/13.8	- /13.2	- /23.9	11.0/29.0	- /28.5	0.6/ -

Stage IV (Table 4) shows no large fluctuations in the northern/central stock, except for 1978 and 1987. The highest values are generally observed in spring and summer, and the lowest during the autumn and early winter months. The southern stock shows greater fluctuations than the northern/central stock, with low values during 1963-1974. From 1975 on, an increase can be observed, and a maximum is reached in spring 1982.

In both stocks, the highest values occur in spring and the lowest in autumn-winter.

The mean values of stages V and VI (Table 5) in the northern/central stock were relatively constant during 1961-1971, while high values occurred in 1962, 1965, 1968-1969 and 1985-1987. The maximum values occur in the spring months and the minimum in autumn.

The southern stock does not present marked tendencies and the mean values show similar variations through time.

The highest values tend to occur in the spring months, and the lowest in autumn and early winter.

Annual Cycles of Maturity Stages

Fig. 4 shows the seasonal cycles of maturity stages I to VI for the 1960s and 1970s for the northern/central stock, while Fig. 5 shows the corresponding data for the southern stock.

As might be seen, the monthly variations and the annual cycles of the different maturity stages confirm the results obtained by other authors on maturation and spawning of the Peruvian anchoveta (Miñano 1958, 1968; Jordán and Chirinos de Vildoso 1965; Einarsson et al. 1966; Santander and Sandoval de Castillo 1969; Jordán 1980; Santander 1981; Peña and Carrasco, MS).

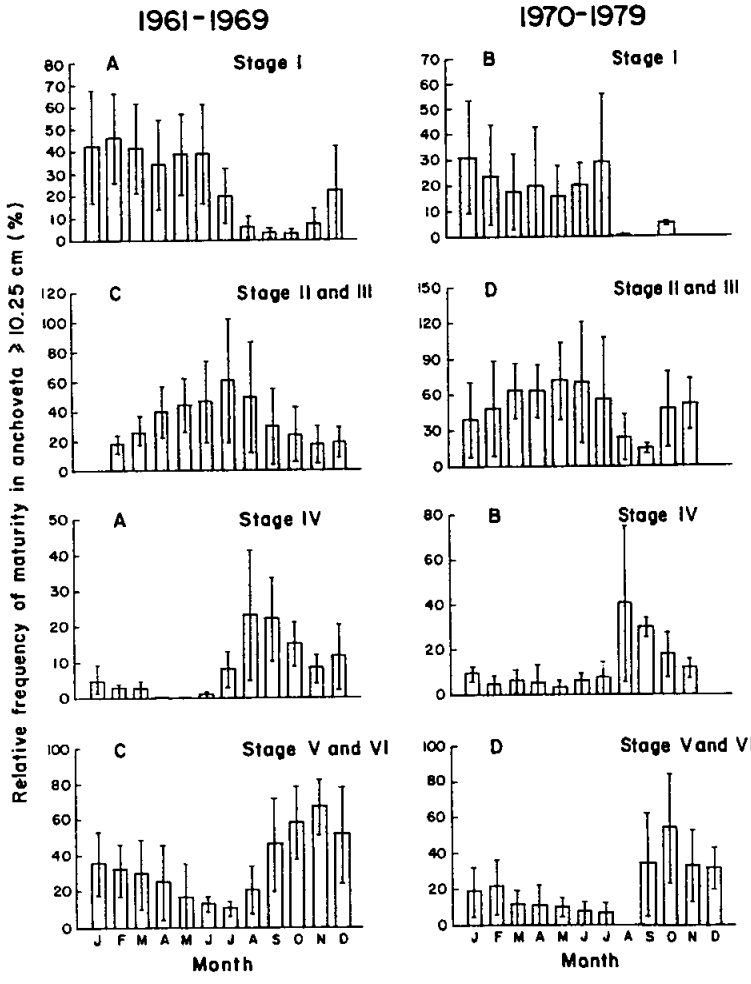

Fig. 4. Relative frequency of maturity stages I-VI in anchoveta sampled off northern/central Peru, from 1961 to 1969 and 1970 to 1979.

Fig. 4. Frecuencia relativa de los estadíos de madurez I-VI de anchovetas muestreadas en el área norte/central del Perú durante 1961 a 1969 y de 1970 a 1979.

Table 4. Relative frequency (%) of sexual maturity stage IV of male and female anchoveta (6.25 - 19.25 cm TL) in the northern/central and southern areas of Peru, 1961-1987.

Tabla 4. Frecuencia relativa (%) del estadio de madurez sexual IV para anchoveta machos y hembras (6.25 - 19.25 cm LT) en las áreas norte/centro y sur del Perú, 1961-1987.

Year	January	February	March	April	May	June
1961	- / -	- / -	4.0/ -	0.1/ -	- / -	0.6/ -
1962	15.3/ -	4.9/ -	8.1/ -	0.4/ -	- / -	0.3/ -
1963	6.8/ -	5.0/ -	1.9/11.3	0.4/ 0.3	0.2/ -	1.3/ -
1964	4.8/ 0.7	4.0/ -	1.6/ -	0.5/ 0.2	0.5/ 0.3	2.1/ 5.0
1965	0.9/ -	3.3/ -	0.3/ -	- / -	0.2/ -	2.1/ -
1966	4.7/ 0.8	1.4/ 2.7	2.1/ 8.6	0.5/ 6.4	0.3/ 1.4	- / -
1967	2.2/ 2.9	2.5/ 1.5	4.4/ -	0.8/ -	0.0/ -	- / -
1968	3.2/ 0.1	0.4/ 0.2	0.2/ -	0.1/ 0.1	- / -	- / -
1969	1.0/ -	- / -	- / -	0.1/ -	- / -	- / 0.4
1970	3.1/ 0.2	8.4/ -	1.5/ -	1.2/ -	0.4/ -	15.6/ 2.2
1971	- / -	- / -	2.9/ -	0.2/ -	0.0/ -	- / -
1972	- / -	- / -	0.9/ 0.2	1.9/ -	5.4/ -	7.3/ -
1973	- / -	- / -	20.3/ 0.1	25.9/ 0.3	- / -	- / 1.3
1974	- / 2.3	- /10.1	12.6/ 0.8	5.7/ 0.3	- / -	- / -
1975	3.9/ 5.0	6.8/ 3.9	4.1/ 7.3	3.1/ 4.2	2.3/ 9.0	- / -
1976	3.6/ 0.8	0.1/ 1.0	2.0/ 0.7	0.1/ 0.9	0.3/ 0.3	1.8/ 0.4
1977	28.6/10.8	- / 7.9	- / 5.2	14.1/ 3.5	14.0/ 3.7	- / 8.7
1978	- / 5.6	- / 8.4	- / -	1.1/ -	1.2/ 6.1	1.2/14.9
1979	- / 8.6	- /10.6	8.6/ 7.2	3.4/ 3.7	- / 1.4	- / 8.4
1980	- /11.1	- / 6.2	- / 6.2	14.5/ 5.1	12.1/ 5.5	24.6/ 2.5
1981	- / 2.3	- / 8.4	- / 7.9	25.9/ 4.2	14.1/ 4.7	33.5/17.9
1982	- / 8.9	31.8/ 1.7	29.3/ 6.7	8.6/ 2.4	24.2/20.0	27.0/ -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	- / -	- /35.9	- / -	- /42.4	20.2/ -	5.0/20.9
1985	33.2/18.8	32.4/15.0	31.8/ -	- / 7.9	- / -	6.9/41.9
1986	3.9/18.0	1.5/ -	2.8/22.6	2.1/ 1.8	10.3/ 2.7	26.7/ 5.3
1987	5.0/ 3.7	9.2/18.5	8.8/ 6.1	7.2/22.3	15.9/ -	17.7/39.3

Year	July	August	September	October	November	December
1961	14.7/ -	21.5/ -	41.1/ -	16.4/ -	3.5/ -	4.2/ -
1962	6.1/ -	25.3/ -	34.2/ -	26.0/ -	11.5/ -	9.9/ -
1963	7.5/21.7	19.9/38.4	16.7/24.3	16.9/14.3	14.4/ 4.3	7.9/ 1.0
1964	9.4/23.8	26.6/18.8	13.1/ 0.6	9.7/ -	2.7/ -	3.2/ 3.4
1965	3.5/ 8.9	- / -	1.5/ 0.6	6.1/ -	17.1/ -	21.4/ 0.3
1966	- / -	- / -	21.3/ 2.1	13.1/ -	- / -	31.3/ 3.6
1967	- / -	- / -	19.5/14.8	13.3/ 1.8	5.9/ -	12.7/ -
1968	- / 9.5	- / 1.0	25.2/ 1.6	12.9/ -	8.7/ -	9.5/ -
1969	- / 0.1	- / -	28.8/30.6	23.3/ 8.4	4.5/ 1.4	6.0/ 0.1
1970	- / -	- / -	36.6/ 5.0	25.8/ 0.5	17.1/ 4.0	11.2/ -
1971	- / -	- / -	24.1/ -	9.2/ -	7.0/ -	1.3/ 1.0
1972	- / -	- / -	- / -	- / -	- / 4.9	9.2/ 1.2
1973	- / 4.7	- / -	- / -	- / -	- / 4.7	- / 3.3
1974	- / -	- / -	- / -	17.0/ 1.7	7.1/ 1.6	- / -
1975	- / -	- / -	- / -	14.8/ 3.8	- / 7.5	5.9/18.8
1976	5.8/ -	- / -	- / -	30.3/ 6.1	42.3/13.7	36.9/15.4
1977	- /19.2	- /17.5	- /16.2	- /11.2	- /13.6	- / 8.2
1978	9.9/18.4	- / -	62.4/21.9	84.8/ 3.7	19.2/ 6.2	10.2/ 9.0
1979	- /23.4	- /15.5	- /16.6	- /17.6	- /34.2	- /38.4
1980	- / -	- / -	- / 9.1	- /22.8	- /15.9	- / 1.3
1981	- /19.6	- /36.7	- /27.3	- /23.9	20.3/21.2	34.5/ 5.6
1982	24.2/45.0	- /57.3	- / -	14.2/36.4	18.9/ -	- / -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	31.8/21.7	- / -	- / -	- /36.3	- / -	- / -
1985	39.4/24.0	40.2/11.0	8.9/33.0	24.0/13.4	4.4/21.6	3.6/46.7
1986	27.6/ -	5.1/ 9.1	12.7/ 5.5	4.4/23.4	37.9/10.2	9.9/14.9
1987	12.1/12.7	- /12.2	- /10.3	48.8/12.2	- /11.7	71.1/14.3

Table 5. Relative frequency (%) of sexual maturity stages V and VI of male and female anchoveta (6.25 - 19.25 cm TL) in the northern/central and southern areas of Peru, 1961-1987.

Tabla 5. Frecuencia relativa (%) del estadio de madurez sexual V y VI para anchoveta machos y hembras (6.25 - 19.25 cm LT) en las áreas norte/centro y sur del Perú, 1961-1987.

Year	January	February	March	April	May	June
1961	- / -	- / -	31.5/ -	61.8/ -	57.1/ -	36.1/ -
1962	66.5/ -	56.3/ -	50.9/ -	56.6/ -	37.3/ -	10.4/ -
1963	45.2/ -	58.3/ -	51.9/28.6	30.9/43.3	18.5/18.8	4.8/ -
1964	50.0/ 4.1	23.7/ 3.4	15.6/ 6.4	15.3/ 8.4	8.8/ 8.1	10.4/13.0
1965	36.5/ -	42.7/10.6	55.8/ 6.4	24.4/ 7.9	19.7/ 0.4	14.6/ 0.6
1966	13.2/ 0.9	9.7/ 7.2	12.4/36.3	13.0/29.8	0.4/31.8	- / -
1967	35.5/ 1.1	7.9/ 0.2	11.8/ -	11.1/ 0.2	3.0/ -	4.6/ 0.5
1968	22.9/ 5.5	28.5/ -	35.1/ 1.2	10.2/ 0.1	3.7/ 0.6	- / -
1969	19.6/39.8	- /33.6	6.4/ 7.6	7.8/ -	2.7/ -	- / -
1970	1.5/34.2	7.7/20.3	9.5/15.8	4.3/ 2.2	1.4/ -	0.8/ -
1971	- / -	- / -	1.0/14.6	0.5/ 2.5	- /21.7	1.0/ -
1972	- / -	- /10.2	8.8/ 5.9	4.5/ -	13.2/ -	30.0/ -
1973	- / -	- / -	9.4/ 2.9	27.0/ 4.3	- /27.5	- /51.9
1974	- /16.6	- /30.0	36.0/ 8.5	35.6/ 0.3	26.7/ -	- / -
1975	23.2/25.0	6.7/14.2	20.2/ 4.7	12.6/ 6.1	20.2/ 9.4	- / -
1976	29.6/ 2.9	51.3/ 0.9	8.1/ 3.9	4.1/ 2.1	5.4/ 1.0	2.9/ 1.2
1977	22.5/23.3	- /26.9	- /26.8	13.9/ 9.5	2.1/ 2.8	- / 9.9
1978	- /12.6	- /19.5	- / -	2.3/ -	3.1/ 2.6	5.2/15.6
1979	- /64.6	- /55.9	2.7/57.5	7.9/17.1	- /18.8	- /47.9
1980	- /36.0	- /10.2	- /33.1	13.8/57.8	7.4/33.6	7.9/68.9
1981	- / 3.7	- /11.4	- /13.5	24.2/41.4	33.7/15.7	40.2/50.2
1982	- /25.9	59.5/ 9.9	48.0/18.1	26.4/33.9	19.3/39.1	14.9/ -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	- / -	- /38.0	- / -	- /18.8	19.8/ -	- /61.7
1985	20.5/15.6	21.6/25.2	2.4/ -	- / 5.7	- / -	1.1/55.7
1986	4.8/79.8	0.8/ -	0.9/11.9	0.9/ 1.9	7.7/ 6.8	20.2/10.1
1987	81.2/85.3	50.8/59.9	22.8/35.7	26.0/28.2	41.2/ -	70.9/37.6

Year	July	August	September	October	November	December
1961	11.2/ -	12.1/ -	26.8/ -	62.5/ -	82.0/ -	89.1/ -
1962	2.9/ -	6.0/ -	22.9/ -	29.1/ -	48.7/ -	62.4/ -
1963	1.0/16.1	22.0/14.4	33.9/53.2	43.9/25.6	62.8/ 7.1	51.8/ 7.9
1964	23.4/11.5	44.7/67.3	86.0/79.5	87.9/76.9	88.2/22.4	61.3/ 1.6
1965	17.4/ 5.6	- / -	9.6/11.0	34.2/13.6	30.8/19.6	17.2/ 0.6
1966	- / -	- / -	49.6/79.3	56.6/52.3	- / -	50.3/ 3.8
1967	- / -	- / -	80.1/ 0.6	77.9/73.5	77.3/37.5	59.8/ -
1968	- /21.2	- /84.9	58.0/51.1	79.2/75.2	83.0/ -	73.2/75.5
1969	- / 0.3	- / -	51.1/62.3	57.0/76.6	68.3/66.8	2.6/15.6
1970	- / -	- / -	55.5/70.2	61.9/67.2	32.7/54.2	57.0/35.7
1971	- / -	- / -	28.9/66.4	47.0/28.9	11.6/40.6	5.9/21.3
1972	- / -	- / -	- / -	- / -	- /35.4	53.2/45.3
1973	- /63.3	- / -	- / -	- / -	- /66.4	- /54.3
1974	- / -	- / -	- / -	77.5/53.5	71.0/79.5	- / -
1975	- / -	- / -	- / -	79.8/74.0	- /75.9	47.1/30.6
1976	6.4/ -	- / -	- / -	51.0/45.2	30.8/32.3	24.1/34.4
1977	- /62.1	- /58.5	- /80.5	- /83.9	- /76.6	- /21.9
1978	7.3/72.2	- / -	18.2/72.0	8.9/55.2	21.6/63.7	4.2/80.7
1979	- /43.7	- /63.8	- /82.3	- /70.4	- /59.7	- /55.9
1980	- / -	- / -	- /84.0	- /75.7	- /75.8	- / 1.7
1981	- /61.1	- /59.9	- /68.1	- /60.7	77.8/38.4	55.7/15.3
1982	14.9/39.4	- /42.7	- / -	84.7/51.5	81.1/ -	- / -
1983	- / -	- / -	- / -	- / -	- / -	- / -
1984	- /71.7	- / -	- / -	- /60.6	- / -	- / -
1985	32.0/63.3	55.4/89.0	89.4/63.3	65.9/79.6	10.3/70.0	- /45.4
1986	59.6/ -	94.9/ 2.1	87.0/73.7	93.2/67.3	42.2/54.5	60.6/40.2
1987	80.2/73.5	- /74.6	- /65.8	40.1/58.9	- /59.9	28.3/85.7

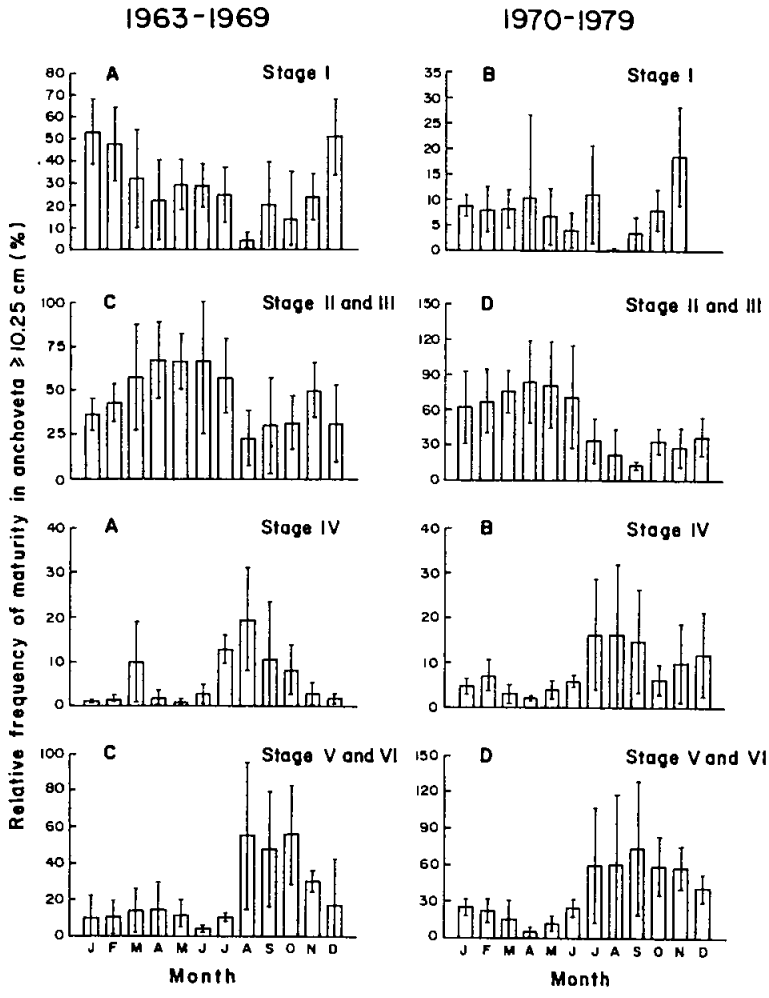

Fig. 5. Relative frequency of maturity stages I-VI in anchoveta sampled off southern Peru from 1963 to 1969 and 1970 to 1979.

Fig. 5. Frecuencia relativa de los estadíos de madurez I-VI de anchovetas muestreadas en el área sur del Perú durante 1963 a 1969 y de 1970 a 1979.

Consistent differences between the northern/central and the southern stock did not appear. Maturity stage I showed its highest percentages during the 1960s, a period in which a large quantity of juvenile fish were caught (IMARPE 1965).

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References

Einarsson, H., L.A. Flores and J. Miñano. 1966. El ciclo de madurez de la anchoveta peruana *(Engraulis ringens)*, p. 128-135. *In* I. Seminario Latinoamericano sobre el Océano Pacífico Oriental, Universidad Nacional Mayor de San Marcos, Lima-Perú.

Jordań, R. and A. Ch. de Vildoso. 1965. La anchoveta (*Engraulis ringens* J.) Conocimiento actual sobre su biología ecología y pesquería. Informe Inst. Mar Perú-Callao 6. 52 p.

Jordań, R. 1980. Biology of the anchoveta. *In* Summary of the present knowledge, p. 249-276. *In* Proceedings of the Workshop on the Phenomenon Known as "El Niño", Guayaquil, Ecuador, 4-12 December 1974. United Nations Educational, Scientific and Cultural Organization, Paris.

IMARPE. 1965. La pesquería de la anchoveta. Informe Inst. Mar Perú-Callao 1(1):1-15.

IMARPE. 1973. Third session of the panel of experts on the population dynamics of the Peruvian anchovy. Bol. Inst. Mar Perú-Callao 2(9): 552-559.

Miñano, J. 1958. Algunas apreciaciones relacionadas con la anchoveta peruana y su fecundidad. Bol. Cient. Cia. Admin. Guano 34: 11-34.

Miñano, J. 1968. Estudio de la fecundidad y ciclo sexual de la anchoveta (*Engraulis ringens* J.) en la zona de Chimbote. Bol. Inst. Mar Perú-Callao 1(9): 507-533.

Pauly, D. and I. Tsukayama, Editors. 1987a. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusemmanarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama. 1987b. On the implementation of management-oriented fishery research: the case of the Peruvian anchoveta, p. 1-13. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pellón, J., N. Peña and J. Mendo. 1988. Reporte de datos de madurez sexual de la anchoveta *(Engraulis ringens)*, 1861-1987. Informe Inst. Mar Perú-Callao 92. 77 p.

Peña, N. and S. Carrasco. 1988. Principales aspectos pesqueros y biológicos de los recursos anchoveta *Engraulis ringens* y sardina *Sardinops sagax* en los años 1986 y 1987. MS presentado al Simposio sobre Recursos Vivos y Pesquerías en el Pacífico Sudeste, Chile, 9-13 Mayo, 1988.

Santander, H. 1981. Patrones de distribución y fluctuaciones de desoves de anchoveta y sardina, p. 180-192. *In* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao, Volumen Extraordinario.

Santander, H. and O. Sandoval de Castillo. 1969. El desove de la anchoveta *(Engraulis ringens)* en los períodos reproductivos de 1961-1968. Ser. Informe Esp. Inst. Mar Perú-Callao 40: 1-6.

Mean Monthly Distribution, Abundance and Production of Anchoveta Eggs off Peru (4-14°S), 1964-1971 and 1972-1986*

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Abstract

This contribution is based on the detailed analysis (resolution: half-degree squares) of 90 maps of anchoveta *(Engraulis ringens)* egg standing stock off Peru (4-14°S), published in 1987 by H. Santander (IMARPE, Callao, Peru). It pertains to surveys conducted from 1964 to 1986. Monthly means were computed for each half-degree square using 3x3x3 running averages, i.e., involving all adjacent squares of a given month and square, and the adjacent squares of the preceding and following months. Monthly maps of egg distribution are presented, averaged over the periods 1964 to 1971 and 1972 to 1986, which are the phases preceding and following the 1972-1973 El Niño and the coincident stock collapse, respectively.

It is shown that the center of gravity of anchoveta egg production has shifted to the south along the coast. Also, the relationship between the two egg production seasons (August-October, January-March) has changed: egg production was much higher in spring than summer from 1964 to 1971, but was, from 1972 to 1986, slightly higher in summer. Overall, mean daily egg production was reduced from about 3.13×10^{13} in 1964-1971 to about 2.2×10^{13} in 1972-1986.

Resumen

Esta contribución se basa en un análisis detallado (resolución: cuadrado de medio grado) de 90 mapas de producción de huevos de anchoveta *(Engraulis ringens)* frente a Perú (4-14°S), publicados en 1987 por H. Santander (IMARPE, Callao, Perú). Estos se refieren a prospecciones realizadas de 1964 a 1986. Los promedios mensuales fueron calculados para cada cuadrado de medio grado usando promedios moviles de 3x3x3; esto es, involucrando todos los cuadrados adyacentes de un determinado cuadrado y mes, y los cuadrados adyacentes del mes precedente y siguiente. Se presentan mapas mensuales de distribución de huevos, promediados para los períodos 1964 a 1971 y 1972 a 1986, que son las fases precedente y siguiente al Niño 1972-1973 y el coincidente colapso del stock, respectivamente.

Se muestra que el centro de gravedad de la producción de huevos de anchoveta se ha desplazado al sur. Asimismo, la relación entre las dos estaciones de producción de huevos (Agosto-Octubre, Enero-Marzo) ha cambiado: la producción de huevos fué mucho mas alta en primavera que en el verano de 1964 a 1971, pero fue ligeramente mas alta en el verano de 1972 a 1986. En general, el promedio diario de producción de huevos se redujo de alrededor de 3.13×10^{13} en 1964-1971 hasta alrededor de 2.2×10^{13} en 1972-1986.

*ICLARM Contribution No. 503.

Introduction

The anchoveta *(Engraulis ringens)* once supported off Peru the largest single-species fishery of the world (Tsukayama and Palomares 1987). The collapse of this fishery, coincident with the 1972-1973 El Niño, has been, in earlier years, attributed to this hydrographic anomaly but the data presently available suggest that the purse seine fishery was the main culprit (see Muck, this vol.). The need to better manage this resource makes it particularly important to identify the key factors which determine recruitment of anchoveta. The present study is concerned with a process most likely to belong to these factors: the apparent rate of production of eggs by the anchoveta stock. The word "apparent", which will be omitted henceforth, refers to the fact that the rates of egg production derived and presented further below do not account for egg mortality, which is covered by Pauly and Soriano (this vol.).

Also, the geographical distribution of this egg production will be presented. However, due to limitations of the available data, the pertinent maps will refer only to monthly 'climatological' averages for two periods - 1964 to 1971 and 1972 to 1986. This division of the available data into two sets was chosen to cover two crucial phases: one of high anchoveta biomasses, lasting from the beginning of egg survey work to the 1972-1973 El Niño, and of generally low, but highly variable biomasses, lasting from 1972 to 1986 (see Pauly and Palomares, this vol.).

Materials and Method

The present contribution, extracted from Senocak (1988), is based entirely on the 90 maps of egg distribution in Santander (1987), pertaining to the area off Peru comprised between 4 and 14°S and based on surveys conducted from 1964 to 1986. Santander (1987) provides details on these surveys. Of this information, only the map number, the year and the month are reported here (Table 1). Sampling was performed from 50 m to the surface with a Hensen net 175 cm long, 70 cm aperture diameter and 300 mm meshes.

Table 1. Within- and between-year availability of anchoveta egg distribution maps used for this contribution.[a]
Tabla 1. Disponibilidad dentro de años y entre años, de mapas de distribución de huevos de anchoveta usados en esta contribución.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total No. of maps
1964			1	2		3			4			5	5
1965			6	7			8				9		4
1966		10			11				12		13		4
1967					14				15		16		3
1968		17							18			19	3
1969	20						21		22				3
1970					23				24	25	26		4
1971					27			28			29		3
1972		30					31/32	33	34/35	36		37	8
1973	38		39			40/41	42	43	44		45		8
1974		46			47			48	49		50		5
1975		51						52	53			54	4
1976	55						56	57			58		4
1977			59	60			61	62/63		64/65			7
1978				66			67			68		69	4
1979		70					71		72		73		4
1980	74								75				2
1981		76		77					78	79			4
1982		80							81			82/83	4
1983													0
1984									84			85	2
1985		86	87					88	89				4
1986					90								1
Total No. of Maps	4	9	5	5	6	3	9	9	17	6	9	8	90

[a] Numbers for different months and years refer to the map numbers in Santander (1987).

The original station records were not accessible to the authors; hence, this work is based on the maps of egg abundance assembled since 1964 by H. Santander and colleagues at IMARPE, of which all had been redrawn at ICLARM, Manila, using a base map and standardized labeling schemes (Table 2).

The surveys documented through Santander's maps did not all cover the investigation area as defined in Fig. 1. However, no large-scale interpolation or extrapolation were undertaken here to compensate for this deficit. Rather, strict rules were applied for small-scale (within half-degree square) interpolations (Fig. 2), i.e., larger areas not covered during a given survey were not included in any of the analyses.

Each half-degree square included in the analysis was divided up into 100 subunits and the egg abundance (d) estimated for each subunit, based in class means in Table 2.

Table 2. Class limits and assumed class means of anchoveta egg abundance maps in Santander (1987), in eggs/m^2.
Tabla 2. Límites de clase y clase media asumida de los mapas de densidad de huevos de anchoveta presentados por Santander (1987), en huevos/m^2.

First group of maps		Second group of maps[a]	
Class intervals	Means	Class intervals	Means
		1 - 100	50
1 - 500	250	101 - 500	300
501 - 1000	750	501 - 1000	750
1001 - 4000	2500	1001 - 2000	1500
>4000	5000[b]	>2000	3000

[a] Refers only to map nos. 8, 20-24, 28, 31 and 40.
[b] Used here instead of 5013 in Santander (1987).

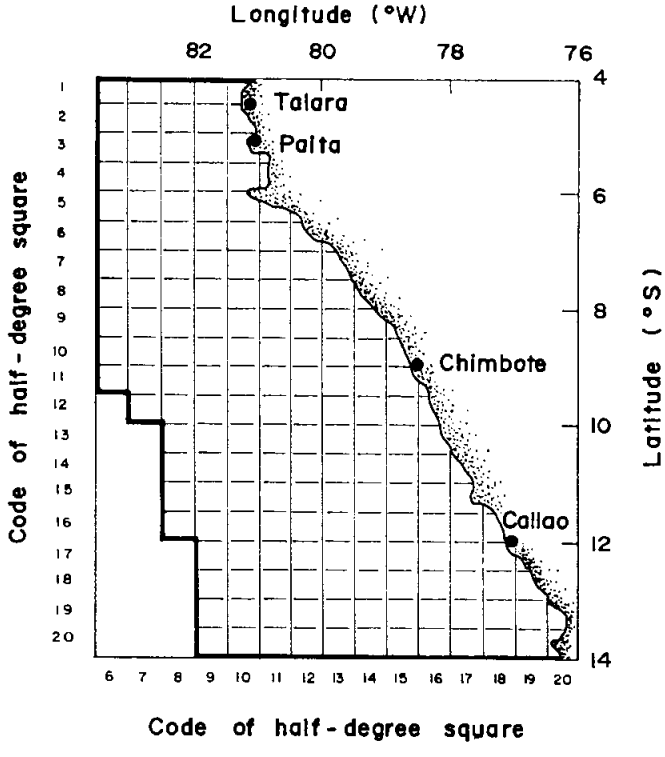

Fig. 1. Investigation area off Peru (4-14°S) showing towns mentioned in the text and numbering system for the 182 half-degree squares used to digitize information in the 90 egg distribution maps of Santander (1987). Area includes only half-degree squares covered during at least one egg survey from 1964 to 1986.
Fig. 1. Area de investigación frente a Perú (4-14°S), mostrando los lugares mencionados en el texto y el sistema de numeración para los 182 cuadrados de medio grado, usados para registrar la información de los 90 mapas de distribución de huevos reportados por Santander (1987). El area incluye sólo a los cuadrados de medio grado donde se realizó por lo menos una prospección de huevos de 1964 a 1986.

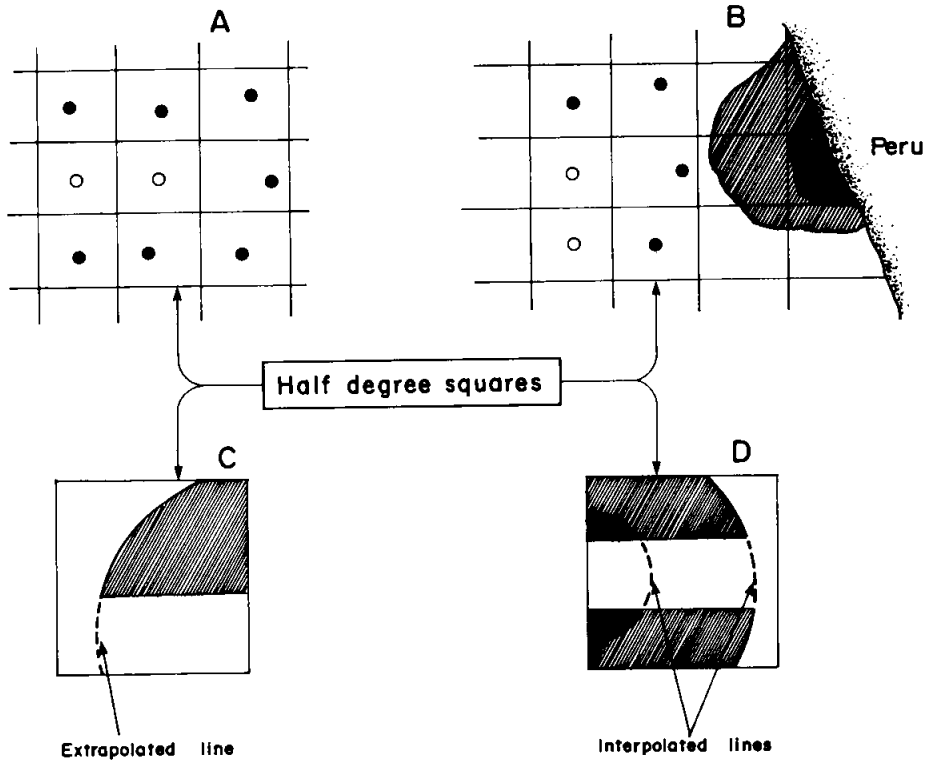

Fig. 2. Schematic representations of rules for interpretation of maps in Santander (1987). A: In cases where half-degree squares without observation (o) were surrounded by zero observation (•), the encircled squares were assumed to also contain a zero observation. B: When isolines of egg densities along the coast were clearly delimited by zero values, seaward squares without observations were assumed to contain no eggs. C and D: Interrupted isolines in maps, due to missing stations, were extrapolated or interpolated by eye, following the trend of the lines within the half-degree squares.

Fig. 2. Representación esquemática de reglas para la interpretación de los mapas de Santander (1987). A: En los casos donde el cuadrado de medio grado sin observación (o) esta indicado por observación cero (•), se asume que el cuadrado circunscrito también contiene observación cero. B: Cuando las isolíneas de densidades de huevos a lo largo de la costa están claramente delimitadas por valores cero, se ha asumido que los cuadrados hacia la costa y sin observaciones tampoco contiene huevos. C y D: Las isolíneas interrumpidas en los mapas, debido a estaciones ausentes, fueron extrapoladas o interpoladas al ojo, siguiendo la tendencia de las líneas dentro del cuadrado de medio grado.

The mean abundance of eggs per m² (E_j) in a given half degree during a given survey and square (j) was then estimated from:

$$E_j = (\Sigma n_1 d_1) N_j^{-1} \qquad \text{... 1)}$$

where N_j is the number of subunits in square (j), n_1 the number of subunits of a given egg abundance level (see Table 2), and d_1 the mean number of eggs per m² for that group of subunits. Note that directly under the coast, squares with $N < 100$ were rather frequent (see Fig. 1).

The estimated development time of anchoveta eggs were taken, for the years 1964-1982 from Table 3 in Santander (1987). For the following period, which lasted to the end of 1986, development time (D, in days) was estimated from

$$\log_{10} D = 6.953 - 4.09 \log_{10} (T + 26) \qquad \text{... 2)}$$

where T is the sea surface temperature (SST, in °C), and which was derived by Pauly (1987) from equation (5) in Pauly and Pullin (1988) and from empirical data in Santander and Sandoval de Castillo (1973). The temperature used to represent the Peruvian coast from 4 to 14°C south for the years 1982-1986 are means of the monthly temperatures for Talara, Paita, Chimbote and Callao (see Table 2 and Figs. 3 and 4).

Table 3. Mean monthly sea surface temperature at Talara, Paita, Chimbote and Callao (Peru), 1984-1986, in °C.[a]
Tabla 3. Promedios mensuales de la temperatura superficial del mar en Talara, Paita, Chimbote y Callao (Perú), 1984-1986 (en °C).

	Talara			Paita			Chimbote			Callao		
Month	1984	1985	1986	1984	1985	1986	1984	1985	1986	1984	1985	1986
Jan	(19.9)	(18.9)	20.8	19.9	18.9	21.5	20.5	19.5	20.0	16.0	15.0	14.7
Feb	(23.5)	(21.0)	23.5	23.5	21.0	22.3	20.2	18.8	21.2	16.2	15.2	17.0
Mar	(22.5)	(22.7)	19.6	22.5	22.7	20.7	19.7	20.3	20.0	17.0	15.6	15.9
Apr	(19.8)	(19.5)	18.8	19.3	19.0	18.1	19.9	18.5	19.5	18.0	15.0	15.4
May	(18.0)	16.3	18.9	17.4	16.0	18.0	18.8	17.6	18.3	16.3	14.9	15.3
Jun	(17.6)	18.1	17.9	17.0	17.8	16.9	17.8	17.6	17.8	15.6	14.9	15.5
Jul	(17.1)	16.9	19.1	16.5	16.4	17.9	18.9	17.1	17.8	15.5	15.1	15.5
Aug	(16.9)	16.6	18.5	16.3	15.7	17.5	18.0	17.1	18.7	15.3	14.7	16.1
Sep	(17.1)	16.7	17.2	16.5	15.9	16.0	18.0	17.5	18.6	14.7	14.5	15.7
Oct	(17.1)	16.9	18.9	16.5	16.1	18.4	18.8	18.2	18.0	14.6	14.6	15.0
Nov	(17.6)	16.7	20.0	17.0	16.7	19.6	19.0	18.3	20.3	15.1	14.3	15.8
Dec	(17.6)	18.7	20.5	17.0	18.1	20.0	19.3	19.1	21.5	14.8	14.7	16.5

[a] Estimates in brackets derived from regression in Fig. 4 and from Paita values; values for 1983 were not needed, given the absence of egg maps in that year.

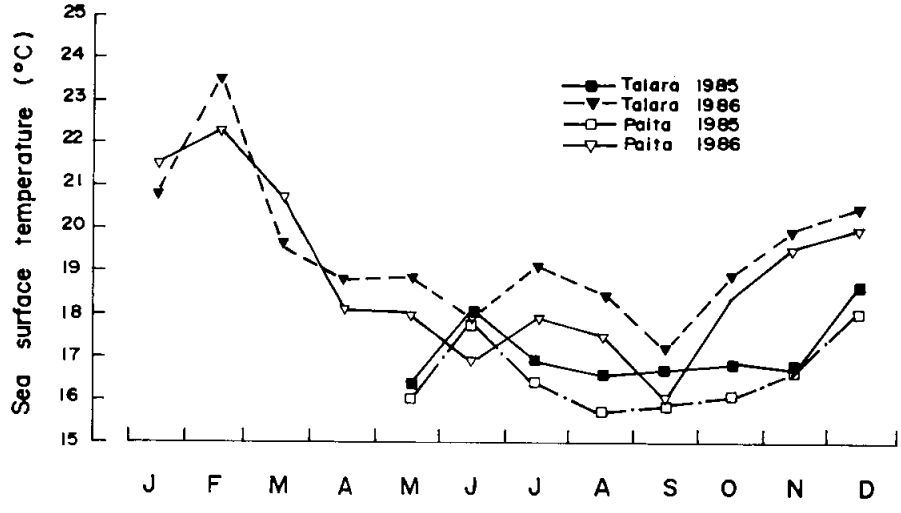

Fig. 3. Mean monthly sea surface temperature at Talara and Paita, Peru, 1985 and 1986 (from IMARPE, unpublished data).
Fig. 3. Promedios mensuales de temperatura superficial en Talara y Paita, Perú, 1985 y 1986 (de IMARPE, datos no publicados).

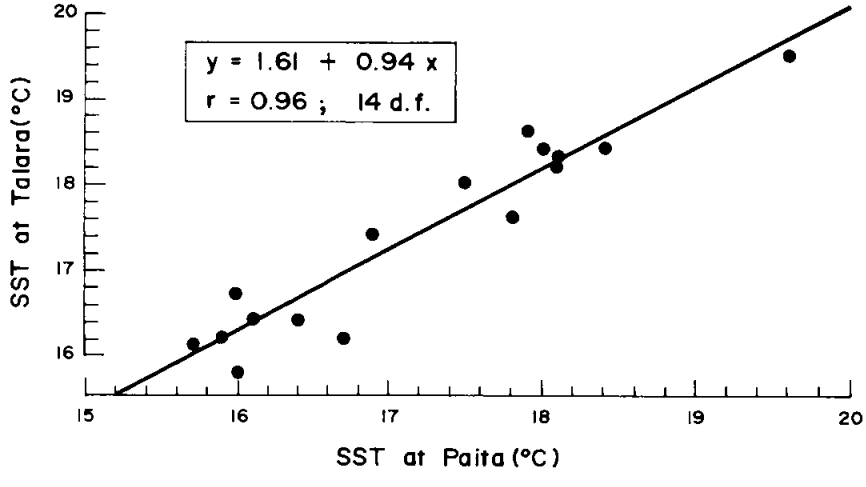

Fig. 4. Regression of sea surface temperature at Talara *vs.* sea surface temperature at Paita (May-December 1985 and May-December 1986), as used to predict missing SST values for Talara.
Fig. 4. Regresión de la temperatura superficial del mar en Talara vs. temperatura superficial del mar en Paita (Mayo-Diciembre 1985 y Mayo-Diciembre 1986), utilizada para predecir los valores ausentes de la temperatura superficial del mar de Talara.

Daily anchoveta egg production per m² (P_d) was then computed, for each half-degree square (j) and each survey/month using

$$P_{dj} = E_j * D_{-1} \qquad \text{... 3)}$$

The resulting maps turned out to have numerous gaps and were rather difficult to interpret. Therefore, a 3x3x3 interpolation scheme (see Fig. 5) was used to smoothen the data. This resulted in the elimination of gaps while simultaneously leading to the emergence of interpretable spatial patterns. Without missing values, the smoothing scheme in Fig. 5 will not lead to biased means, but to reduced variance (Sager 1971).

After smoothing, the monthly values of P_{dj} were averaged for the periods 1964 to 1971 and 1972 to 1986.

Santander's maps were Mercator projections, i.e., the east-west extent (e.g., in km) of a one-degree "square" changes with latitude (see Table 4). These values were used to convert the smoothed egg production estimates per m² within each half-degree square into production estimates per total area.

Finally, the geographic center of gravity of the anchoveta egg production was computed for each of the 12 months in the two periods by multiplying the production in each half-degree square by the latitude and longitude of its center, then computing the (weighted) average latitudes and longitudes by month.

Table 4. Relationship between degree of latitude and km equivalent at 4-14°S.[a]
Tabla 4. Relación entre grado de latitud y su equivalencia en km de 4-14°S.

Latitude (°South)	Km. equivalent of one degree longitude
4	112.04
5	110.89
6	110.70
7	110.48
8	110.23
9	109.95
10	109.63
11	109.27
12	108.89
13	108.47
14	108.02

[a] From Klein (1894).

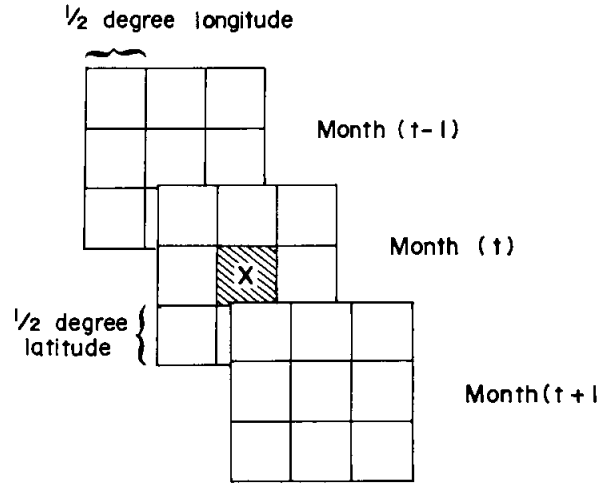

Fig. 5. Schematic representation of 3x3x3 smoothing scheme in space and time. This scheme was also used for interpolation of missing values, but only when observations were available for at least 2 out of the 27 half-degree squares.
Fig. 5. Representación esquemática del arreglo emparejado de 3x3x3 en el espacio y tiempo. Este esquema también fue empleado para interpolar valores ausentes, pero sólo cuando se dispuso por lo menos de observaciones en 2 de los 27 cuadrados de medio grado.

Results and Discussion

The smoothed "climatological" maps of monthly anchoveta egg production obtained here for the periods 1964 to 1971 and 1972 to 1986 are presented here in Figs. 6a, 6b, 6c and 6d. As might be seen, maximum egg production generally occurs in a single band right along the coast, although there are indications in certain months (e.g., February or October, first and second period) of two distinct spawning "centra" (*sensu* Mathisen, this vol.), one at about 8°S, the other at about 13°S.

The center of gravity for both series (1964 to 1986) and all months combined is 9°42'S, which is very close to the value of 9°48'S that can be estimated from Table 2 of Santander (1987). This implies that Santander's large-scale extrapolation of limited surveys (and maps) to

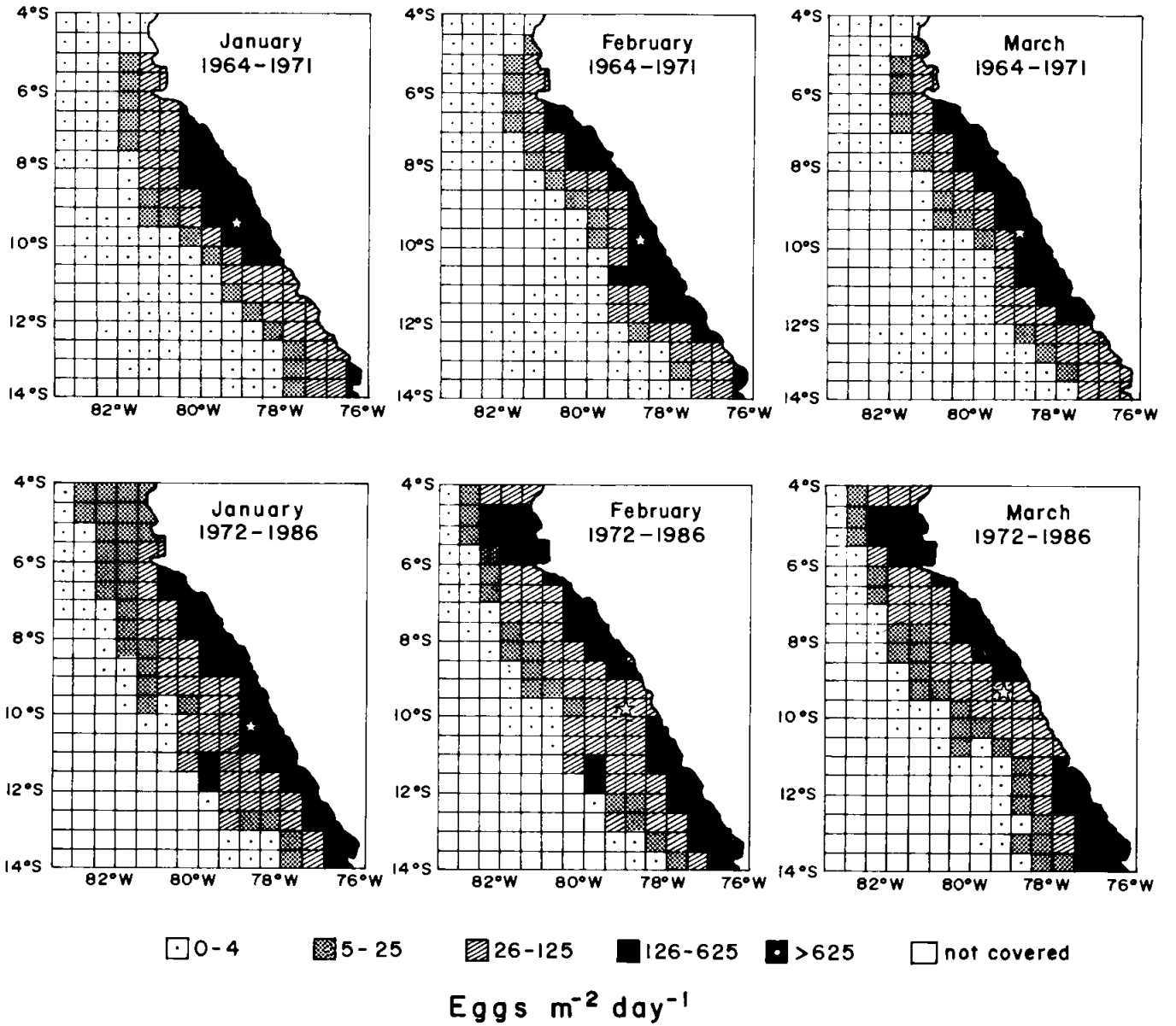

Fig. 6a. Geographic distribution of mean monthly anchoveta egg production (eggs/m^2/day) for the months of January, February and March during two periods (above 1964-1971; below 1972-1986). The large white star indicates center of gravity of the production values.

Fig. 6a. Distribución geográfica de los promedios mensuales de producción de huevos de anchoveta (huevos/m^2/dia) para los meses de Enero, Febrero y Marzo, durante dos períodos (arriba 1964-1971; abajo 1972-1986). La estrella blanca indica el centro de gravedad de los valores de producción.

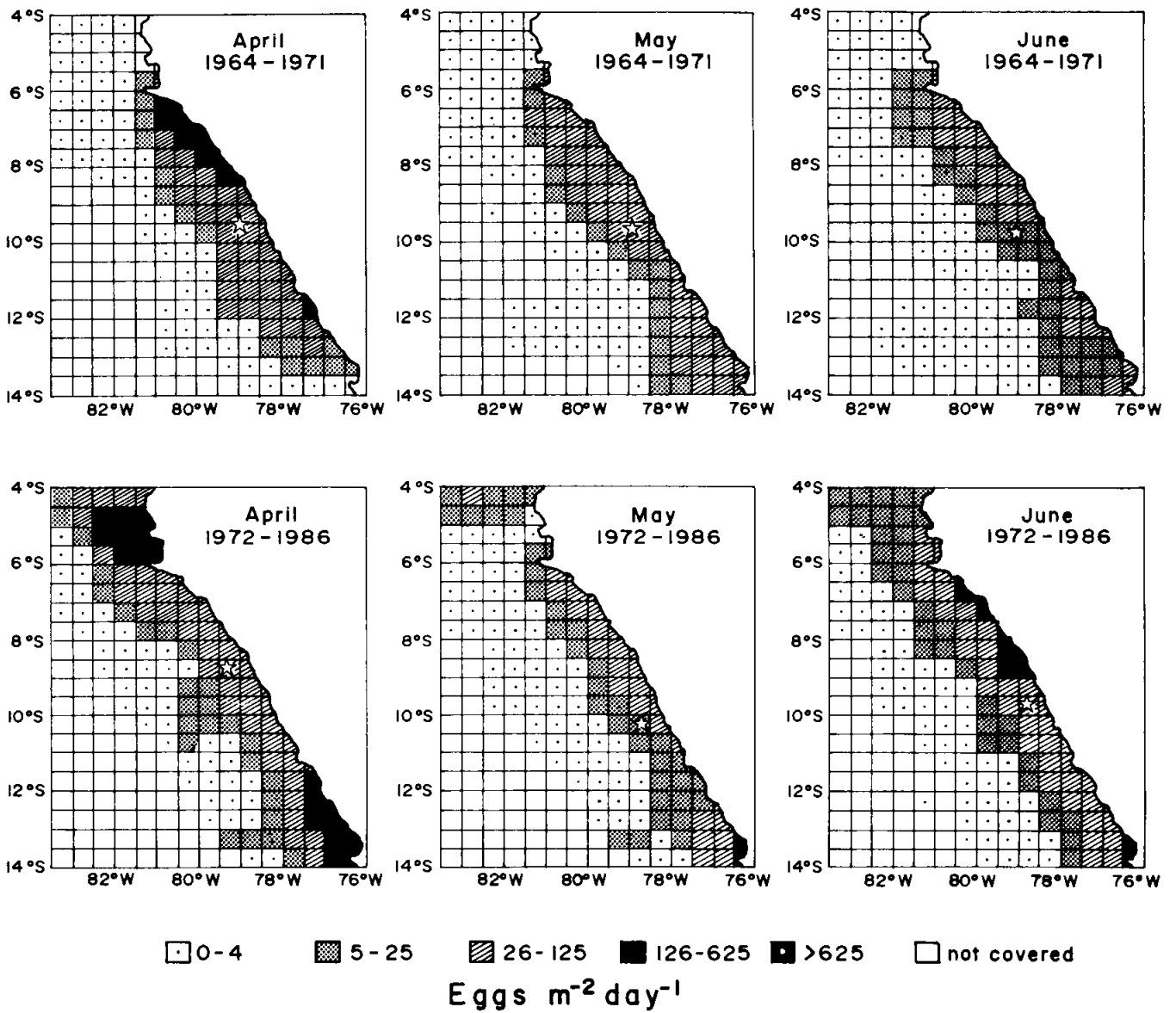

Fig. 6b. Geographic distribution of mean monthly anchoveta egg production (eggs/m^2/day) for the months of April, May and June during two periods (above 1964-1971; below 1972-1986). The large white star indicates center of gravity of the production values.

Fig. 6b. Distribución geográfica de los promedios mensuales de producción de huevos de anchoveta (huevos/m^2/dia) para los meses de Abril, Mayo y Junio, durante dos períodos (arriba 1964-1971; abajo 1972-1986). La estrella blanca indica el centro de gravedad de los valores de producción.

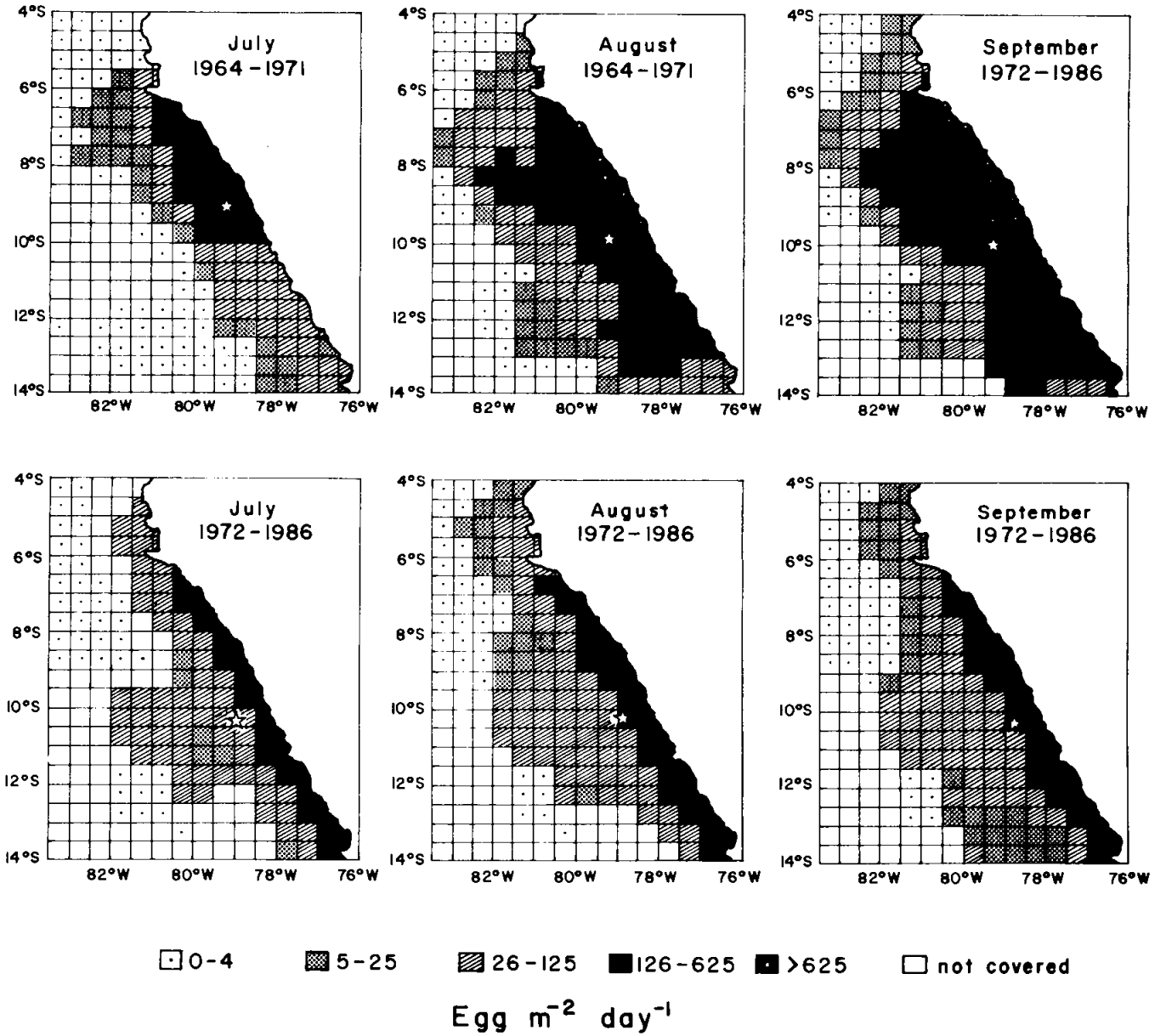

Fig. 6c. Geographic distribution of mean monthly anchoveta egg production (eggs/m^2/day) for the months of July, August and September during two periods (above 1964-1971; below 1972-1986). The large white star indicates center of gravity of the production values.

Fig. 6c. Distribución geográfica de los promedios mensuales de producción de huevos de anchoveta (huevos/m^2/dia) para los meses de Julio, Agosto y Septiembre, durante dos períodos (arriba 1964-1971; abajo 1972-1986). La estrella blanca indica el centro de gravedad de los valores de producción.

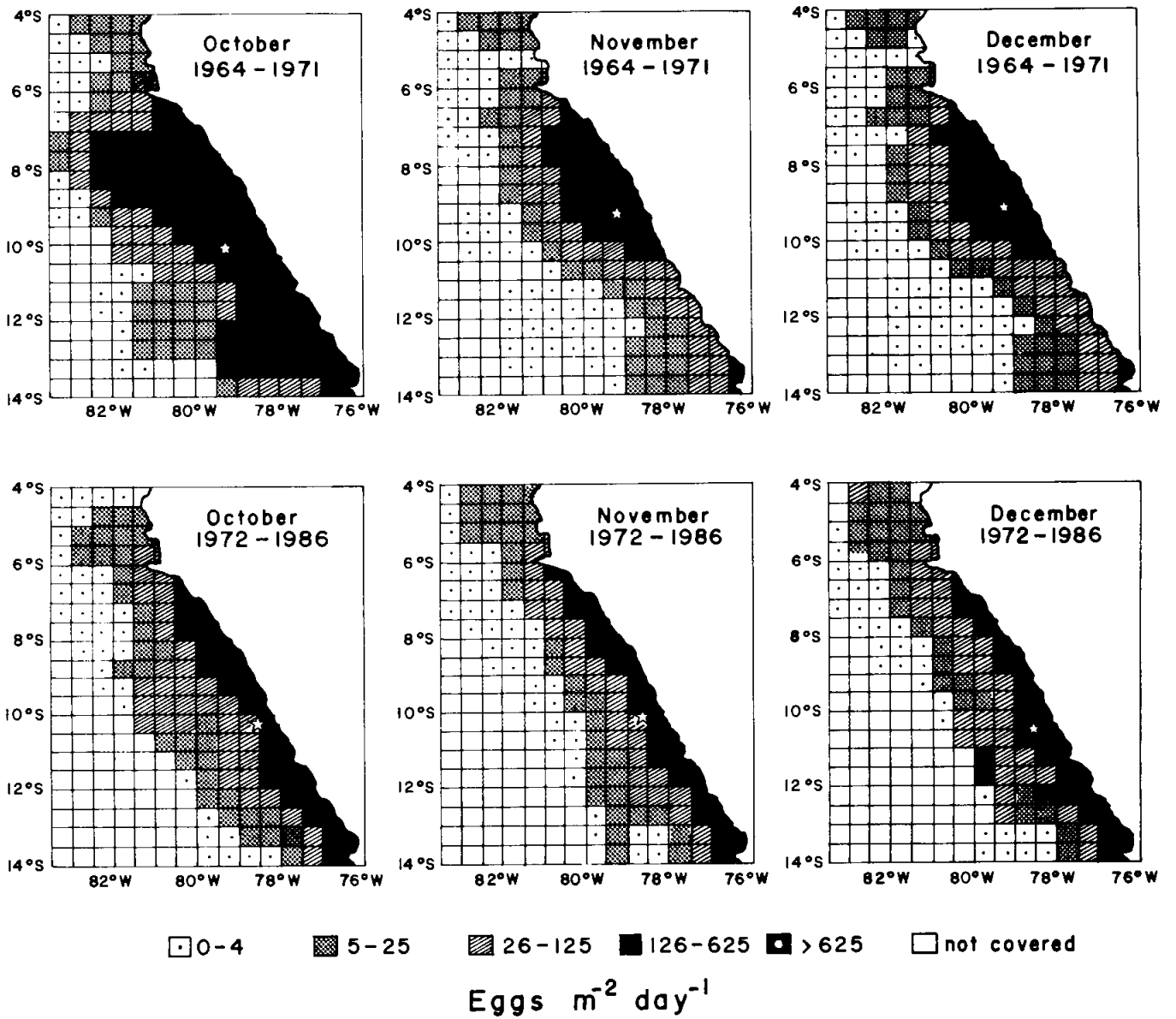

Fig. 6d. Geographic distribution of mean monthly anchoveta egg production (eggs/m^2/day) for the months of October, November and December during two periods (above 1964-1971; below 1972-1986). The large white star indicates center of gravity of the production values.

Fig. 6d. Distribución geográfica de los promedios mensuales de producción de huevos de anchoveta (huevos/m^2/dia) para los meses de Octubre, Noviembre y Diciembre, durante dos períodos (arriba 1964-1971; abajo 1972-1986). La estrella blanca indica el centro de gravedad de los valores de producción.

the whole of the northern-central coast of Peru (4-14°S) did not lead to any bias that would shift the north-south balance.

Fig. 7 presents the center of gravity of anchoveta egg production off Peru on a monthly basis, for each of the two periods distinguished here. As might be seen, spawning of anchoveta in 1972-1986 involved more seasonal changes than it did in 1964-1971.

Also, a shift southward along the coast appears to have occurred. This may be in line with the "southernization" hypothesis of Palomares et al. (1987), which states that *Engraulis ringens* off northern/central Peru have become, over the last decades, more similar to their southern counterparts - in terms of various aspects of their biology - than they were earlier.

Fig. 8 presents, finally, monthly averaged estimates of total anchoveta egg production off Peru (4-140°S) for the two periods considered here. The similarity between the two curves involves:

i) evidence of two peaks per year, one lasting from January to March ("summer"), the other from August to October ("spring") and

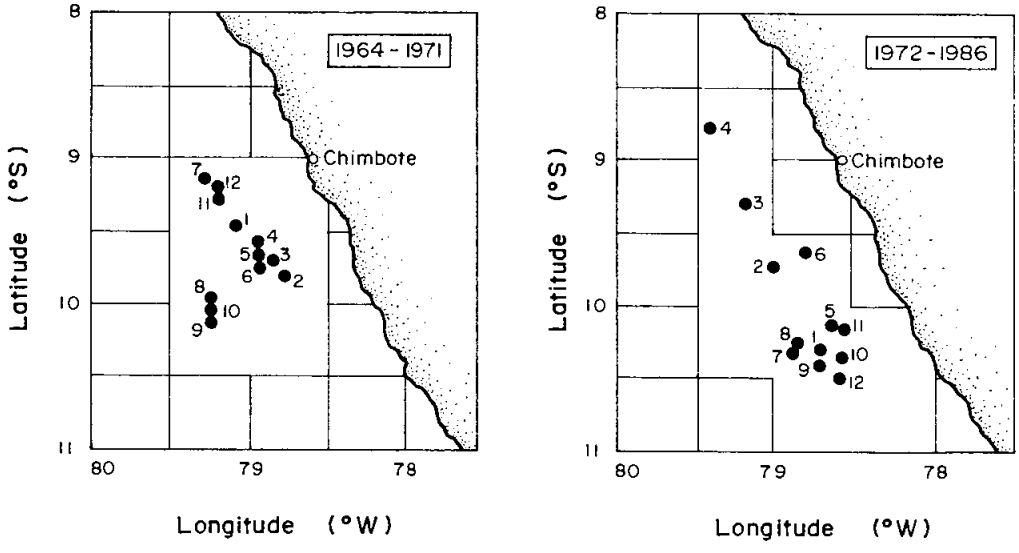

Fig. 7. Location changes of center of gravity of anchoveta egg production along the Peruvian coast, 4-14°S (1-12 = January-December). Left: monthly changes from 1964 to 1971. Right: monthly changes from 1972 to 1986. (Note wider range and southeastern shift in later period.)

Fig. 7. Cambios en la ubicación de los centros de gravedad de producción de huevos de anchoveta a lo largo de la costa peruana, 4-14°S (1-12 = Enero-Diciembre). Izquierda: Cambios mensuales de 1964 a 1971. Derecha: Cambios mensuales de 1972 a 1986. (Nótese para los últimos años una mayor amplitud y un cambio hacia el sur).

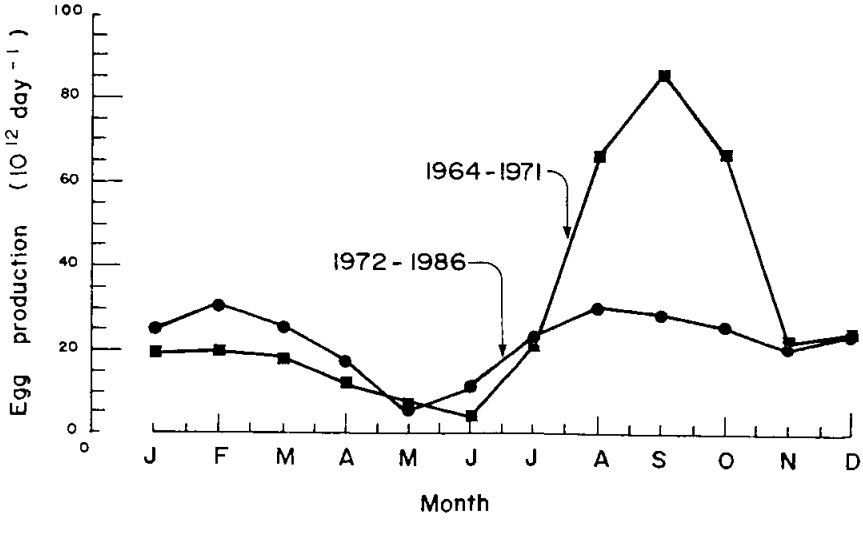

Fig. 8. Mean monthly egg production of anchoveta off Peru (4-14°S) for the periods before and after the 1972/1973 El Niño. (Note marked difference in the September peak.)

Fig. 8. Promedios mensuales de producción de huevos de anchoveta frente a Perú (4-14°S) para los períodos anterior y posterior al Niño 1972/1973. (Nótese la marcada diferencia en el máximo de Septiembre).

ii) a production minimum in May-June ("fall").

However, it is the difference between these two curves which strikes us most. In the first period (1964-1971), the spring peak was much larger than the summer peak, while both peaks are more or less equal in the second period (1972-1986).

A number of hypotheses could be presented to explain this large difference (Senocak 1988). However, as pointed out in the Introduction, the egg production rates estimated here are *apparent* rates, i.e., they do not account for egg mortality. We shall, therefore, abstain from suggesting here a cause for the change reflected in Fig. 8. The reader is invited, however, to consult Pauly and Soriano (this vol.) for a follow-up on anchoveta egg production and mortality.

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References

Klein, H. 1894. Mathematische Geographie. Verlag J.J. Weber, Leipzig.

Palomares, M.L., J. Muck, J. Mendo, E. Chúman de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982, p. 117-141. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. 1987. Managing the Peruvian ecosystem: a synthesis, p. 325-342. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and R.S.V. Pullin. 1988. Hatching time in spherical pelagic, marine fish eggs in response to temperature and egg size. Environ. Biol. Fish. 22(4): 261-271.

Sager, G. 1971. Eigenarten der übergreifenden Mittelwertbildung. Monatsber. Dt. Akad. Wiss. Berlin 13(2): 86-97.

Santander, H. 1987. Relationships between anchoveta egg standing stock of parent biomass off Peru, 4-14°S, p. 179-207. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Santander, H. and O. Sandoval de Castillo. 1973. Estudio sobre la primera etapa de vida de la anchoveta. Informe Inst. Mar Perú-Callao 4: 1-30.

Senocak, T. 1988. Verteilung und Dichteabhängige Sterblichkeit der Eier von *Engraulis ringens* vor Peru. Institut für Meereskunde, Christian-Albrecht Universität, Kiel, 74 p. M.S. thesis.

Tsukayama, I. and M.L. Palomares. 1987. Monthly catch and catch composition of Peruvian anchoveta *(Engraulis ringens)* (northern-central stock, 4-14°S), 1953 to 1982, p. 89-108. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Production and Mortality of Anchoveta *(Engraulis ringens)* Eggs off Peru*

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Abstract

The egg production of anchoveta was estimated by month from 1953 to 1985 based on estimates of mature female biomass batch fecundity and related factors for the period 1953-1985 off Peru (4-14°S). These theoretical estimates of production were related to empirical estimates derived from egg surveys conducted from 1964 to 1985. This yielded estimates of egg mortality; a multiple regression model including parent stock size, sardine biomass, SST and SST anomaly explained a large fraction of the variance of these egg mortality estimates. However, how results suggest parent *concentration* (rather than parent stock size) to be the key parameter affecting anchoveta egg mortality, a hypotheses which will have to be tested in a future contribution.

Resumen

Se estimó la producción de huevos mensual de la anchoveta peruana (4-14°S) de 1953 a 1985 basado en estimaciones de la fecundidad biomasa de hembras maduras y factores relacionados para el período 1953-1985 frente a Perú (4-14°S). Estas estimaciones de producción teóricas fueron relacionadas con estimaciones empíricas obtenidas de cruceros de evaluación de huevos realizados de 1964 a 1985. Esto proporcionó estimaciones de mortalidad de huevos; un modelo de regresión múltiple que incluye el tamaño del stock de padres, biomasa de sardina, TSM y anomalías de TSM, explicó una gran parte de la varianza de estos estimados de mortalidad de huevos. Sin embargo, como los resultados lo sugieren, la concentración de padres (más que el tamaño del stock de padres) es el parámetro clave que afecta la mortalidad de huevos, una hipótesis que deberá ser probada en una contribución futura.

Introduction

Recruitment to a stock depends on (i) the size of the spawning stock and (ii) the survival of the eggs and larvae. Within fishery biology, an immense literature exists on how to forecast the recruitment of fish stock given a knowledge of spawning stock size, i.e., from the "top-down" (reviews in Ricker 1954; Cushing 1988). There have also been numerous attempts to approach the recruitment problem from the "bottom-up", i.e., through detailed analyses of the factors controlling the survival of eggs and larvae (see, e.g., papers in Sharp 1980 and Rothschild 1986).

While generally, "bottom-up" approaches have been more costly, more data intensive, yet less successful than "top-down" approaches in providing management advice, it is nevertheless clear that management of important fish resource species should be based on an understanding of all aspects of their life history, including the early stages.

In the case of the Peruvian anchoveta, sufficient data are available on the dynamics of the parent stock, and on the distribution and density of the eggs to justify an attempt to identify the major causes of anchoveta egg mortality.

*ICLARM Contribution No. 507.

Materials and Methods

Two sources of data were tapped for this contribution:

i) length-structured biomass estimates obtained by VPA (Pauly and Palomares, this vol.) and which were used to estimate parent biomass, mature female biomass and egg production, by month, for the period January 1953 to July 1985, using a model to be briefly described further below; and

ii) Ninety maps of anchoveta egg distribution based on egg surveys conducted from 1964 to 1985, and which were published and subjected to preliminary analyses by Santander (1987) and Senocak et al. (this vol.).

The model used here to estimate the monthly reproductive output (RO), i.e., egg production, of anchoveta has the form:

$$RO_i = \sum_{j=1}^{n} B_{ij} \cdot P_{ij} \cdot A_j \cdot S_k \cdot PF_j \cdot RF \qquad \text{... 1)}$$

where j is the number of length classes for which, in a given month i, anchoveta biomass estimates are available (see Table 1 for the definition of the other terms).

Fig. 1 gives an example of the type of maps published by Santander (1987) and the first five columns of Table 2 summarize the key information pertaining to or extracted from these maps. Most important here is the fifth column, i.e., the estimates of egg standing stock, derived by planimetry (Santander 1987). [Some of these maps represented surveys which had covered less than the 4-14°S stretch of the Peruvian coast used here as reference. The estimated egg standing stocks for these maps have been, in these cases, extrapolated to the whole reference area using a procedure documented in Santander (1987). The detailed planimetry of Senocak et al. (this vol.), which did not involve any large-scale extrapolation, shows that no detectable bias was introduced by Santander's extrapolation procedure.]

Table 1. Specifications of the multiplicative model used by Pauly and Soriano (1987) to estimate the egg production of Peruvian anchoveta (equation 1), by month (i), based on biomass data by length class (j)[a].

Tabla 1. Especificaciones del modelo multiplicativo usado por Pauly y Soriano (1987) para estimar la producción de huevos de anchoveta (ecuación 1) por meses (i) basado en datos de biomasa por clase de longitud (j).[a]

Variable or constant	Definition	(units)	Remarks and/or source of estimate
B_{ij}	Biomass of male and female anchoveta	(tonnes)	From VPA III output of Pauly and Palomares (this vol.)
P_{ij}	Fraction of mature fish	(dimensionless)	Derived from logistic curve with shape and position varying with SST (see Pauly and Soriano 1987)
A_j	Size-specific factor relating anchoveta fecundity per unit weight to length	(dimensionless)	See Tables 2 and 3 in Pauly and Soriano (1987)
S_k	No. of spawnings per month, k=1 (January); k=12 (December)	(1/t)	From Table 3 in Pauly and Soriano (1987), based on Jordan (1980)
PF_j	Fraction of females in parent stock	(dimensionless)	From Fig. 4 and Table 3 in Pauly and Soriano (1987), based on Clark (1954), Miñano (1958) and Jordan (1959)
RF	Relative batch fecundity	(eggs/g)	Value of 596/g female taken from Santander et al. (1984)
10^9	Factor for adjusting gram to tonne	(dimensionless)	Used, but not given in Equation (1)
n	Number of length classes used in month (i)	(dimensionless)	Variable between months

[a] See Pauly and Soriano (1987) for further details on model derivation and specification and on data sources.

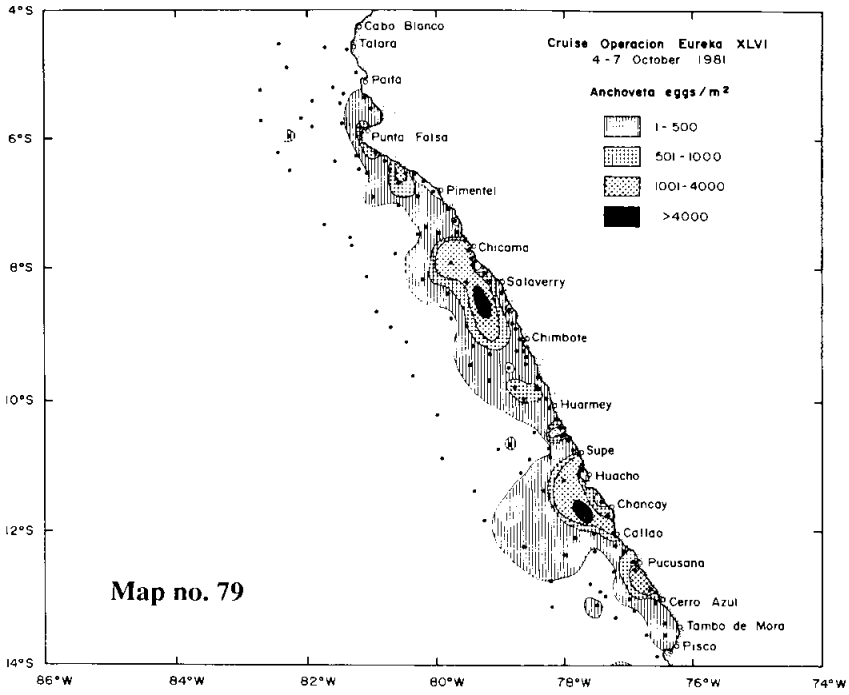

Fig. 1. Anchoveta egg distribution off Peru (4-14°S), in early October 1981. Details on this map (No. 79 in Santander 1987), given here as an example, are provided in Table 2.

Fig. 1. Distribución de huevos de anchoveta frente al Perú (4-14°S) a comienzos de Octubre 1981. Detalles de éste mapa (No. 79 en Santander 1987), presentado aquí como un ejemplo, se dan en la Tabla 2.

Pauly (1987) had attempted to estimate anchoveta egg mortality by relating theoretical egg production (as estimated via equation 1), to the egg standing stock in Santander's maps. However, the model he used to calculate egg mortality (his equation 4) produced biased estimates when egg mortality was low (J.A. Gulland, pers. comm. to D. Pauly, December 1987), and his whole section on "the cannibalization of anchoveta eggs" (inclusive of his Table 2 and Fig. 4) is thus erroneous.

We used instead an approach suggested by J.A. Gulland (pers. comm.). Defining N_d as the egg standing stock at the end of period D, and R as the initial size of a "cohort" of anchoveta eggs, it follows for that cohort, that:

$$N_d = R\,e^{-ZD} \qquad \text{... 2)}$$

where Z is the egg mortality from spawning/fertilization to hatching and D (days) is the egg development time. The parameter D can be estimated from:

$$\log_{10}D = 6.953 - 4.09\log_{10}(T+26) \qquad \text{... 3)}$$

where T is the sea surface temperature (SST, in °C) and which was derived by Pauly (1987) based on data in Santander and Sandoval de Castillo (1973) and equation (5) in Pauly and Pullin (1988).

Under steady-state condition (assumed here to prevail shortly before, during and after a given egg survey was conducted and/or during a period of one month), equation (2) implies a mean standing stock (N) whose value can be estimated from:

$$\bar{N} = \frac{1}{D}\int_0^D Re^{-ZD} \qquad \text{... 4)}$$

or

$$\bar{N} = \frac{R}{ZD}(1 - e^{-ZD}) \qquad \text{... 5)}$$

Table 2. Summary of data on anchoveta egg surveys conducted from 1964 to 1985 off Peru (4-14°S)[a], with added ancillary information and some derived statistics.

Tabla 2. Resumen de los datos de los cruceros de evaluación de huevos de anchoveta llevados a cabo de 1964 a 1985 frente al Perú (4-14°S) con alguna información adicional y estadísticas derivadas.

Running no.	Map no.	Year	Month	Map standing stock (egg x 1012)[a]	Daily reproductive output (egg x 1012)[b]	Anchoveta parent stock (t x 106)[b]	Sardine biomass[c] (t x 106)	Egg development time (day)[d]	Z (day-1)[e]	Estimated Z (day-1)[f]
1	1	1964	Mar	27.4	16.8	5.01	0.32	1.53	-	0.238
2	2		Apr	17.0	3.35	3.19	0.31	1.74	-	0.251
3	3		Jun	12.9	4.71	1.04	0.30	2.02	-	0.076
4	4		Sep	137.0	68.8	1.54	0.31	2.10	0.049	0.555
5	5		Dec	60.3	(1.89)	(0.532)	0.34	2.02	-	0.138
6	6	1965	Mar	51.4	35.8	7.36	0.36	1.37	-	0.248
7	7		Apr	8.03	7.20	8.26	0.37	1.27	0.206	0.373
8	8		Jul	53.3	20.7	3.30	0.38	1.55	-	3.457
9	9		Nov	44.0	60.3	3.07	0.35	1.72	1.212	3.396
10	10	1966	Feb	16.2	19.7	6.55	0.33	1.37	0.822	0.249
11	11		May	4.94	1.19	3.10	0.31	1.78	-	0.428
12	12		Sep	418.0	74.4	1.44	0.30	2.14	-	0.407
13	13		Nov	97.4	123.0	2.50	0.30	1.96	1.139	1.001
14	14	1967	May	6.36	0.704	1.33	0.30	1.89	-	0.162
15	15		Sep	292.0	49.1	0.998	0.30	2.19	-	0.250
16	16		Nov	116.0	52.4	1.09	0.30	2.25	0.018	0.108
17	17	1968	Feb	50.2	32.0	2.70	0.30	1.77	0.134	0.100
18	18		Sep	169.0	185.0	2.74	0.30	1.98	0.921	1.524
19	19		Dec	15.5	127.0	2.16	0.31	1.85	7.722	0.723
20	20	1969	Jan	22.0	16.5	2.35	0.31	1.60	0.225	0.462
21	21		Jul	9.42	19.5	1.72	0.32	1.80	2.002	1.155
22	22		Sep	82.3	69.4	1.77	0.32	1.84	0.527	2.422
23	23	1970	May	22.1	53.8	14.10	0.30	1.61	2.330	1.741
24	24		Sep	82.0	(259.0)	(3.60)	0.30	1.89	3.104	2.866
25	25		Oct	22.6	(253.0)	(3.60)	0.30	1.82	10.989	3.581
26	26		Nov	9.05	(135.0)	(3.60)	0.30	1.87	13.369	1.956
27	27	1971	May	107.0	1.24	3.02	0.30	1.60	-	0.697
28	28		Aug	12.7	95.4	3.83	0.47	1.70	7.353	5.493
29	29		Nov	29.3	178.0	3.72	0.98	1.85	6.006	3.385
30g	30	1972	Feb	2.08	(44.3)	(2.59)	1.50	1.21	20.661g	0.233
31	31/32		Jul	13.2	(33.1)	(1.77)	2.18	1.29	2.385	2.755
32	33		Aug	23.8	(79.8)	(1.38)	2.18	1.42	3.324	6.717
33	34/35		Sep	7.19	(120.0)	(1.12)	2.18	1.57	15.924	8.129
34	36		Oct	5.47	(106.0)	(0.946)	2.18	1.55	21.505	6.810
35	37		Dec	62.3	9.70	2.34	2.18	1.26	-	0.347
36	38	1973	Jan	35.2	(5.06)	(3.05)	2.18	1.08	-	0.094
37	39		Mar	41.3	(10.7)	(3.07)	2.18	1.27	-	0.181
38	40/41		Jun	19.8	(2.75)	(4.71)	2.18	1.94	-	1.244
39	42		Jul	18.9	(20.4)	(9.53)	2.18	2.06	0.915	1.880
40	43		Aug	109.0	(23.5)	(4.44)	2.18	2.16	-	1.139
41	44		Sep	60.9	(52.4)	(6.70)	2.17	2.12	0.634	0.616
42	45		Nov	70.7	(170.0)	(2.28)	2.17	1.85	2.43	3.395
43	46	1974	Feb	86.4	(69.5)	(2.27)	2.15	1.67	0.381	0.257
44	47		May	3.44	(2.79)	(1.55)	2.13	1.61	0.34	0.954
45	48		Aug	85.2	(173.0)	(1.58)	2.14	1.91	1.967	2.540
46	49		Sep	64.7	(116.0)	(0.864)	2.15	2.04	1.766	1.155
47	50		Nov	29.6	(93.7)	(0.941)	2.17	1.85	3.183	1.169
48	51	1975	Feb	40.7	(29.3)	(1.73)	2.20	1.69	0.243	0.210
49	52		Aug	56.0	(105.0)	(1.37)	2.20	2.04	1.841	1.167
50	53		Sep	55.6	(196.0)	(1.78)	2.19	2.06	3.465	1.610
51	54		Dec	67.4	40.5	1.71	2.12	1.98	0.182	0.694
52	55	1976	Jan	17.0	(50.8)	(2.22)	2.10	1.84	3.007	0.447
53	56		Jul	53.8	22.8	1.93	1.98	1.50	-	4.768
54	57		Aug	53.6	57.3	2.06	2.03	1.54	0.705	8.885
55	58		Nov	19.2	81.2	2.16	2.18	1.64	4.352	6.748
56	59	1977	Mar	45.9	(9.30)	(1.68)	2.37	1.35	-	0.191
57	60		Apr	.313	(2.70)	(1.53)	2.42	1.35	-	0.402
58	61		Jul	28.0	(23.9)	(0.821)	2.52	1.77	0.507	1.832
59	62/63		Aug	25.4	(49.0)	(0.632)	2.48	1.87	1.85	1.823
60	64/65	1977	Oct	17.1	42.5	3.13	2.39	1.94	2.433	0.997
61	66	1978	Apr	2.67	(0.901)	(1.19)	2.42	1.54	-	0.448
62	67		Jul	64.7	(4.83)	(0.394)	2.52	1.94	-	0.538
63	68		Oct	6.44	(22.2)	(0.377)	2.39	1.94	3.432	1.116
64	69		Dec	25.5	(5.54)	(0.621)	2.24	1.82	-	0.833
65	70	1979	Feb	21.6	13.5	1.14	2.32	1.63	0.025	0.193
66	71		Jul	30.1	10.2	0.492	2.49	1.80	-	1.175
67	72		Sep	66.2	26.7	0.385	2.50	1.87	-	1.786
68	73		Nov	69.8	15.8	0.283	2.52	1.66	-	1.256
69	74	1980	Jan	21.8	3.72	0.461	2.53	1.58	-	0.372
70	75		Sep	68.2	28.9	0.360	2.57	1.94	-	1.219
71	76	1981	Feb	27.3	21.2	1.63	2.57	1.58	0.277	0.268
72	77		Apr	10.3	4.39	1.80	2.57	1.66	-	0.494
73	78		Sep	18.1	111.0	1.16	2.57	2.92	6.188	1.651
74	79		Oct	74.5	158.0	1.59	2.57	1.87	2.097	3.915
75	80	1982	Feb	86.4	69.7	2.36	2.57	1.58	0.329	0.336
76	81		Sep	31.6	127.0	0.782	2.98	1.78	4.01	4.220
77	82/83		Dec	9.79	9.96	0.412	3.60	1.03	0.10	0.060
78	84	1984	Sep	49.6	2.71	0.0394	3.76	2.08	-	0.174
79	85		Dec	85.6	1.06	0.114	3.21	1.96	-	0.173
80	86	1985	Feb	96.2	3.66	0.269	2.84	1.93	-	0.029
81	87		Mar	7.76	4.33	0 603	2.65	1.78	-	0.076
82	88		Aug	47.4	30.1	0.602	2.12	2.10	0.289	0.491
83	89		Sep	38.0	(12.9)	(0.187)	2.15	2.08	-	0.361
84	90	1986	May	10.8	(0.163)	(0.327)	2.34	1.91	-	0.174

[a] Adapted from Santander (1987, Table 3).
[b] From (part of) equation (1) and biomasses estimated by Pauly and Palomares (this vol.).
[c] From Table 1 in Muck (this vol.), with monthly values interpolated between annual means (used from June/July); these estimates are very crude and need refinement, based on future VPA estimates of sardine biomasses.
[d] From equation (3) and SST in Pauly and Tsukuyama (1987) for 1953 to 1982, and from Senocak et al. (this vol.) from 1983 to 1985.
[e] From equation (6).
[f] From equation (9).
[g] Outlier, not used for estimates of parameters of equations (6) and (9).

Both N and R can be turned into egg production rates through division by D, i.e.,

$$\frac{N/D}{R/D} = \frac{1 - e^{-ZD}}{ZD} \qquad \text{... 6)}$$

N/D then corresponds to the above-mentioned map standing stock estimates divided by egg development time (see also Senocak, this vol.), while R/D corresponds to the output of equation (1), reexpressed on a daily basis.

Various plausible multiple regression models were then applied to the data of Table 2, our aim being to identify biologically acceptable factors explaining the observed variability in egg survival. The Rojas/Alamo database on anchoveta food and feeding habits (see Rojas de Mendiola, this vol.; Alamo, this vol.; and Pauly et al., this vol.) was also tapped for data on anchoveta egg cannibalism and the results were used to help interpret the output of our egg mortality models.

Results and Discussion

Parental Biomass and Egg Production, 1953 to 1985

Fig. 2 and Tables 3, 4 and 5 present the results obtained by applying equation (1) to the biomass data generated by Pauly and Palomares (this vol.). The estimates of parental biomass in Fig. 2 resemble those published earlier by Pauly and Soriano (1987). As was the case earlier, the lone independent estimate of parental biomass obtained for August/September 1981 using the egg production method (Santander et al. 1984) is very close to our estimates of parental biomass for that period (see also Table 3, footnote).

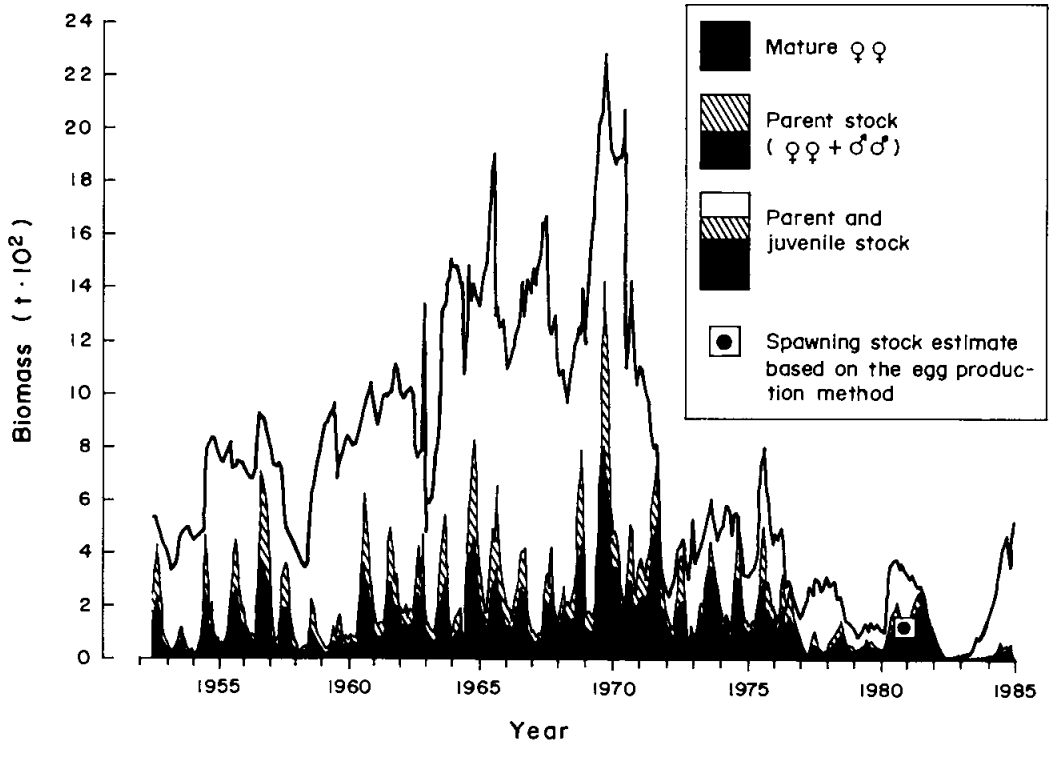

Fig. 2. Total biomass, parent (=mature) stock and biomass of mature female anchoveta off Peru (4-14°S), January 1953 to July 1985. Note strong, regular seasonal oscillations and very good match with independent spawning stock estimate in August/ September 1981 by Santander et al. (1984).

Fig. 2. Biomasa total, stock de padres (=maduros) y biomasa de anchovetas hembras maduras frente al Perú (4-14°S), Enero 1953 a Julio 1985. Notar la fuerte y regular oscilación estacional y una muy buena concordancia con la estimación independiente del stock desovante en Agosto/Septiembre 1981 de Santander et al. (1984).

Table 3. Estimated biomass of mature female and male anchoveta *(Engraulis ringens)* off Peru (4-14°S), January 1953 to July 1985 (in tonnes). Note that estimates for the early/mid-1970s tend to be biased upward (see text).[a]

Tabla 3. Biomasa estimada de anchovetas maduras (Engraulis ringens) *hembras y machos frente al Perú (4-14°S), Enero 1953 a Julio 1985 (en toneladas). Notar que los valores para comienzos y mediados de 1970 tienden a estar sobreestimados (ver texto).*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	2,324,629	3,687,629	4,255,910	3,354,697	1,780,670	759,621	675,923	444,380	322,403	192,221	236,800	325,083
1954	778,346	1,190,877	958,377	470,370	306,811	214,251	343,315	130,482	150,946	163,288	306,942	1,397,974
1955	4,628,339	3,299,281	1,448,142	2,109,215	862,341	784,263	705,329	466,236	584,753	421,088	670,558	1,086,364
1956	2,511,945	4,049,643	4,450,385	2,986,737	2,341,447	1,952,697	1,820,396	1,424,517	973,275	780,623	884,357	773,870
1957	1,407,115	7,022,473	6,651,020	6,078,912	5,823,122	4,335,316	2,842,668	1,079,831	547,811	707,394	752,574	3,120,840
1958	3,280,197	3,526,073	3,371,224	1,882,582	1,072,449	699,824	624,921	195,383	227,089	286,092	432,654	276,946
1959	606,482	2,214,714	1,807,238	1,372,257	869,253	640,095	422,105	383,747	334,340	376,378	519,242	1,166,015
1960	698,823	1,402,145	1,602,622	1,021,144	699,377	840,562	702,882	869,485	838,234	802,908	811,071	1,797,878
1961	4,050,912	6,233,816	4,684,939	4,031,832	3,236,062	1,977,297	1,307,135	1,285,905	1,260,206	1,342,832	1,348,396	1,685,565
1962	4,776,121	4,918,827	3,830,377	2,923,596	3,214,620	2,279,411	1,895,947	1,781,146	2,094,791	1,494,146	1,863,795	1,777,456
1963	2,136,645	3,503,178	4,254,088	2,913,276	4,657,700	1,355,650	1,478,852	1,184,660	1,131,397	1,059,453	1,182,109	1,909,215
1964	3,845,888	4,974,556	5,426,498	3,193,788	1,384,392	1,041,711	971,146	1,462,987	1,542,929	1,852,280	525,536	703,178
1965	4,154,754	6,281,776	7,360,888	8,261,310	6,437,582	4,036,225	3,297,160	2,580,483	1,687,431	2,063,787	3,068,186	4,878,389
1966	4,440,739	6,549,658	4,728,831	3,409,429	3,102,499	2,081,105	1,899,162	1,929,042	1,435,945	2,241,601	2,504,874	2,933,097
1967	4,057,425	4,122,205	4,176,276	2,099,257	1,334,167	1,031,783	1,123,584	836,175	997,957	961,965	1,089,122	2,658,287
1968	3,197,645	2,702,713	4,174,045	2,097,710	1,860,501	1,145,809	1,632,899	2,107,437	2,744,281	2,007,215	2,155,906	1,964,527
1969	2,345,165	2,769,932	6,324,308	6,935,128	7,895,689	4,133,864	1,715,978	1,760,900	1,771,295	1,660,915	1,582,342	2,133,276
1970	6,310,369	10,787,530	14,137,810	11,135,920	9,698,282	7130761	4,779,425	4,848,070	4773541	4,473,689	3,000,746	2,543,317
1971	1,895,066	3,194,843	5,098,249	4,817,334	3,015,614	2,350,503	3,121,872	3,827,084	3466583	3,018,701	3,724,288	3,800,192
1972	5,886,226	6,889,323	7,445,824	4,767,073	3,136,134	2,713,880	2,138,707	1,690,730	1,348,869	1,227,993	1,140,384	2,337,956
1973	3,768,454	3,882,752	3,840,114	1,524,991	815,748	582,377	1,175,937	541,483	816,565	1,341,442	2,163,379	1,972,436
1974	2,597,888	3,543,061	4,410,033	4,155,136	3,360,099	3,040,496	2,408,332	1,971,782	1,441,163	1,611,421	1,676,850	1,126,649
1975	1,010,533	2,187,394	5,053,889	4,045,153	2,830,089	1,514,035	1,496,137	1,264,570	1,304,127	1,410,340	1,279,203	1,710,247
1976	2,127,963	4,190,732	5,050,645	2,679,496	2,930,559	2,578,082	1,934,089	2,059,849	1,234,449	1,582,157	2,160,741	3,214,625
1977	1,918,159	2,460,301	2,663,668	2,557,887	1,853,953	1,374,297	1,053,084	752,210	506,851	313,111	128,175	195,377
1978	245,908	806,537	1,063,143	833,071	425,599	207,846	273,494	247,411	332,788	505,281	734,338	869,859
1979	1,002,829	1,138,779	1,388,163	1,118,577	618,940	463,546	491,525	480,336	384,936	330,773	283,047	363,351
1980	461,452	523,174	705,087	545,491	635,123	518,556	528,168	419,273	360,454	356,880	382,628	480,753
1981	929,657	1,630,146	1,708,486	1,804,618	2,128,345	1,604,501	1,382,503	1,434,416	1,160,744	1,590,016	1,568,468	1,849,099
1982	2,031,170	2,363,049	2,525,817	2,195,488	2,184,578	1,476,403	1,481,406	838,298	781,703	790,185	670,058	412,029
1983	120,318	23,904	5,454	7,087	17,376	21,052	8,318	3,638	3,271	4,106	5,000	6,446
1984	9,966	14,545	29,025	42,545	62,900	35,087	41,590	42,797	39,407	65,037	96,077	113,573
1985	197,855	268,764	603,246	406,172	445,338	498,387	391,979	-	-	-	-	-

[a]The mean of the values for August and September is (1434416 + 1160744)/2 = 1.297580, or 1.3 x 10^6 tonnes, very close to the independent estimate of 1.2 x 10^6 tonnes of Santander et al. (1984).

Table 4. Estimated biomass of mature female anchoveta *(Engraulis ringens)* off Peru (4-14°S), January 1953 to July 1985 (in tonnes). Note that estimates for the early/mid-1970s tend to be biased upward (see Table 3 and text).

Tabla 4. Biomasa estimada de anchovetas (Engraulis ringens) *hembras maduras frente al Perú (4-14°S), Enero 1953 a Julio 1985 (en toneladas). Notar que los valores para comienzos y mediados de 1970 tienden a estar sobreestimados (ver Tabla 3 y texto).*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	1,321,212	2,014,939	2,275,717	1,801,389	965,765	426,267	389,939	265,458	185,938	110,709	139,214	184,368
1954	429,495	650,656	536,331	276,803	189,279	139,294	219,618	85,966	94,424	101,666	189,623	828,052
1955	2,522,634	1,819,346	829,857	1,193,904	503,620	464,845	426,699	289,324	365,414	272,767	443,084	707,374
1956	1,526,926	2,352,075	2,572,280	1,817,512	1,450,474	1,251,817	1,203,284	986,455	662,526	550,157	623,856	559,713
1957	818,338	3,698,823	3,510,480	3,232,838	3,049,771	2,288,889	1,502,866	585,645	299,382	389,275	414,063	1,630,828
1958	1,896,764	1,902,070	1,817,655	984,118	592,998	391,414	355,133	118,092	138,124	174,493	262,950	161,936
1959	333,331	1,156,546	959,565	753,630	484,261	370,056	253,737	234,677	193,313	217,767	300,051	651,279
1960	365,556	736,150	861,472	580,851	419,607	515,849	450,584	564,575	552,077	531,202	526,773	1,115,724
1961	2,373,017	3,538,035	2,700,905	2,368,130	1,928,769	1,224,675	828,860	823,744	815,505	872,371	869,044	1,064,992
1962	2,832,774	2,896,403	2,348,297	1,840,781	2,015,436	1,469,378	1,252,760	1,198,712	1,411,393	1034031	1,268,713	1,204,870
1963	1,375,350	2,123,551	2,511,024	1,795,522	2,939,777	841,235	913,842	735,298	696,602	652,689	744,581	1,158,849
1964	2,146,985	2,715,533	2,997,359	1,850,239	848,986	659,378	630,918	960,219	1,015,379	1,227,516	294,556	403,778
1965	2,676,725	3,818,796	4,353,884	4,648,581	3,580,680	2,269,759	1,850,283	1,469,941	977,384	1207475	1,776,023	2,762,433
1966	2,406,010	3,478,431	2,574,854	1,930,134	1,836,428	1,290,514	1,215,856	1,268,462	977,172	1,536,607	1,754,989	2,092,552
1967	2,759,539	2,538,842	2,559,680	1,327,411	822,522	643,145	710,856	545,855	661,927	656,376	752,256	1,813,840
1968	2,090,197	1,756,402	2,580,961	1,419,964	1,257,604	801,035	1,147,133	1,496,569	1,959,417	1,466,828	1,570,893	1,404,380
1969	1,516,585	1,627,485	3,472,801	3,839,018	4,309,745	2,339,228	1,054,600	1,097,834	1,122,922	1,057,294	1,012,820	1,299,171
1970	3,555,944	6,043,169	8,022,568	6,647,045	6,075,676	4,744,813	3,377,803	3,478,003	3,479,941	3,216,208	2,171,110	1,795,029
1971	1,265,653	1,964,446	2,971,928	2,685,583	1,758,190	1,401,111	1,872,242	2,334,073	2,227,656	2,056,919	2,555,923	2,618,777
1972	4,050,227	4,809,750	5,271,819	3,316,578	1,981,685	1,692,488	1,387,116	1,174,567	1,027,277	924,213	787,335	1,341,532
1973	1,990,209	2,110,506	2,155,432	923,170	514,383	386,946	851,625	391,547	606,030	1,018,524	1,650,892	1,583,212
1974	2,099,287	2,792,510	3,459,558	3,257,313	2,653,672	2,363,980	1,955,769	1,632,632	1,186,710	1,354,742	1,342,611	877,815
1975	775,308	1,464,269	3,113,251	2,593,830	1,923,235	1,118,888	1,129,588	989,220	1,039,252	1,148,818	1,077,513	1,451,570
1976	1,811,819	2,795,350	2,998,613	1,700,991	1,801,625	1,530,117	1,145,651	1,234,141	792,898	1,012,637	1,390,817	1,920,117
1977	1,110,230	1,402,801	1,574,778	1,605,820	1,253,189	1,002,394	806,196	600,132	416,590	260,225	95,584	124,228
1978	146,899	431,767	569,676	458,174	250,568	127,332	171,093	62,729	222,000	341,871	499,929	589,969
1979	637,459	731,523	895,537	731,496	406,464	321,374	341,140	335,095	275,129	236,665	201,065	241,088
1980	308,531	343,108	446,921	347,099	411,600	344,778	364,262	303,403	266,986	268,496	288,103	355,013
1981	652,317	1,051,476	1,112,970	1,196,661	1,420,186	1,124,657	1,015,496	1,068,897	896,331	1210,731	1,217,515	1,457,802
1982	1,606,276	1,851,687	2,006,827	1,771,793	1,762,474	1,206,989	1,215,206	713,321	676,012	672,629	565089	339,891
1983	88,086	17,161	2,987	3,630	9,161	11,052	4,735	2,420	2,304	2,804	3,370	4,269
1984	6,246	9,086	18,053	25,778	41,675	24,282	28,511	30,013	27,958	45,221	64,723	75,672
1985	128,788	175,265	376,325	269,785	301,652	342,614	273,543	-	-	-	-	-

Table 5. Estimated monthly reproductive output by the anchoveta stock off Peru (4-14°S), January 1953 to July 1985, in billion eggs (i.e., x 10^9). The values for the early/mid-1970s are overestimates (see Tables 3, 4 and text).

Tabla 5. Estimación mensual de la producción de huevos del stock de anchoveta frente al Perú (4-14°S), Enero 1953 a Julio 1985, en billones de huevos (es decir x 10^9). Los valores para comienzos y mediados de 1970 están sobreestimados (ver Tablas 3, 4 y texto).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	223,001	417,595	277,665	56,483	11,271	50,263	151,742	279,131	217,516	149,058	156,856	34,823
1954	60,900	137,709	102,567	17,793	5,183	37,383	140,422	148,742	163,292	194,956	259,386	191,144
1955	315,471	403,509	174,539	56,349	9,335	73,434	208,382	361,279	618,567	603,340	792,571	250,866
1956	374,074	758,040	607,044	135,692	37,093	296,722	904,731	1,981,312	1,561,567	1,632,756	1,381,554	280,881
1957	155,591	517,390	381,124	94,086	23,095	156,332	300,852	357,408	244,835	380,447	299,984	141,887
1958	518,700	445,033	339,109	23,393	8,296	49,545	142,436	163,321	253,806	361,256	384,722	34,239
1959	44,404	146,000	114,313	30,434	6,993	54,097	128,467	294,425	226,750	295,232	305,874	110,823
1960	29,557	101,636	115,909	29,071	9,226	101,566	301,887	910,650	1,241,628	1,422,102	1,076,289	388,551
1961	528,572	1,079,356	597,202	139,173	40,253	239,320	502,711	1,185,258	1,589,138	1,954,018	1,402,278	324,524
1962	608,424	969,642	693,496	145,039	52,135	336,026	882,237	2,065,840	3,172,399	2,892,567	2,501,054	480,932
1963	420,475	835,661	634,301	131,410	77,738	168,788	506,827	952,468	1,125,873	1,206,342	1,110,459	305,934
1964	323,521	561,300	501,471	100,526	20,036	141,186	418,582	1,499,760	2,063,507	2,895,659	242,803	77,668
1965	794,962	1,487,000	1,110,642	216,088	51,141	281,229	640,907	1,279,788	1,186,701	1,750,467	1,810,299	505,548
1966	288,570	551,604	385,616	91,841	36,815	252,329	756,715	1,982,197	2,232,726	4,068,163	3,710,504	953,446
1967	1,016,306	1,120,565	832,521	118,315	21,812	138,367	452,102	897,621	1,471,914	1,814,239	1,571,817	731,381
1968	662,502	894,911	834,520	154,923	45,590	258,786	1,050,496	3,229,639	5,549,850	5,038,703	3,950,467	665,776
1969	510,700	606,165	616,716	174,754	56,303	312,715	603,249	1,494,839	2,081,500	2,217,373	1,627,657	357,585
1970	594,626	1,577,838	1,666,492	436,584	163,688	1,269,115	3,088,409	7,588,246	10,352,370	10,445,460	5,413,273	875,599
1971	481,033	961,559	855,984	134,621	38,304	259,789	982,472	2,958,945	4,479,487	5,702,904	5,347,169	1,133,995
1972	1,602,956	3,296,360	2,867,123	428,504	64,603	443,638	1,236,406	3,015,993	4,355,195	4,285,281	1,942,809	300,584
1973	193,709	429,375	416,083	63,714	13,875	101,969	779,360	886,931	1,915,416	3,897,503	4,827,496	1,115,445
1974	1,412,494	3,040,711	2,869,610	679,645	188,187	1,325,342	3,395,300	6,711,189	5,785,994	7,996,841	5,022,691	631,701
1975	499,349	1,039,876	1,202,590	273,601	79,166	461,409	1,373,710	3,009,560	4,306,292	5,679,465	4,381,157	1,254,503
1976	1,506,248	2,362,314	1,217,878	219,638	64,788	354,618	706,656	1,775,937	1,755,170	2,376,781	2,434,723	512,852
1977	230,978	422,197	424,027	134,950	45,766	368,202	952,937	1,808,994	1,769,965	1,316,274	296,443	49,160
1978	40,253	82,948	78,159	18,911	5,278	25,020	104,061	275,860	508,464	923,167	1,030,519	245,475
1979	195,182	376,880	351,158	74,649	14,198	106,376	317,198	709,652	801,274	767,934	473,503	93,963
1980	115,443	196,023	168,802	32,054	13,022	94,896	319,551	706,241	867,625	1,040,662	841,643	203,865
1981	295,708	594,822	478,298	131,578	52,624	381,288	1,106,638	2,774,401	3,323,482	4,888,765	3,874,244	997,701
1982	1,030,399	1,951,983	1,644,554	366,554	120,343	679,860	1,926,211	2,943,836	3,818,172	4,287,944	2,659,675	308,748
1983	46,929	14,002	527	43	75	708	2,161	4,972	7,098	9,153	8,319	2,066
1984	2,177	4,870	6,674	1,986	1,427	7,769	25,091	65,242	81,401	143,562	141,249	32,941
1985	46,425	102,543	134,229	29,575	11,480	108,643	255,221	-	-	-	-	-

However, the parental biomass estimates, and hence, the estimates of reproductive output for some months (especially during the early 1970s), are different from the values than would have been estimated based on available independent estimates of biomass (Pauly and Palomares, this vol.). Thus, in order for our estimates of egg mortality to be as accurate as possible, we have replaced, in Table 6, the VPA-based estimates of parental biomass (and reproductive output) by proportionally adjusted independent biomass estimates (and by the corresponding estimate of the reproductive output, respectively) in all cases when two biomass estimates for the same month differed by more than 5%. The adjusted estimates are given in brackets in Table 2.

The Evidence for Egg Cannibalism in Anchoveta

Fig. 3A presents a plot of ln(N/(D·P)) *vs.* parental stock size (P) for the period 1964 to 1985. As might be seen, there is a strong negative correlation between the egg survival index (ln(N/(D·P))) and parent stock, suggesting a strong impact of parental stock on egg mortality rate. This confirms an earlier plot of Santander (1987) based on maps covering the period 1964 to 1982 and on the parental biomass estimates of Pauly and Soriano (1987).

However, parental biomass is not the only factor affecting anchoveta egg survival, and we have derived, to illustrate this, the model:

$$\ln(N/(D \cdot P)) = 33.23 - 2.15\log_{10}P - 2.50T + 0.063T^2 \qquad \text{... 7)}$$

where T is the SST in °C and where $R^2 = 0.594$ (see also Fig 3B and Table 6). Fig. 4 shows that the residuals of this model lack structure, as required for multiple linear regression. Equation (7), it must be realized, is only one of the many possible models, and should not be taken as representing final identification of factors affecting anchoveta egg survival.

Interesting here is Fig. 5 which shows the dependent variable of equation (7) as a function of temperature. As might be seen, some curvature is apparent, as implied by the significant squared term in equation (7).

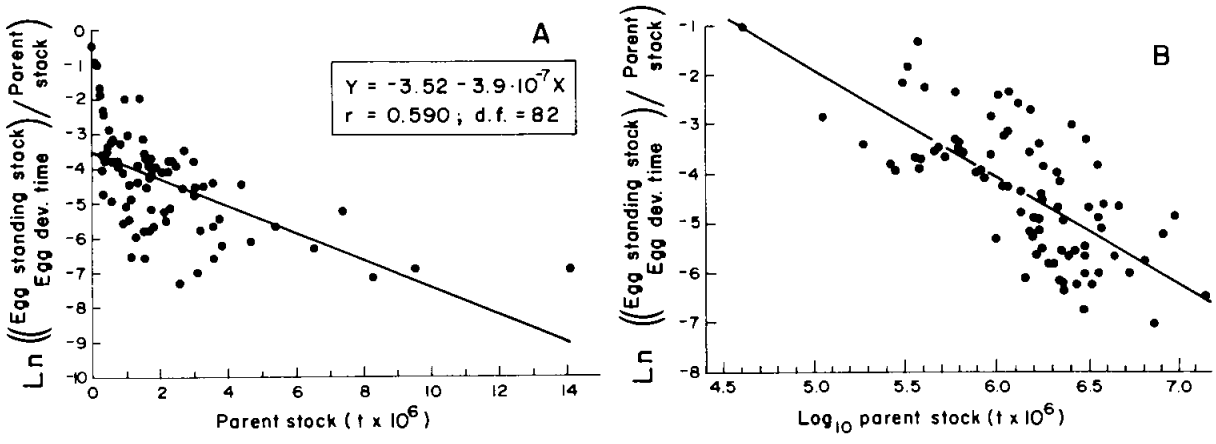

Fig. 3. Evidence of density-dependence in anchoveta egg survival.

A. Bivariate plot, as used to derive Ricker-type stock-recruitment relationships.

B. Plot of the residuals of equation (7) *vs.* the line linking the index of egg survival (Y-axis) and parental stock. Note markedly improved fit over Plot A, resulting from the inclusion of SST and SST^2 as variables (see text).

Fig. 3. Evidencia de la densodependencia en la sobrevivencia de huevos de anchoveta.

A. Ploteo bivariado, tal como es usado para derivar la relación stock-reclutamiento de Ricker.

B. Ploteo de residuales de la ecuación (7) vs la línea que relaciona el indice de sobrevivencia de huevos (eje Y) y el stock de padres. Notar el mejor ajuste en relación al ploteo A, a consecuencia de la inclusión de TSM y TSM^2 como variables (ver texto).

Table 6. Statistics of multiple regression linking anchoveta egg survival index and its predictor variables (equation 7; degrees of freedom = 80, R = 0.771).

Tabla 6. Datos estadísticos de la regresión múltiple que relaciona el indice de sobrevivencia de huevos de anchoveta y sus variables predictoras (ecuación 7; grados de libertad = 80; R = 0.771).

Variables	(Units)	Estimates	Standard errors[a]
ln (N/(D·P))	(eggs 10^9/ days · tonnes)	(independent variable)	0.952
$\log_{10}$ parent stock	(tonnes)	-2.147	0.257
Sea surface temp (SST)	(°C)	-0.250	0.942
$(SST)^2$	$(°C)^2$	0.0627	0.0245

[a] Standard error of Y-estimate

Taking the partial derivative of equation (7) with respect to temperature:

$$\frac{\delta \ln (N/(D \cdot P))}{\delta T} = 2\,(0.0663)T - 2.50 \qquad \text{... 8)}$$

and setting it equal to zero allows estimation of the temperature (T_{min}) at which ln (N/(D·P)) is minimum, i.e., T_{min} = 19.8°C.

Thus, our analysis of Santander's maps provides evidence for:

i) parental cannibalism on anchoveta eggs; and

ii) a parabolic relationship between egg mortality and SST, with maximum close to the upper limit of the optimal temperature range of anchoveta (about 15-20°C).

One multiple regression model we derived, using the data in Table 2, to explain variability of our estimates of egg mortality, is:

$$\log_{10}Zegg = -23.7 + 0.608\log_{10}P + 0.379\log_{10}S + 0.505A_T + 2.4T - 0.0751T^2 \qquad \text{... 9)}$$

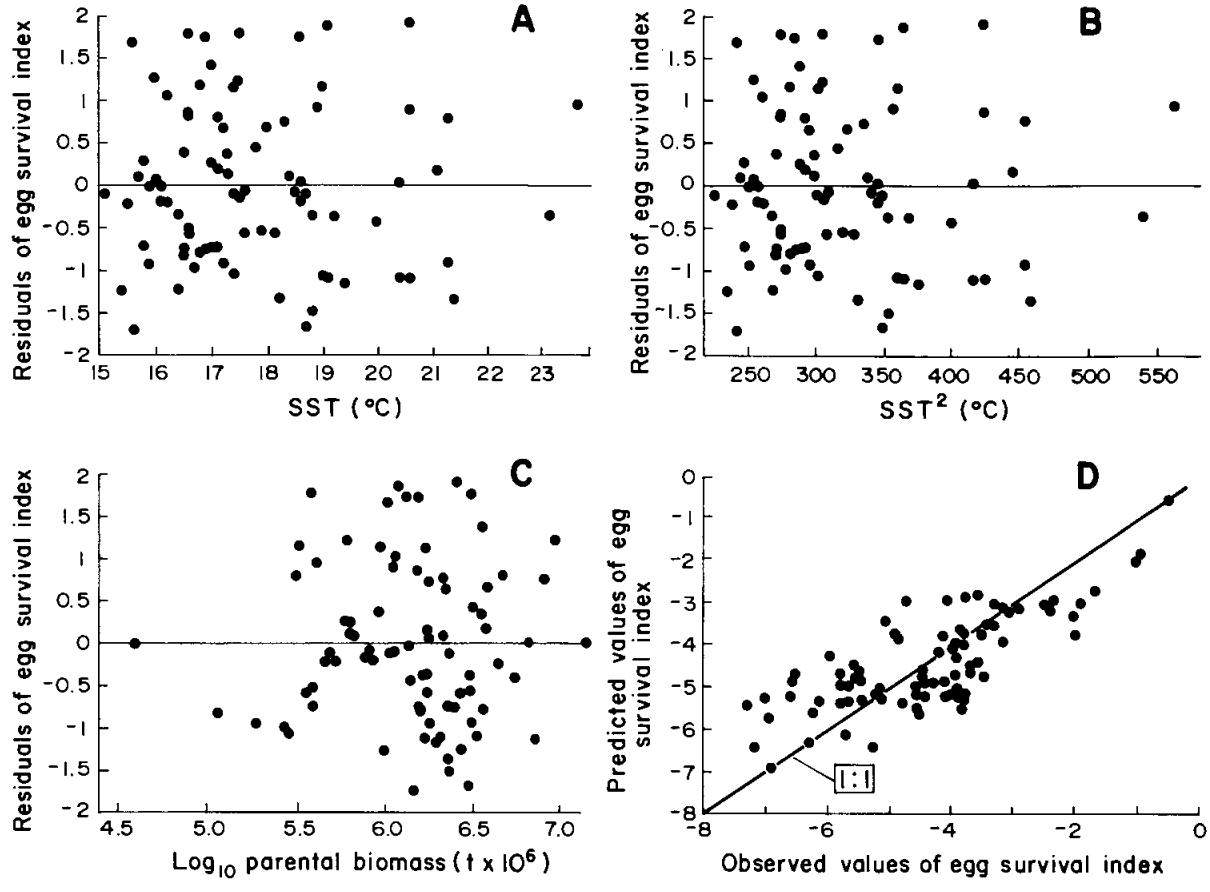

Fig. 4. Selected features of model represented by equation (7). A-C: residuals of equation (7) linking egg survival index and its predictor variables. Note absence of structure. D: plot of observed *vs.* predicted values of the egg survival index.

Fig. 4. Características seleccionadas del modelo representado por la ecuación (7). A-C: residuales de ecuación (7) relacionando el índice de sobrevivencia de huevos y sus variables predictoras. Notar la ausencia de estructura. D: ploteo de valores observados vs valores predictivos del índice de sobrevivencia de larvas.

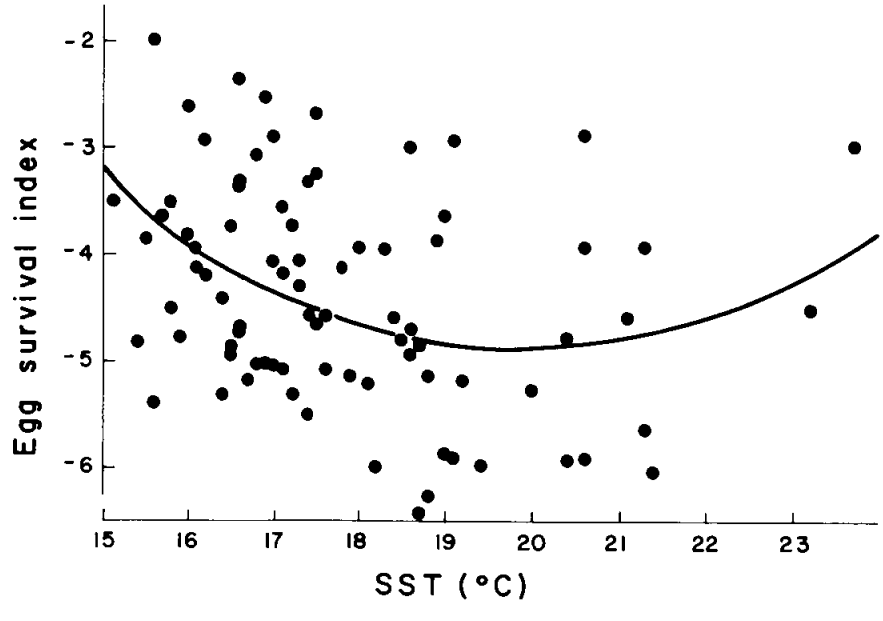

Fig. 5. Relationship of egg survival index and SST; note curvature, suggesting a minimum at 19.8°C.

Fig. 5. Relación entre el índice de sobrevivencia de huevos y TSM; notar curvatura, sugiriendo un mínimo a 19.8°C.

which has an $R^2 = 0.562$ and whose statistics are given in Table 7. Fig. 6 shows that this model gives a particularly good fit to SST and SST anomaly, and a lesser fit to the biological variables (parent stock and sardine stock). Again, SST has a parabolic relationship with egg mortality. Taking the partial derivative of equation (9) with respect to T gives:

$$\frac{\delta \log_{10} Z_{egg}}{\delta T} = 2.4 - 2(0.0751)\,T \qquad \text{... 10)}$$

which set equal to zero and solved for T gives $T_{max} = 16.0°C$.

Thus, we find again that anchoveta egg mortality has a peak within the range of temperature that is optimal for anchoveta.

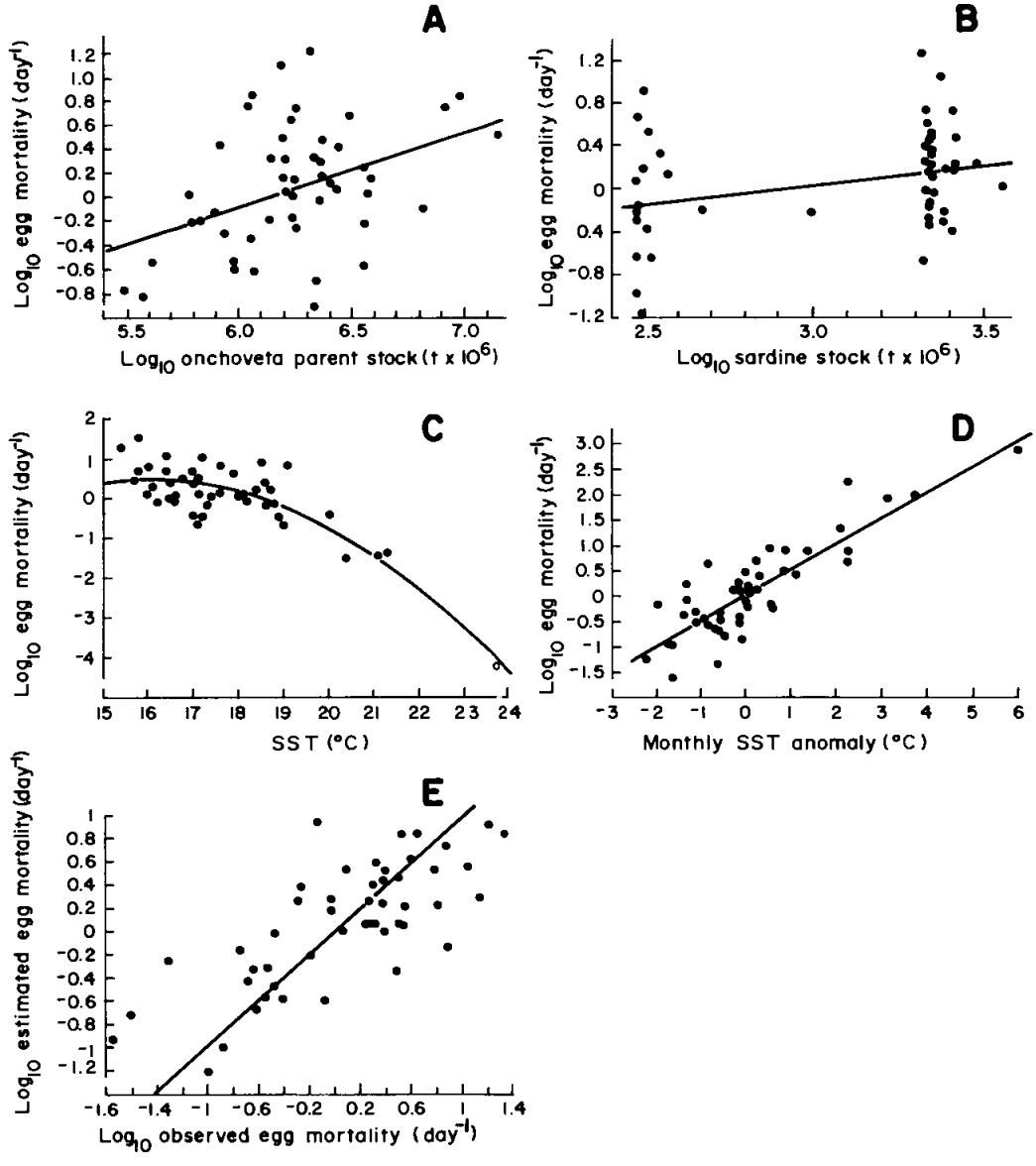

Fig. 6. Relationship between anchoveta egg mortality and its predictor variables. The solid lines of Plots A-D represent the axes of equation (9), with intercepts set at the mean of all other variables; the dots represent the residuals, plotted from the solid lines. Plot E shows the predicted *vs.* the observed mortalities. Note overall good fit of equation (9) to the data, the absence of structure in the residuals, and the strong relationship between mortality, SST and SST anomaly.

Fig. 6. Relación entre la mortalidad de huevos de anchoveta y sus variables predictoras. Las líneas sólidas de los ploteos A-D representan el eje de la ecuación (9), con interceptos fijados al promedio de todas las otras variables; los puntos representan los residuos, ploteados de las líneas sólidas. El Ploteo E muestra la mortalidad estimada vs la observada. Notar el buen ajuste general de la ecuación (9) a los datos, la ausencia de estructura en los residuos y la fuerte relación entre mortalidad, TSM y la anomalía de TSM.

Table 7. Statistics of equation (9), relating anchoveta egg mortality and its predictor variables (degrees of freedom = 43; R = 0.751).
Tabla 7. Datos estadísticos de la ecuación (9), que relaciona la mortalidad de huevos de anchoveta y sus variables predictoras (grados de libertad = 43; R = 0.751).

Variables	(Units)	Estimates	Standard errors[a]
$\log_{10}$ egg mortality	(day^{-1})	(indep. variable)	0.4937
$\log_{10}$ parent stock	(tonnes)	0.6078	0.2851
$\log_{10}$ sardine stock	(tonnes)	0.3788	0.2160
SST anomaly (A_T)	(°C)	0.5049	0.0758
Sea surface temp. (SST)	(°C)	2.4007	0.6881
$(SST)^2$	$(°C)^2$	-0.0751	0.0185

[a] Standard error of Y-estimate.

Fig. 6D, which shows the *positive* partial correlation between anchoveta egg mortality and SST anomaly, suggests, however, that the observed parabolic relationship between SST and egg mortality do not reflect a causal linkage. Rather, SST, which fluctuates seasonally, is lowest in September-October (see Fig. 8 and Bakun 1987), during a period when anchoveta concentrate under the coast for spawning (Jordán 1971; FAO 1981; Csirke, this vol.).

Anchoveta feed during the spawning season and hence, the peak consumption of anchoveta eggs by adult anchoveta occurs in September-October (Fig. 7; Table 8). This could explain the apparent relationships between SST and egg mortality. As for SST anomaly, we assume that it is linked with anchoveta egg mortality via two mechanisms: (1) increased predation on anchoveta eggs by zooplankton and other predators not included in our models, and whose metabolic rate and hence, food consumption, can be expected to increase when the SST anomaly increases and (2) increased concentration of anchoveta within the small inshore patches of low SST waters that remain during high SST anomalies (Muck et al., this vol.).

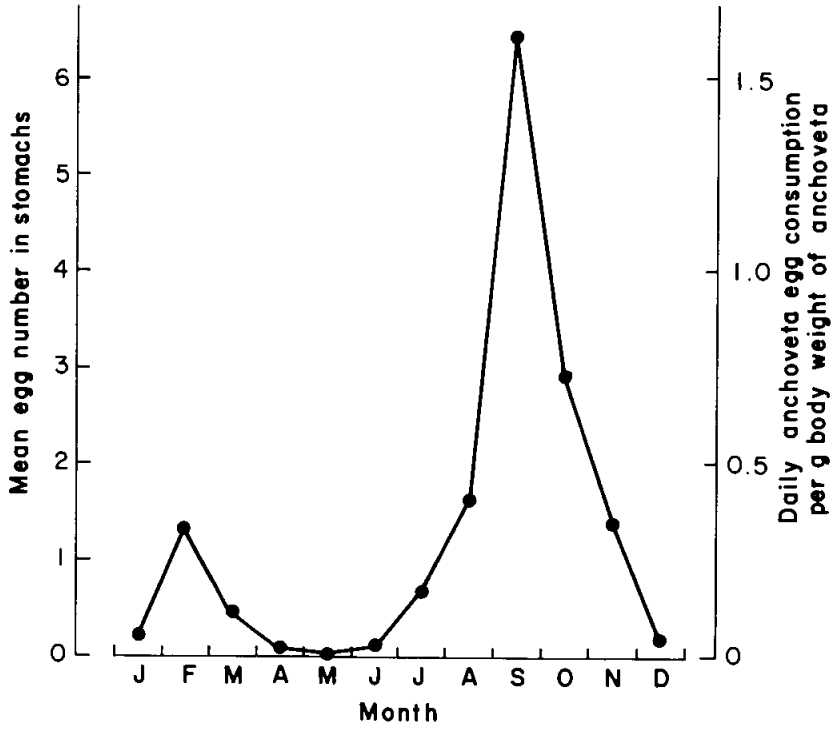

Fig. 7. Mean number of anchoveta eggs in the stomach of anchoveta sampled from 1953 to 1982 by Rojas de Mendiola (this vol.) and Alamo (this vol.), as extracted from their database (see Table 8 for details). Note strong seasonality, with a major peak during the major spawning season (September/ October) and a minor peak during the minor spawning season (February/March). The scale on the right side provides an approximate conversion to egg consumption rate (see Table 8).
Fig. 7. Número promedio de huevos de anchoveta en el estómago de anchoveta muestreada de 1953 a 1982 por Rojas de Mendiola (este vol.) y Alamo (este vol.), extraido de su base de datos (ver tabla 8 para detalles). Notar la fuerte estacionalidad, con un pico mayor durante la estación de desove principal (Septiembre/Octubre) y un pico menor durante la estación de menor desove (Febrero/Marzo). La escala del lado derecho proporciona una conversión aproximada de la tasa de consumo de huevos (ver Tabla 8).

Equation (9) predicts, for anchoveta eggs in August/September 1987, a value of Z = 2.13 day^{-1}; this is much higher than the value of 0.91 day^{-1} presented by Santander et al. (1984).

Data are available which might allow resolving this discrepancy, and testing of the hypotheses presented above. Notably, a detailed analysis of the Rojas/Alamo database on anchoveta stomach contents emphasizing seasonal and interyear variations of egg cannibalism (i.e., going beyond the mean seasonal cycle in Fig. 8), and combined with corresponding estimates of anchoveta concentration, could contribute toward elucidating the role of egg cannibalism in anchoveta population dynamics.

Table 8. Data for quantification of egg cannibalism in anchoveta, as extracted from the Rojas/Alamo database (see Rojas de Mendiola, this vol.; Alamo, this vol.; Pauly et al., this vol.).
Tabla 8. Datos para la cuantificación del canibalismo de huevos de anchoveta, extraidos de la base de datos de Rojas/Alamo (ver Rojas de Mendiola, este vol.; Alamo, este vol.; Pauly et al., este vol.).

Month	No. of anchoveta with sampling month and record for eggs	No. of anchoveta with eggs in the stomach	Total no. of eggs in stomach	Mean eggs per anchoveta stomach	Daily Anchoveta egg consumption[a]
January	616	38	126	0.205	0.051
February	769	77	1000	1.300	0.325
March	852	22	379	0.445	0.111
April	633	17	60	0.095	0.024
May	409	7	17	0.042	0.010
June	266	6	34	0.128	0.032
July	589	23	401	0.681	1.170
August	996	204	1632	1.639	0.410
September	1698	520	10935	6.440	1.610
October	869	99	1664	1.915	0.479
November	1057	112	1469	1.390	0.348
December	971	53	188	0.194	0.048

[a] Approximate daily anchoveta egg consumption per g body weight of anchoveta (see also Fig. 7), as computed from the daily ration of 0.448 g estimated by Pauly et al. (this vol.) for anchoveta of about 20 g live weight, and a mean stomach content of 0.122 g. The quotient of mean stomach content over ration is ≈ 3.7, but this estimate of turnover rate was increased to 5 to account for the facts that (1) most stomachs with eggs were sampled early mornings, when stomach contents are less than average and (2) that eggs are more rapidly digested than other food items.

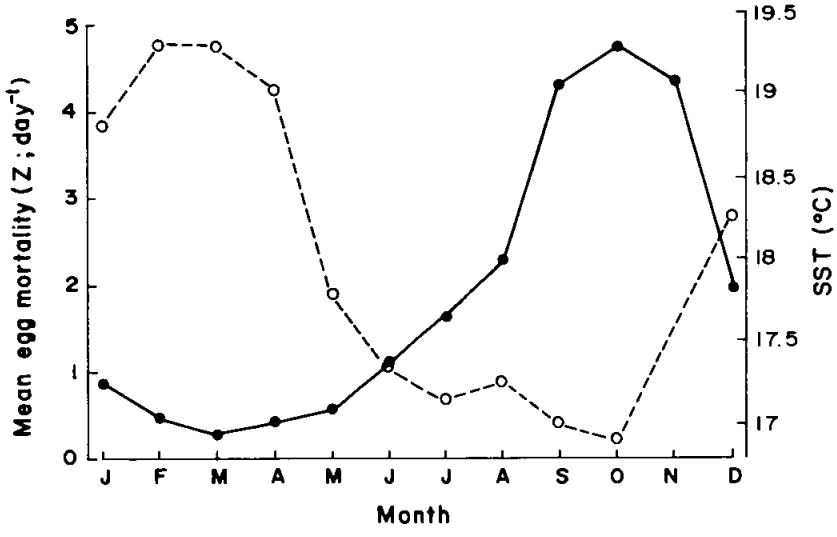

Fig. 8. Solid line: annual cycle of mean monthly anchoveta egg mortality, 1964 to 1985, based on map-specific Z values in Table 2, or on estimates from equation (9) when these could not be computed via equation (6); monthly means were smoothed over 3 months. Note strong summer peak, coincident with peak occurrence of eggs in anchoveta stomachs (see Fig. 7). Dotted line: mean seasonal cycle of sea surface temperature, as derived using only SST values for the months represented in Table 2, and smoothing over 3 months.
Fig. 8. Línea sólida: ciclo anual del promedio mensual de la mortalidad de huevos de anchoveta, 1964 a 1985, basado en valores de Z obtenidos de mapas específicos de la Tabla 2, o en estimaciones de la ecuación (9) cuando éstos no pudieron ser computados por la ecuación (6); los promedios mensuales fueron suavizados mediante promedio corrido de 3 meses. Notar el fuerte pico de verano, coincidente con la ocurrencia del pico de huevos en los estómagos de anchoveta (ver Fig. 7). Línea interrumpida: ciclo estacional promedio de la temperatura superficial derivado usando solo valores de TSM para los meses presentados en la Tabla 2, y suavizados con promedios corridos de 3 meses.

References

Alheit, J. 1986. Egg cannibalism *versus* egg predation: their significance in anchovies. ICES C.M. 1986/H:59, Pelagics Cttee, 9 p.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Clark, F.N. 1954. Biología de la anchoveta. Bol. Cient. Cia. Admin. Guano 1(1): 98-132.

Cushing, D.H. 1988. The study of stock and recruitment, p. 105-128. *In* J.A. Gulland (ed.) Fish population dynamics. 2nd ed. J. Wiley and Sons, New York.

FAO. 1981. Atlas of the living resources of the sea. Prepared by the FAO Fisheries Department. FAO Fish. Ser., Rome.

Jordán, R. 1959. Observaciones sobre la biología de la anchoveta (*Engraulis ringens* J.) de la zona pesquera de Huacho. Bol. Cient. Cia Admin. Guano 35(11): 3-22 + app.

Jordán, R. 1971. Distribution of anchoveta *(Engraulis ringens)* in relation to the environment. Inv. Pesq. 35(1): 113-126.

Jordán, R. 1980. Biology of the anchoveta. I: Summary of the present knowledge, p. 249-276. *In* Proceedings of the Workshop on the Phenomenon known as `El Niño', Guayaquil, Ecuador, 4-12 December 1974. United Nations Educational, Scientific and Cultural Organization, Paris, 284 p.

Miñano, J. 1958. Algunas apreciaciones relacionadas con la anchoveta peruana y su fecundidad. Bol. Cient. Cia. Admin. Guano 34: 11-24.

Pauly, D. 1987. Managing the Peruvian upwelling ecosystem: a synthesis, p. 325-342. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and R.S.V. Pullin. 1988. Hatching time in spherical pelagic marine fish eggs in response to temperature and egg size. Environ. Biol. Fish 21(2): 261-271.

Pauly, D. and M. Soriano. 1987. Monthly spawning stock and egg production of Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1982, p. 167-178. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559-623.

Rothschild, B.J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, 277 p.

Santander, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru (4-14°S), p. 179-207. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Santander, H. and O. Sandoval de Castillo. 1973. Estudio sobre las primeras etapas de vida de la anchoveta. Informe Inst. Mar Perú-Callao 41(1):28.

Santander, H., J. Alheit and P.E. Smith. 1984. Estimación de la biomasa de la población desovante de anchoveta Peruana *Engraulis ringens* en 1981 por aplicación del "metodo de produccion de huevos". Bol. Inst. Mar. Perú-Callao 8(6):213-250.

Sharp, G.O., Editor. 1980. Workshop on the effect of environmental variation on the survival of larval pelagic fishes. Intergov. Oceanogr. Comm. Workshop Rep. No. 28. 323 p.

Relationships Between Anchoveta Spawning Strategies and the Spatial Variability of Sea Surface Temperature off Peru

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Abstract

Time series of sea surface temperature (SST) of nine shore stations along the entire Peruvian coast (4-17°S), available on a monthly basis for the period 1950-1988, were analyzed with reference to the spatial and temporal variability of SST and related standard deviation, and discussed with regard to the spawning strategies of the Peruvian anchoveta (*Engraulis ringens*).

Resumen

Se presenta un análisis de las series de tiempo de la temperatura superficial del mar (TSM) para nueve estaciones costeras del Perú (4-17°S) para el período 1950-1988. Los resultados son analizados con respecto a la variabilidad temporal y local de la TSM y su respectiva desviación estandar, y es discutido con respecto a las estrategias de desove de la anchoveta (*Engraulis ringens*).

Introduction

Time series of spatial means of sea surface temperature (SST) for the area 4-14°S have been reported in Pauly and Tsukayama (1987) and Bakun (1987), and have become important information for modelling purposes (e.g., Muck and Pauly 1987; Muck and Fuentes 1987; Muck and Sanchez 1987; Muck a, b, this vol.; Muck et al., this vol.; Mendo et al., this vol.; Pauly and Soriano, this vol.)

Priority is given in these studies to the analyses of temporal changes in SST (seasonality, El Niño events) expressed as mean values for the whole area (4-14°S). However, little has been reported on the spatial (e.g., north-south) distribution of SST and the temporal and spatial variability of that distribution.

SST provides information on physical conditions of the ecosystem (temperature, upwelling, turbulence,primary production, see e.g., Medina (1979); Enfield (1981); Muck et al. (1987); Mendo et al. (this vol.)). On the other hand, the SST-standard deviation (SST-SD) of a number of simultaneous (monthly) measurements of SST values taken along the coast refers to its stochastic nature.

It might be the latter one which determines the degree of distinctness in evolutionary adaptations of life cycle strategies.

Data Acquisition

The monthly SST time series analyzed here, pertaining to nine shore stations, cover a period of 38 years (1950-1988) and are documented in Muck et al. (1989).

The nine shore stations are: Talara (04°34'S); Paita (05°05'S); Puerto Chicama (07°43'S); Chimbote (09°05'S); Don Martín (11°02'S); Callao (12°04'S); Pisco (13°40'S); San Juan (15°21'S); and Ilo (17°38'S).

The missing values in the original data set (= 24%, referring almost exclusively to the first decade (1950-1960)) were linearly interpolated by Muck et al. (1989) in all cases where only one or two months were missing, or estimated by linear regression between the time series of neighboring stations when the missing sequence was of three months or more (Muck et al. 1989). The SST-SD values used throughout this contribution express the standard deviation of the nine measurements available for each month from 1950 to 1988.

Diskette 1 (see Appendix I) provides the uncorrected SST time series for the nine shore stations.

Results and Discussion

The SST-anomalies derived from the data presented above show the typical oscillation between abnormally warm periods (El Niño events) and abnormally cold periods. Between 1950 and 1987, there were five periods with positive anomalies >1°C, eight periods with positive anomalies >0.5°C, five periods with negative anomalies <-0.5°C and one period with a negative anomaly <-1°C (Fig. 1).

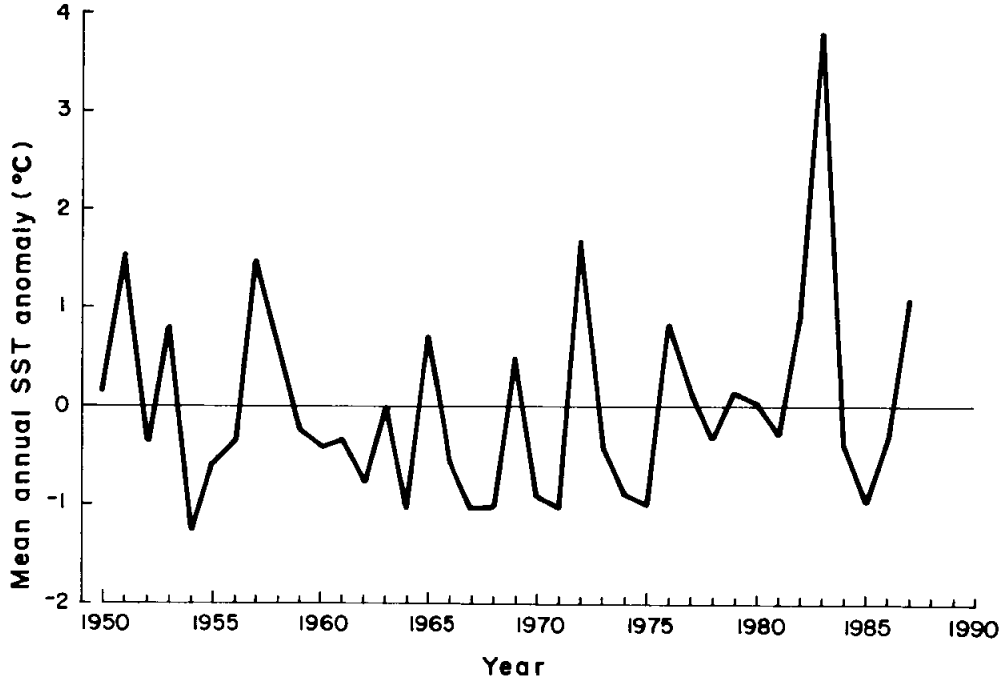

Fig. 1. Time series of mean annual sea surface temperature anomaly off Peru, 1950-1987.
Fig. 1. Serie de tiempo de los promedios anuales de anomalías de la temperatura superficial del mar frente a Perú, 1950-1987.

The curve of the annual anomaly of the SST-SD-values (Fig. 2) shows a pattern similar to that of Fig. 1: years with SST-anomalies were also years with SST-SD-anomalies. In other words, the differences of SST between the nine shore stations along the Peruvian coast are higher during years with El Niño events than during normal ones, and conversely lower during cold years.

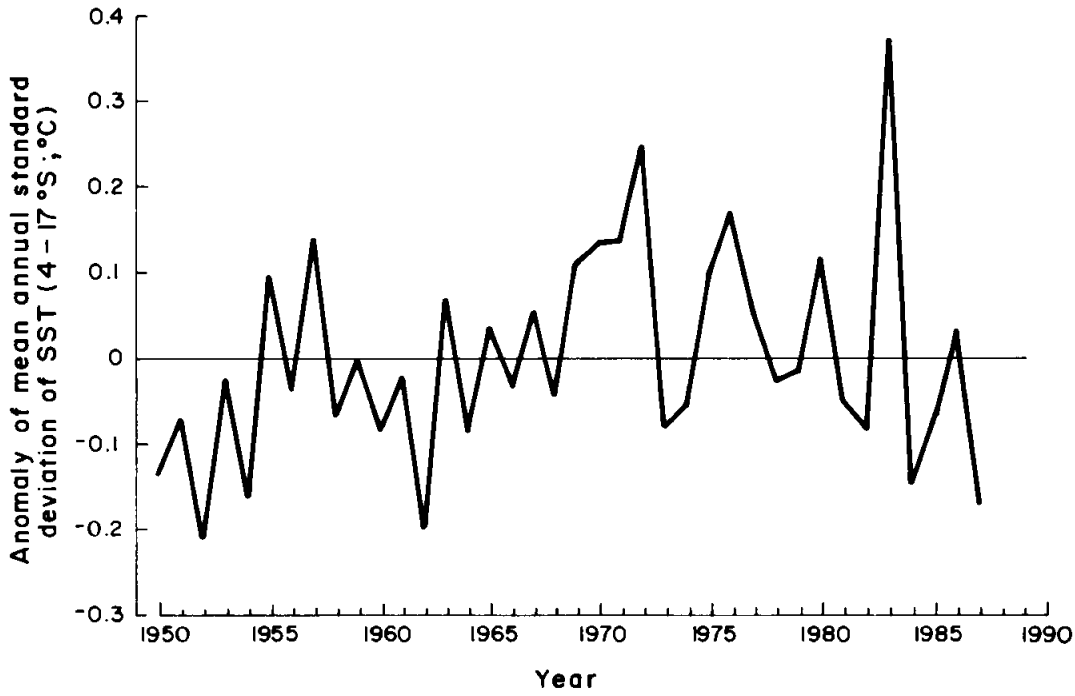

Fig. 2. Time series of anomalies of mean annual standard deviation of sea surface temperature from nine coastal stations off Peru (4-17°S).

Fig. 2. Serie de tiempo de anomalías de los promedios anuales de las desviaciónes estandar de la temperatura superficial del mar, en nueve estaciones costeras frente a Perú (4-17°S).

Comparing the curves of Fig. 1 and Fig. 2, it is notable that during the 1972 and 1976 El Niño events, the positive SST-SD-anomalies occur well before the SST-anomalies.

Indeed, a detailed analysis of the spatial and temporal pattern of SST-anomalies during the very strong El Niño in 1982-1983 shows a clear north-south propagation of SST-anomalies and also shows that the maximum SST-anomaly occurs in the south of Peru (near San Juan-Ilo) about three months later than in the north (near Talara-Paita).

Plotting the mean monthly SST-SD-values from 4-17°S, we obtain Fig. 3, which shows clearly two periods with different regimes: a period of very high SST-SD-values between April and July (autumn, early winter) and a longer period of low SST-SD between August and March (mid-winter, spring, summer).

Low values of monthly SST-SD means that during the 38 years covered here, the temperature variations within a given month were low (=high stability). Thus, the spatial mean of all monthly SST-SD-values in Fig. 3 can be interpreted as an index of the spatial homogeneity of SST. In other words, the high values of the mean monthly SST-SD occurring in May and June indicate low spatial homogeneity of SST, while the very low SST-SD-values during August-October suggest that during this period, the whole area covered here (4-17°S) has very similar characteristics (i.e., is very homogeneous).

Thermal variability can be assumed to reflect the dynamics of other physical properties of the pelagic ecosystem such as upwelling, turbulence, primary production, and depth of the mixed layer. Thus, generalizing my interpretation of the dynamics of SST-SD, I suggest that the curve given in Fig. 3 expresses changes from periods of environmental stability to periods of environmental perturbations, or with reference to the communities within the ecosystem, from periods of low to periods of high environmental uncertainty.

When comparing Fig. 3 with Fig. 7 in Pauly (1987) on the seasonal cycle of anchoveta spawning behavior, I found a surprising coincidence: maximum spawning activity (October) generally falls in the month with the lowest environmental perturbations and almost no spawning occurs during May-June, when the SST-SD-values are highest. The same match is found when one compares the second smaller spawning peak of February-March with the corresponding SST-SD-values.

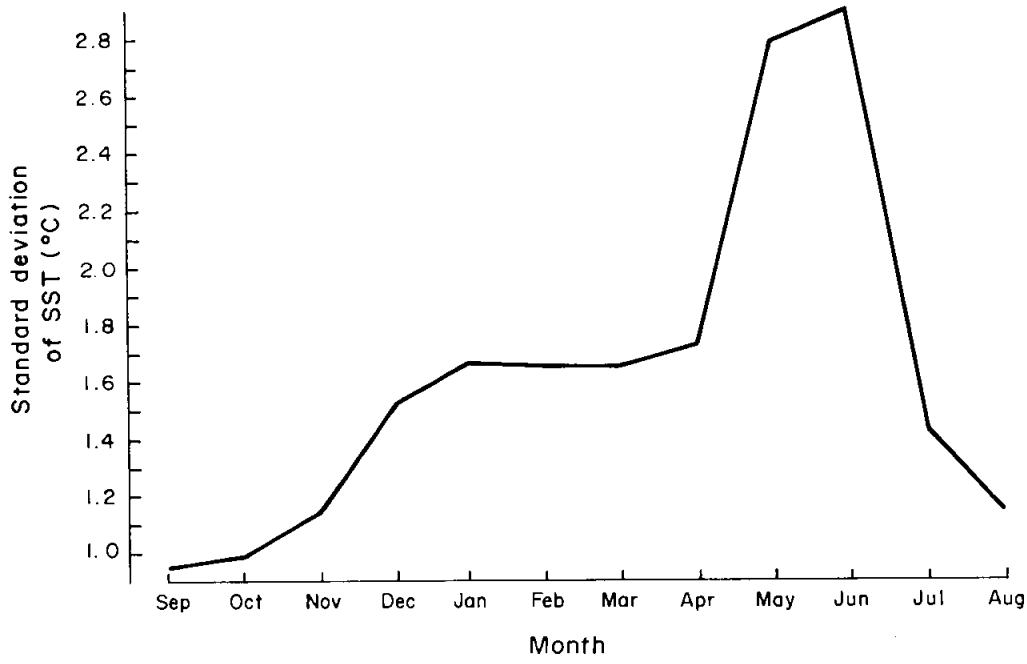

Fig. 3. Mean standard deviation of SST between nine coastal stations off Peru (4-17°S), monthly averages based on data for the years 1950 to 1987. High values suggest lack of homogeneity along the coast and hence low predictability of reproductive success. Note low values during August-November, i.e., the major spawning season of anchoveta.

Fig. 3. Promedios de desviaciones estandar de la TSM en nueve estaciones costeras frente a Perú (4-17°S), promedios mensuales basados en datos de los años 1950 a 1987. Los altos valores sugieren falta de homogeneidad a lo largo de la costa y por la tanto bajo poder de prediccion del éxito reproductivo. Nótese los bajos valores durante Agosto-Noviembre, es decir, durante la estación principal de desove de anchoveta.

Plotting monthly data of the fraction of mature females from Callao and Chimbote samples (Jordan 1980, in Pauly and Soriano 1987) *vs.* the SST-SD for these areas (Table 1) led to Fig. 4. This indicates a strong negative correlation between the percentage of mature females in catch samples and the values of SST-SD for the corresponding months.

I interpret these findings as an expression of a long-term evolutionary adaptation of anchoveta spawning to seasons with different environmental uncertainty: the main spawning event occurs during periods when there is a high probability that environmental conditions will be "as always" (i.e., differing little from the long-term mean values).

While seasonal spawning peaks occur, it must also be noted that some anchoveta spawn throughout the year. Paulik (1981) wrote on this:

> "The anchoveta, with 2- or 3-year classes in its population, cannot afford the luxury of gambling on the weather. Lack of spawning success in a single year could be disastrous. So anchoveta hedges its bet by spawning over the entire year and increasing its chances of encountering favorable conditions during some part of the extended spawning season".

Thus, the question arises: Are there two different spawning strategies of two genetically different anchoveta (sub)populations, one spawning mainly from September to November, the other throughout the year?

Fig. 5 shows the trend of October values of SST-SD (i.e., during the main spawning season) from 1950 to 1987. In this graph, low SST-SD-values imply that spawning in October was the "right" thing to do, while high values of SST-SD indicate that spawning over the whole year was the better strategy. As might be seen, this graph suggests that from the mid-1960s to the mid-1980s, spawning over the whole year was the better strategy. This should have led to a reduced fitness of the fish adapted to spawning mainly from September to November, and hence to a reduction of their proportion in the overall population, relative to anchoveta with a tendency to spawn year-round. The findings of Senocak et al. (this vol.) support this hypothesis.

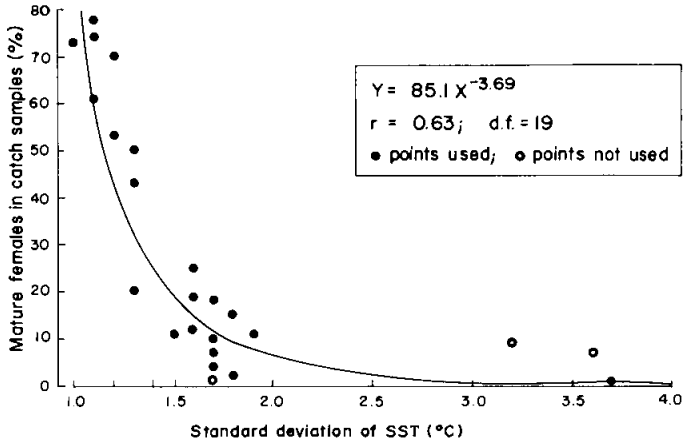

Fig. 4. Relationship between the relative abundance of mature female anchoveta in catch samples (Callao, Chimbote) and the standard deviation of mean monthly SST for these locations (see text for data sources).
Fig. 4. Relación entre la abundancia relativa de anchoveta hembras maduras en las muestras (Callao, Chimbote) y las desviaciones estandar de los promedios mensuales de la TSM para estos lugares (ver texto para fuente de datos).

Table 1. Monthly mean SST (°C) and SST-standard deviation of nine shore stations along the Peruvian coast for the period 1950-1987.*
Tabla 1. Promedios mensuales de la TSM (°C) y de la desviación estandar de la TSM de nueve estaciones costeras a lo largo de la costa peruana para el período 1950-1987.

	Talara 04°34'S		Paita 05°05'S		Chicama 07°43'S		Chimbote 09°05'S		D. Martin 11°02'S		Callao 12°04'S		Pisco 13°40'S		S. Juan 15°21'S		Ilo 17°38'S	
	SST	sd	SST	sd	SST	sd	SST	sd	SST	sd	SST	sd	SST	sd	SST	sd	SST	sd
Jan	20.4	1.6	20.1	1.8	17.6	1.9	20.8	1.7	17.9	1.8	16.9	1.9	21.9	1.3	15.7	1.6	16.8	1.4
Feb	21.7	2.1	21.7	1.8	18.8	1.9	21.7	1.6	18.8	1.6	17.7	1.8	22.3	1.0	16.3	1.7	17.1	1.4
Mar	21.5	2.0	21.6	1.9	18.7	1.7	21.7	1.7	18.9	1.7	18.3	1.7	22.4	1.2	16.1	1.5	16.8	1.4
Apr	20.1	2.3	19.7	2.3	17.9	2.1	21.0	1.7	18.0	1.7	17.8	1.8	22.0	1.3	15.6	1.1	16.5	1.2
May	18.7	3.8	18.2	3.8	17.4	2.2	19.5	3.7	16.9	3.3	17.3	1.7	21.1	1.2	14.8	2.6	15.7	2.8
Jun	18.5	3.7	17.8	3.8	17.1	2.0	18.5	3.6	16.3	3.3	16.3	3.2	20.2	1.2	14.4	2.6	15.3	2.7
Jul	18.3	1.9	17.3	2.0	16.7	1.3	18.6	1.6	16.4	1.5	16.3	1.3	19.8	1.3	14.5	13.0	15.3	1.0
Aug	17.7	0.9	16.7	1.3	16.2	0.9	18.3	1.3	16.0	1.4	15.9	1.2	19.6	1.1	14.2	1.1	14.9	1.0
Sep	17.7	0.9	17.0	1.5	15.9	0.7	18.0	1.1	15.5	1.0	15.5	1.0	19.7	0.7	13.7	0.8	14.7	0.9
Oct	17.9	1.0	17.0	1.4	15.8	0.8	18.5	1.1	15.8	1.0	15.5	1.1	20.0	0.7	13.9	0.8	15.0	0.9
Nov	18.2	1.4	17.5	1.5	16.0	1.2	19.1	1.2	16.3	1.2	15.8	1.3	20.4	0.8	14.3	0.9	15.5	1.0
Dec	18.6	1.8	18.3	1.7	16.6	1.7	19.8	1.5	17.0	1.5	16.4	1.6	21.2	1.0	14.9	1.3	16.3	1.4
Annual mean	19.1	2.0	18.6	2.1	17.1	1.5	19.6	1.8	17.0	1.7	16.6	1.6	20.9	1.1	14.9	1.4	15.8	1.4

*Based on the SST-time series given in Muck et al. (1989).

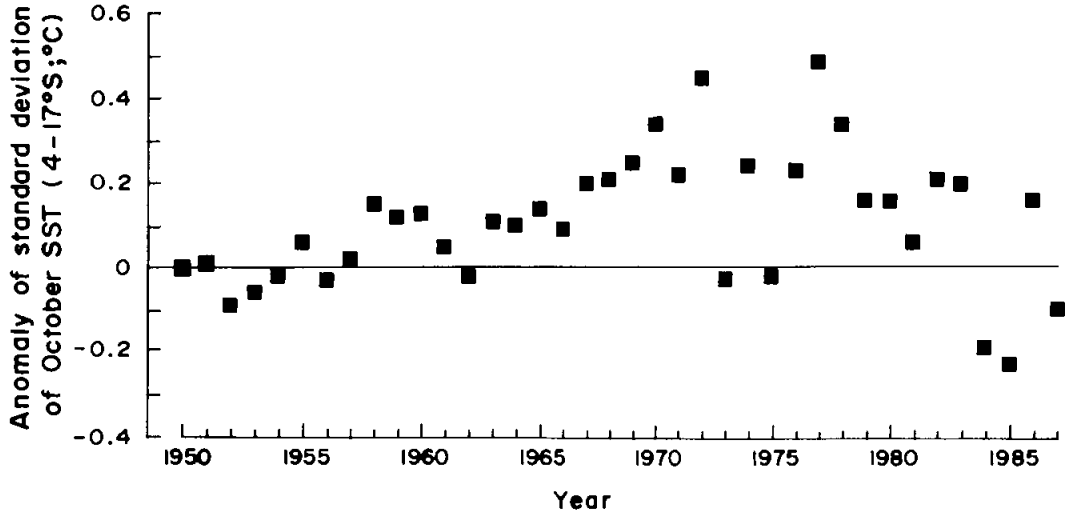

Fig. 5. Trend of October SST-SD anomaly; values > 0 imply that October conditions along the coast of Peru are highly variable (unpredictable) and that hence, the optimum spawning strategy would be to spawn year-round.
Fig. 5. Tendencia de la anomalia de la desviación estandar de TSM de Octubre; los valores > 0 implican que las condiciones a lo largo de la costa peruana son altamente variables (no predecibles) y que por lo tanto, la óptima estrategia para el desove sería desovar durante todo el año.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Enfield, D.B. 1981. El Niño: eastern boundary response to interannual forcing, 213-254. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. Wiley-Interscience, New York.

Jordán, R. 1980. Biology of the anchoveta I: Summary of the present knowledge, p. 249-276. *In* Proceedings of the Workshop on the Phenomenon known as "El Niño", Guayaquil, Ecuador, 4-12 December 1974. United Nations Educational, Scientific and Cultural Organization, Paris. 284 p.

Medina, F.A. 1979. A study of wind, oceanic temperature and hydrography in the upwelling area off Peru. Oregon State University, Corvallis. 62 p. M.S. thesis.

Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Muck, P. and G. Sánchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Muck, P., O. Sandoval de Castillo and S. Carrasco. 1987. Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Peru, p. 268-275. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Muck, P., I. Tsukayama and E. Ferrandis. 1989. Temperaturas superficiales del mar a lo largo de la costa peruana, para el período 1950-1988. Inf. 94. Inst. Mar. Perú-Callao.

Paulik, G.J. 1981. Anchovies, birds and fishermen in the Peru Current, p. 35-79. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. Wiley-Interscience, New York.

Pauly, D. 1987. Managing the Peruvian upwelling ecosystem: a synthesis, p. 325-342. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D. and M. Soriano. 1987. Monthly spawning stock and egg production of Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982, p. 167-178. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D. and I. Tsukayama. 1987. On the implementation of management-oriented fishery research: the case of the Peruvian anchoveta, p. 1-13. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Tetracycline Labelling for Age and Growth Studies in Fish, with Emphasis on the Peruvian Anchoveta

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Abstract

Marking experiments were conducted with fingerlings of anchoveta (*Engraulis ringens*), sardine (*Sardinops sagax*), silversides (*Odonthestes regia*) and Atlantic menhaden (*Brevoortia tyrannus*) using tetracycline baths or injections, or through feeding the experimental fish with *Artemia salina* previously held in tetracycline. The resulting marks on otoliths, scales and vertebrae are clearly visible in ultraviolet light, stable under long-term storage conditions, and hence can serve for validation of age and growth studies or for aging of tropical fishes. Data to estimate the relationships between mark visibility, fish mortality and dosage are given for three of the investigated fish species.

Resumen

Se han realizado experimentos de marcación de juveniles de anchoveta (*Engraulis ringens*), sardina (*Sardinops sagax*), pejerrey (*Odonthestes regia*) y Atlantic menhaden (*Brevoortia tyrannus*) usando baños o inyecciones de tetraciclina o a través de experimentos de alimentación con *Artemia salina*, previamente marcada con tetraciclina. Las marcas resultantes en otolitos, vertebras y escamas son claramente visibles en luz ultravioleta, estables y con capacidad de almacenamiento de larga duración, y por lo tanto sirven para validar estudios de edad y crecimiento o para estimar la edad de peces tropicales. Datos para la estimación de la relación entre visibilidad de marcas, mortalidad de peces y dosis son dados para tres de las especies de peces investigados.

Introduction

The antibiotic known as tetracycline can be used to mark vertebrate bones. Marked bone tissues fluoresce in golden yellow, whereas unmarked bones show only a weak, pale blue fluorescence (Harris 1960). Thus, tetracycline can be used to resolve problems associated with age validation of temperate/cold water fishes (Beamish and McFarlane 1983) or with aging of tropical species.

Example of studies based on these techniques are those of Weber and Ridgway (1962) on sockeye salmon (*Oncorhynchus nerka*), king salmon (*Oncorhynchus tshawytscha*) and rainbow trout (*Salmo gairdneri*), Kobayashi et al. (1964) on *Carassius auratus*, Jones and Bedford (1968) on *Gadus morhua*, Holden and Vince (1973) on *Raja clavata*, Casselman (1974) on *Esox lucius*, Nagiec et al. (1983) on *Coregonus lavaretus*, Smith (1984) on *Triakis semifasciata*, and Dekker (1986) on *Anguilla anguilla*. Unpublished experiments were also conducted in 1970 on anchoveta (*Engraulis ringens*) by A. Málaga of IMARPE, Perú and K.M. Wilbur of Duke University, USA. Table 1 summarizes data from some of these studies. As might be noted, they usually do not indicate the optimal dose for marking the species studied.

Table 1. Tetracycline doses used in various fish marking studies.
Tabla 1. Dosis de tetraciclina usada en varios estudios de marcación de peces.

Species	Source	Type of tetracycline	Doses (mg/g fish)	Medium
Engraulis ringens	Málaga and Wilbur (unpublished)	Acromicyn	0.8	Seawater
Gadus morhua	Jones and Bedford (1968)	Acromicyn	0.025 0.05 0.1	Saline solution Saline solution Saline solution
Esox lucius	Casselman (1974)	Tetracycline hydrochloride	-	-
Raja clavata	Holden and Vince (1973)	Tetracylcine hydrochloride	0.05 0.1	Isotonic solution Isotonic solution
Carassius auratus	Kobayashi et al. (1964)	Acromicyn	0.05 0.1	Isotonic solution Isotonic solution

A strong dose of tetracycline usually results in mortality and in a wide and diffuse band, whose central area, corresponding to the exact time of marking, is difficult to locate. Small doses, on the other hand, result in marks (rings) that are difficult to detect; these doses, however, protect the fish against infections associated with the insertion of, e.g., individual tags. In this study, therefore, a wide range of doses were administered to enable identification of the optimum dosage.

Materials and Methods

The marking experiments reported upon here were conducted on 240 juvenile individuals of four species and three families of pelagic fishes: anchoveta (*Engraulis ringens*, Fam. Engraulidae), sardine (*Sardinops sagax*, Fam. Clupeidae), Atlantic menhaden (*Brevoortia tyrannus*, Fam. Clupeidae) and silverside (*Odonthestes regia*, Fam. Aetherinidae).

These experiments were conducted in Peru in January 1975 and May 1977 with the three Peruvian species, and at the Marine Laboratory of the US National Marine Fisheries Service (NMFS) in Beaufort, North Carolina in May 1976. Some reading and photographing of labelled material were done at the MAFF in Aberdeen, Scotland, in October 1976-April 1977.

The fish used for the experiments were either scooped from commercial purse seines (anchoveta and sardine) or caught with gill nets (silverside and menhaden).

Only fish not affected by netting (i.e., which had survived for 35 days) and which had been feeding actively for at least 20 days were used for the tetracycline marking experiment (Fig. 1). They were kept either in oxygenated 4,000-l tanks, or in floating live boxes anchored off San Lorenzo Island, near Callao, at water temperature of about 15°C. In the latter case, which applied to some anchoveta and silverside, the fish consumed food naturally produced in the boxes. The anchoveta, sardine and silverside in the tanks were fed minced fish flesh supplemented with a commercial fishmeal-based poultry feed, or in some special cases, tetracycline-labelled *Artemia salina*. The menhaden were fed commercial pellets such as generally used at the Beaufort Laboratory of NMFS.

Prior to administration of tetracycline, the individual fish were:

1. exposed, until the respiratory movements slowed down, to a solution of the anesthetic MS 222 (at a concentration of about 1:10,000 in seawater) or of Quinaldine (about one drop per liter of water);
2. measured to the nearest 0.5 cm;

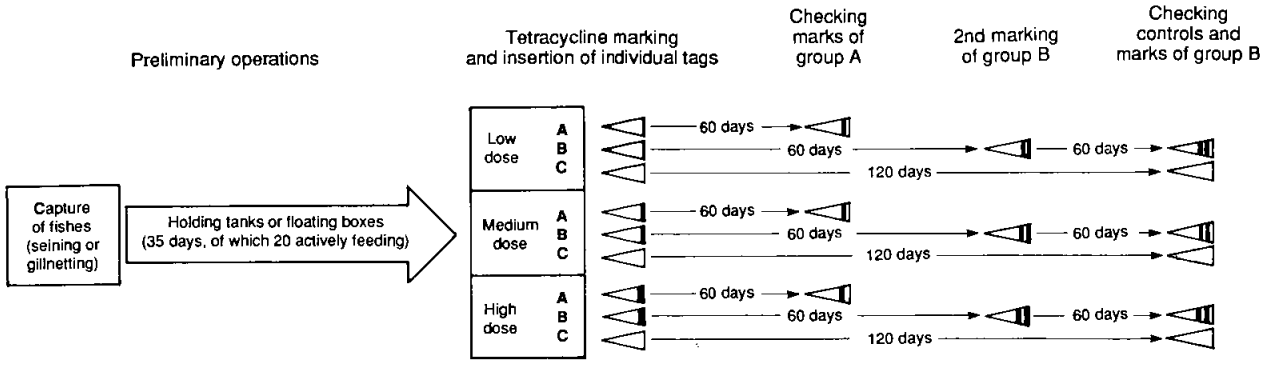

Fig. 1. Schematic representation of the experimental design used for tetracycline marking of anchoveta and other small pelagic fishes. Group A (1 marking) = 25 fish; Group B (2 markings) = 25 fish; Group C (control, no marking) = 10 fish.
Fig. 1. Representación esquemática del diseño experimental usado para la marcación con tetraciclina de la anchoveta y otros peces pelágicos. Grupo A (1 marcación) = 25 peces; Grupo B (2 marcaciones) = 25 peces; Grupo C (control, sin marcación) = 10 peces.

3. weighted to the nearest 0.5 g (the weights were used to compute the required dose of tetracycline);
4. tagged with an individually coded spaghetti tag, inserted into the dorsal muscle just anterior to the first dorsal fin. Internal (magnetic) tags were also inserted into the ventral cavity of anchoveta and sardine.
5. returned to seawater (fish which lost the spaghetti tags administered in (4) were not further considered).

The tetracycline used for the experiments was either chlortetracycline, oxytetracycline or pure tetracycline. No attempts were made to distinguish between possibly different effects of these compounds.

Administration of tetracycline was performed as follows:

i. through intraperitoneal injection of tetracycline-laced hot gelatin into a spot anterior to the pelvic fin, such as to leave the intestine and liver unharmed by the needle (performed between steps (4) and (5) above in the form of a unique dose (0.005, 0.05 and 0.1 mg/g/fish);
ii. through a bath in water with 20 mg of tetracycline per liter for periods lasting from 1 to 10 days (as in Hettler 1984);
iii. force-feeding of pill boxes containing a dose of tetracycline; cumulative doses (0.025-1.000) mg/g fish;
iv. feeding from 1 to 10 days with adult *Artemia salina* that had been kept for 6 days in tetracycline solution (50 mg/l) after a starvation period of 2 days or with larval *Artemia* that had been hatched in 500 mg/l tetracycline solution.

Marked scales, otoliths and vertebrae were kept for occasional reexamination, to assess the stability of the markings under storage conditions.

Results and Discussion

As illustrated in Fig. 2A with regard to anchoveta, tetracycline-induced mortality depends on dose; a 50% mortality within two weeks after marking is induced by a cumulative dose of 0.63 mg/g, administered over a period of 3-5 days. Visibility of tetracycline markings is also strongly dependent on dosage (see Fig. 2B).

The results for the three other species of fishes investigated here were similar, and are summarized in Table 2. Anchoveta and sardine kept in 50 mg/l tetracycline solution bath as well as those fed with *Artemia* previously immersed in tetracycline solution were the ones with the highest percentage of visible markings. In the case of small menhaden ($\overline{L}$ = 3.5 cm, $\overline{W}$ = 6 g), a tetracycline bath produced very visible marks while feeding of *Artemia* larvae hatched in tetracycline solution produced only a weak fluorescence.

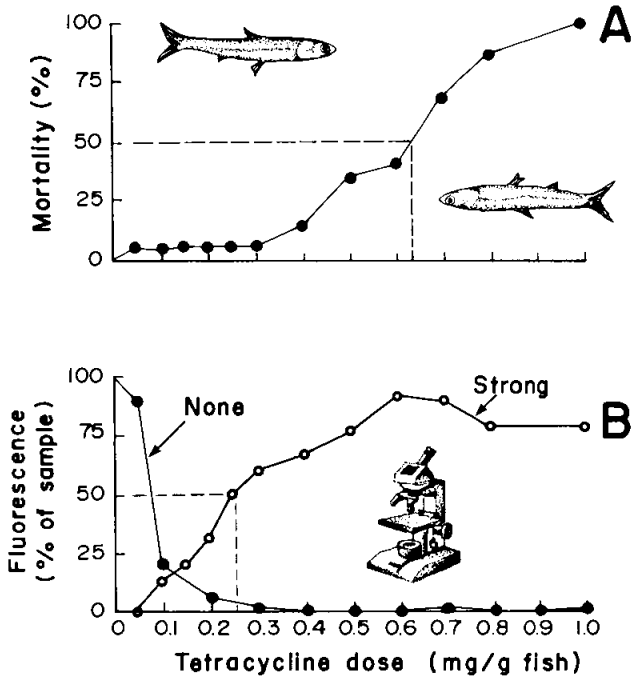

Fig. 2. Response of anchoveta (*Engraulis ringens*) to cumulative tetracycline exposure of 3-5 days (see Table 2 for larger exposures). A. Mortality as a function of dose; 50% mortality occurs at about 0.63 mg/g fish. B. Visibility of marks as a function of dose; 50% of marked samples will have strong marks at a dose of 0.25 mg/g fish.
Fig. 2. Reacción de la anchoveta (Engraulis ringens) *a la exposición acumulada con tetraciclina por 3-5 dias (ver tabla 2 para exposiciones mas largas). A. Mortalidad como una función de la dosis; 50% de mortalidad ocurre acerca de 0.63 mg/g pez. B. Visibilidad de las marcas como función de la dosis; 50% de las muestras marcadas tendrán marcas fuertes a la dosis de 0.25 mg/g pez.*

Table 2. Relationship between cumulative dose of tetracycline, duration of exposure, mortality and visibility of marks in (A) anchoveta ($\bar{l}$ = 11.2 cm; $\bar{w}$ = 13.0 g), (B) sardine ($\bar{l}$ = 14.5 cm; $\bar{w}$ = 16.8 g), and (C) Atlantic menhaden ($\bar{l}$ = 18.0 cm, $\bar{w}$ = 20.0 g).
Tabla 2. Relación entre la dosis acumulada de tetraciclina, duración de la exposición, mortalidad y visibilidad de las marcas en (A) anchoveta ($\bar{l}$ = 11.2 cm; $\bar{w}$ = 13.0 g), (B) sardina ($\bar{l}$ = 14.5 cm; $\bar{w}$ = 16.8 g) y (C) Atlantic menhaden ($\bar{l}$ = 18.0 cm; $\bar{w}$ = 20.0 g).

Cumulative dose (mg/g fish)	Duration of exposure (days)	Fish mortality (%) A / B / C	None A / B / C	Fluorescence (% of sample) Weak A / B / C	Strong A / B / C
0.025	10	3/2/2	85/80/90	15/20/10	0/0/0
0.050	5	5/4/1	90/50/83	10/40/17	0/10/0
0.050	10	4/3/1	71/40/80	30/47/20	0/13/0
0.100	5	4/5/1	20/25/45	66/35/35	14/40/20
0.150	10	5/4/2	10/21/28	70/49/40	20/30/32
0.200	5	5/5/2	6/5/10	62/50/50	32/35/40
0.250	10	5/5/2	5/0/5	45/40/45	50/60/50
0.300	5	5/10/2	1/0/5	39/30/30	60/70/65
0.400	3	15/23/4	1/0/2	31/30/38	68/70/60
0.500	3	35/40/5	0/0/3	22/22/47	78/78/50
0.600	3	40/55/20	0/1/3	7/14/22	93/85/75
0.700	4	69/59/40	1/2/2	9/8/23	90/90/75
0.800	5	87/90/65	0/2/0	21/10/20	79/88/80
1.000	5	100/100/80	1/0/0	20/5/0	79/95/100

Introperitoneous injection of two different doses of tetracycline (0.05 and 0.1 mg/g) led to small differences in the width of the markings, but the smaller dose is better, because the mortality induced is smaller.

The *Artemia* larvae fed to the experimental fish were all strongly fluorescent. All fish fed for six days with these larvae got fluorescent marking of their hard structures.

Overall, fluorescence occurred in all hard structures (scales, otoliths, vertebrae) of all fish, after 24 hours when they had been injected a dose of 0.5 mg/g or after 48 hours when they had been injected a dose of 0.05 mg/g.

Tetracycline marks on material kept in storage tend to fade, but the process is slow, and marks can be observed on scale, otoliths or vertebrae two years after marking. When vertebrae or otoliths are embedded in plastic, the fluorescent mark keeps at least eight months, although the vertebrae (but not the otoliths) may require some polishing for the marks to regain their former intensity.

These results suggest, overall, that tetracycline marking can be used to test various hypotheses concerning growth of fragile, small pelagic fishes such as investigated there, and to validate age readings based on counts of annual or daily (Pannella 1971) otolith rings, or the analysis of length-frequency data.

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References

Arnold, D.E. 1966. Marking fish with dies and other chemicals. Bureau of Sport Fisheries and Wildlife. Technical Paper 10.

Beamish, R.J. and G.A. McFarlane. 1983. Validation of age-determination estimates: the forgotten requirement. Trans. Am. Fish. Soc. 112: 735-743.

Bedford, B.C. 1964. Two mechanical aids for otolith reading. Res. Bull. Int. Comm. N.W. Atlant. Fish (1): 79-81

Casselman, J.M. 1974. Analysis of hard tissue of pike, *Esox lucius* L. with special reference to age and growth, p. 13-17. *In* T.B. Bagenal (ed.) The ageing of fish. Unwin Brothers, Surrey, England.

Dekker, W. 1986. Age reading of eels using tetracycline-labelled otoliths. ICES C.M. 1986/M:16. Anadromous and Catadromous Fish Cttee., 14 p.

Harris, W.H. 1960. A microscopic method for determining rate of bone growth. Nature (London) 188: 1038-1039.

Hettler, W.F. 1984. Marking of otoliths by immersion of marine fish larvae in tetracycline. Trans. Am. Fish. Soc. 113(3): 370-373.

Holden, M.J. and M.K. Vince. 1973. Age validation studies on the centra of *Raja clavata* using tetracycline. J. Cons. CIEM 35: 13-17.

Jones, B.W. and B.C. Bedford. 1968. Tetracycline labelling, as an aid to interpretation of otolith structures in age determinations: a progress report. ICES C.M.1968/Gen:11. 3 p.

Kobayashi S., R. Yuki, T. Furui and T. Kosugiyama. 1964. Calcification in fish and shellfish: tetracycline labelling patterns on scale, centrum and otolith in young goldfish. Bull. Jap. Soc. Sci. Fish. 30(1): 6-13.

Mugiya, Y. and J. Muramatsu. 1982. Time-marking methods for scanning electron microscopy in goldfish otoliths. Bull. Japan Soc. Sci. Fish. 48(9): 1225-1232.

Nagiec, M., C. Nagiec, K. Dabrowski and E. Murawska. 1983. Marking of juvenile whitefish *Coregonus lavaretus* (l.) with tetracycline antibiotics. Acta Ichthyol. et Pisc. 13(2): 47-57.

Ouchi, K. 1969. Effects of water temperature on the scale growth and width of the ridge distance in goldfish. Bull. Japan Soc. Sci. Fish. 35(1): 25-31.

Pannella, G., 1971. Fish otoliths: daily growth layers and periodical patterns, Science (N.Y.). 1/3: 1124-1127.

Smith, S.E. 1984. Timing of vertebral-band deposition in tetracycline-injected leopard sharks. Trans. Am. Fish. Soc. 113(3): 308-313.

Weber, D.D. and G.J. Ridgway. 1962. The deposition of tetracycline drugs in bones and scales of fish and its possible use for marking. Fish Cult. 24(4): 150-155.

Weber, D.D. and G.J. Ridgway. 1967. Marking Pacific salmon with tetracycline antibiotics. J. Fish. Res. Board Can. 24(4): 849-865.

Age and Growth of the Southern Stock of Peruvian Anchoveta Based on Otolith Microstructures and Length-Frequency Analysis

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Abstract

The growth of anchoveta (*Engraulis ringens*) off Ilo, Peru, was determined using otolith interpretation and length-frequency analysis. The suitability of otolith interpretation for anchoveta growth determination is demonstrated. The use of length-frequency methods, jointly with age data, and the correction of length-frequency for recruitment and gear selectivity are discussed.

Resumen

El crecimiento de la anchoveta peruana frente a Ilo, Perú, fué determinado utilizando la interpretación de los otolitos y los análisis de frecuencia de tallas. La adecuación de los otolitos para determinar el crecimiento de la anchoveta peruana fue probada. El uso conjunto de los análisis de frequencia de tallas con los datos de edad y la corrección de los sesgos producidos por el reclutamiento y la selección del arte en las frecuencias de tallas son discutidos.

Introduction

The Peruvian anchoveta (*Engraulis ringens*) occurs off the coast of Peru, with heaviest concentrations along the northern and central areas. Anchoveta adult distribution (Villanueva 1975) and their egg distribution (Santander 1987) suggest the presence, during the spawning periods, of isolated groups which may correspond to genetically distinct subpopulations (Mathisen, this vol.). Anchoveta morphological features (Rojas de Mendiola 1971; Tsukayama 1966) and tagging experiments support the hypothesis that the anchoveta resources in the Peruvian southern area (Atico-Ilo) constitute a stock distinct from the northern/central stock documented in Pauly and Tsukayama (1987).

The growth of the northern/central stock has been studied by Pauly and Tsukayama (1983) and especially by Palomares et al. (1987), who also reviewed earlier studies. In contrast with the northern/central stock, little is known on the growth of the southern stock. In this contribution, the growth of the latter stock is determined by means of otolith interpretations and length-frequency analysis based on otoliths and length-frequency data collected in the southern region of Peru in 1979.

Materials and Methods

The length-frequency data used for this analysis were collected monthly during 1979 by IMARPE staff along the southern coastal area comprising the harbors of La Planchada, Atico, Mollendo and Ilo. A subsample of one pair of otoliths for each 0.5 cm total length interval was obtained from the Ilo samples (n = 163).

The otoliths were studied with a compound microscope following the standard methods developed for temperate water fishes. The periodicity of ring formation was determined based on the progression, during the course of the year, of the ring in the margin of the otolith and by comparing the number of daily increments in the otoliths with the age determined from the rings. For this last method, a subsample of otoliths (n = 18) covering a wide range of ages was prepared for light microscopy, which was performed by applying otolith preparation techniques modified from Brothers (1987).

Age was assigned using the 1st of July as arbitrary birthdate, and an annual age-length key was constructed. The parameters of the von Bertalanffy growth function (VBGF) were estimated by means of the ETAL I program (Gaschütz et al. 1980). As the age-length key does not reflect seasonal changes in growth, the growth curve was fitted without accounting for seasonality.

Fitting of the growth curve to the length-frequency data was done by using the ELEFAN I program (Pauly and David 1981; Pauly 1987; Palomares et al. 1987). Here, the length-frequency data are used to estimate the growth parameters L_∞, K, C (amplitude of the seasonal growth oscillations), and WP (time of minimum growth) of the VBGF modified to include seasonal growth oscillation (Pauly and Gaschütz 1979). Also, Modal Progression Analysis or MPA (George and Banerji 1964; Sparre 1987), as included in the Compleat ELEFAN program package of Gayanilo et al. (1988), was used to determine the mean length and associated statistics of each presumed age group in the available length-frequency samples. These means were then interlinked in a fashion thought to reflect growth.

The MPA routine of the Compleat ELEFAN uses the method of Bhattacharya (1967) for decomposing length-frequency samples into their component (normal) distribution. For comparison, the method of Cassie (1950), was also applied to the data of Table 2.

The growth increments resulting from MPA were treated as if they were tagging/recapture data, using each of the successive mean lengths as if they were tagging (length at age t) and recapture lengths (length at age $t+\Delta t$). The age-at-length data obtained by reading the available otoliths were also used to derive growth increments (i.e, "tagging/recapture" data). This was achieved: (i) by using only the increments between year groups and counting twice the increment between age 1 and 2, which is well represented in the samples (see Table 2) and (ii) by using the appropriate routine of the software documented by Brey et al. (1988). The two sets of growth increment data so obtained were entered, along with that obtained from MPA, into the appropriate routine of the Compleat ELEFAN package, and the latter used - along the lines suggested by Morgan (1987) - to estimate growth parameters by simultaneous analysis of length-frequency and growth increment data (Gayanilo et al. 1988).

To correct for the bias introduced by incomplete recruitment and gear selection, the original length-frequency data were corrected using the methods described in Pauly (1986, 1987). As the probabilities of capture in the southern stock can be assumed to be similar to those in the northern/central stock, the probabilities of capture of Palomares et al. (1987), pertaining to the northern/central stock, were used for the correction. All length-based analyses were then repeated using the corrected length-frequencies.

Results

Otolith Interpretation

Anchoveta otoliths are small elongated bodies with a sharp rostrum and well-developed antirostrum. When observed with a compound microscope and reflected light against a dark background, a concentric pattern of bright (opaque) and dark (translucent or hyaline) rings appeared. The definition of the rings improved when the otoliths were immersed in a dense medium (glycerin). The presence of faint false rings obscured in some cases the otolith interpretation.

Otolith interpretation is a dual process consisting of (1) growth ring identification and interpretation and (2) determination of ring periodicity and validation of results.

To assess the objectivity of the interpretation, the otoliths were read three times; a level of 94% coincidence was obtained which showed consistency in the interpretation. Moreover, in a comparative reading exercise between an expert sardine otolith reader without experience in anchoveta otolith interpretation (Ms. G. Cárdenas, IMARPE) and the author, an agreement of 86% was achieved. Thus, anchoveta otolith interpretation was considered reliable.

The determination of the periodicity of the ring formation was made difficult by the thinness and transparency of the otolith margin. Some error might have occurred in the identification of the ring formed in the edge, principally when the opaque ring was in its initial development. Nevertheless, when plotting the monthly percentage of hyaline rings in the otolith edge along the year, the formation of one hyaline ring per year was evident (Fig. 1).

Under the light microscope, the otoliths showed a recurrent pattern of light and dark rings (Pannella 1971) laid down with daily periodicity (Rojas de Mendiola and Gómez 1981). The increments were enumerated along the posterior otolith radius and the number of increments versus the number of hyaline rings in each otolith were plotted (Fig. 2.). The correlation between both variables was not very high (r = 0.81). This might be due to the bias introduced by the long spawning period of anchoveta (up to 6 months) and to the failure of the light microscope in detecting the thin increments (0.5 - 0.7 µm) laid down in the hyaline rings of fish older than one year (Morales-Nin 1988). Nevertheless, the age in days and in years for age 1 was close enough to validate the periodicity of the first annulus. Therefore, the two validation methods used here provided sufficient evidence of the annual formation of the rings and it can be concluded, therefore, the the age determinations by means of annuli are essentially correct.

Table 1 presents the validated age-length key derived here.

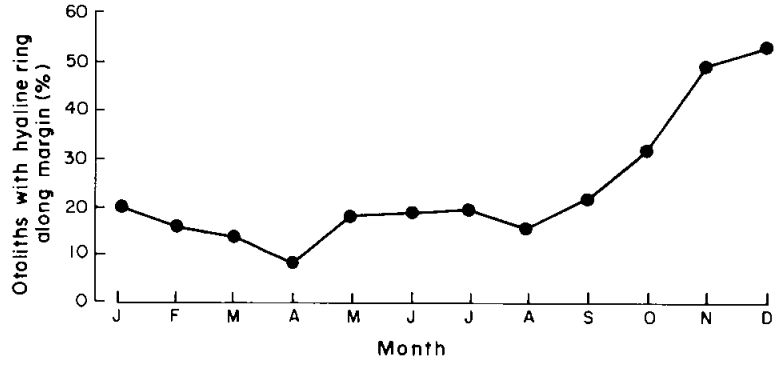

Fig. 1. Percentage of otoliths with a hyaline ring in the margin along the year.
Fig. 1. Porcentaje de otolitos con un anillo hialino en el margen a lo largo del año.

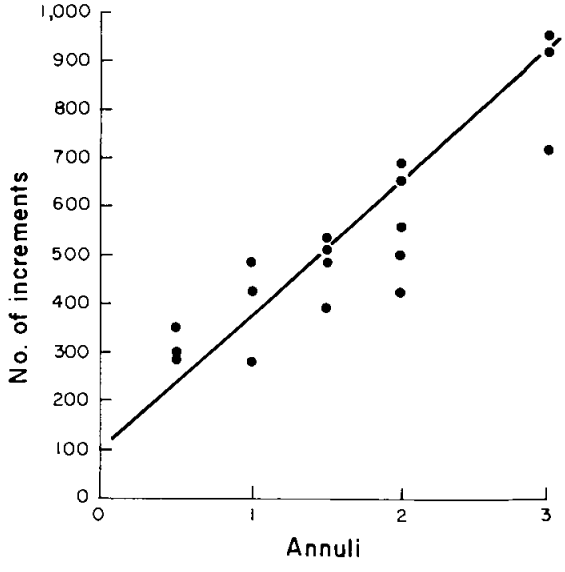

Fig. 2. Correspondence between the age in years (number of annuli) and the age in days (number of increments).
Fig. 2. Correspondencia entre la edad en años (número de annuli) y la edad en días (número de incrementos).

Table 1. Age-length key for the southern anchoveta *(Engraulis ringens)* stock. (Otoliths collected off Ilo during 1979).
Tabla 1. Clave talla-edad para el stock sur de la anchoveta (Engraulis ringens). *(Los otolitos fueron colectados en Ilo durante 1979).*

Total length (cm)	Age groups 0	1	2	3	Total
8.5	1				1
9.0	2				2
9.5	2				2
10.0	3				3
10.5	5				5
11.0	6	2			8
11.5	2	5			7
12.0	2	5			7
12.5	1	8			9
13.0		10			10
13.5		9	1		10
14.0		7	2		9
14.5		6	4	1	11
15.0		2	5	1	8
15.5		3	4	4	11
16.0			7	4	11
16.5			9	3	12
17.0			6	6	12
17.5			4	7	11
18.0			5	3	8
18.5			3	3	6
Total	24	57	50	32	163
Mean length	10.56	13.20	16.29	16.84	-
s.d.	1.00	1.15	1.29	1.06	-

Length-Frequency Analysis

The length-frequency distribution showed notable monthly difference in structure (Table 2).

The analysis of these data using Cassie's (1950) probability paper method and modal progression analysis (MPA) usually suggested the presence of four age groups. However, a fifth group appeared in June (Fig. 3.). The mean lengths obtained for ages 0, 1 and 2 were similar to the means from otolith reading. The mean length of age 3 was different, probably due to overlapping in the length-frequencies caused by the low growth rate of old fishes (Table 3). MPA showed the presence of young fishes following the months of maximum spawning and clear seasonal growth oscillations in the age groups 1 and 2 (Fig. 3).

When the length-frequency data were corrected for recruitment and gear selection, the growth parameters obtained using ELEFAN I showed a clear change and a better fit (Fig. 4B) than without such correction (Fig. 4A, Table 6). The main change was the increase of K, which was higher (Pauly 1986) and hence, closer to the values obtained from otolith readings.

The mean lengths obtained of various age groups estimated by the Bhattacharya method (Fig. 3) and converted into growth increments using MPA are given in Table 4, along with the two sets of growth increments derived from otoliths.

The three sets of growth increment data were analyzed jointly with the length-frequency to improve the fit of the growth parameters. Two independent calculations were done for each set of growth increments, one using the uncorrected length-frequency data, and the other relying on the length-frequency data corrected for incomplete recruitment and gear selection (see Table 5). Table 6 presents the results.

Table 2. Length-frequency of anchoveta catches from the southern area (La Planchada-Ilo) in 1979.
Tabla 2. Frecuencia de tallas de las capturas del área sur (La Planchada-Ilo) en 1979.

Mean length (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
6.0		26										
6.5		26			59							
7.0		0			152							
7.5		465			59							
8.0	2,339	358			59							
8.5	635	1,331	2	269	0						12	334
9.0	4,087	4,723	596	660	1,470		214				0	0
9.5	1,799	3,563	897	2,654	5,431		0				115	118
10.0	10,631	6,539	1,813	7,040	9,353		214				0	1,827
10.5	12,789	6,741	4,592	13,253	15,867		219				51	571
11.0	23,515	10,515	8,005	23,768	31,943	1,628	691			332	84	4,082
11.5	28,184	19,225	13,202	39,022	44,593	3,749	1,248			195	51	12,883
12.0	29,031	25,508	24,953	58,571	55,573	12,361	1822			1,563	103	9,316
12.5	44,726	37,996	41,290	75,625	72,225	28,274	5,102			911	629	12,667
13.0	35,103	35,129	41,975	54,403	50,777	35,651	6,221	88		2,060	983	6,751
13.5	33,093	54,105	57,634	84,212	47,198	40,784	6,857	213		4,360	1,502	4,016
14.0	19,608	28,695	43,634	54,698	38,734	32,394	872	288	294	4,076	2,248	5,693
14.5	8,541	15,695	24,896	63,568	64,382	28,354	4,259	664	1,214	10,621	5,911	24,259
15.0	27,809	19,297	11,652	41,547	69,676	11,615	2,145	756	687	14,737	5,810	98,468
15.5	105,762	93,242	26,358	147,417	131,337	19,329	2,054	7,229	23,538	59,890	21,379	318,947
16.0	349,988	310,547	77,335	276,927	234,495	25,153	3,918	41,408	73,087	246,328	88,131	261,227
16.5	638,572	625,519	166,697	417,280	357,390	65,038	9,249	136,202	164,063	719,565	195,309	130,130
17.0	464,199	403,130	139,961	259,760	230,170	51,920	12,852	104,367	99,386	585,850	141,604	11,338
17.5	174,952	128,482	45,736	88,570	105,576	25,087	6,484	53,726	32,140	278,621	38,554	226
18.0	28,441	684	5,165	6,722	12,318	3,012	1,108	4,779	2,181	32,432	6,160	
18.5	1,705			319	305	2	318	551		2,283	348	
19.0					21							
Sum	2,044,509	1,831,541	736,393	1,716,285	1,579,163	384,351	65,847	350,271	396,590	1,963,824	508,984	902,853

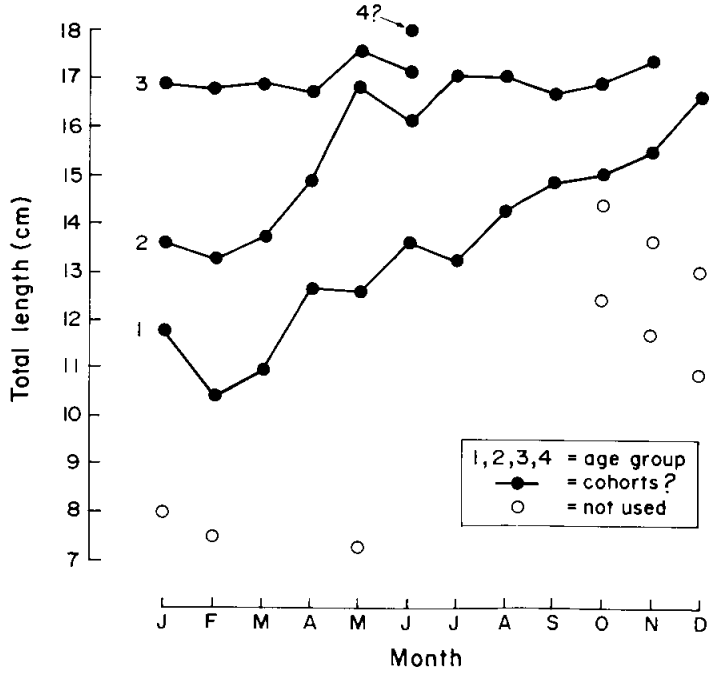

Fig. 3. Mean length at age obtained from MPA. The selected values for each age group have been connected with a line to show the seasonal growth oscillation.
Fig. 3. Tallas medias por edad obtenidas a partir del análisis de progresión modal. Las tallas medias seleccionadas para cada grupo de edad han sido conectadas con una línea para mostrar la fluctuación estacional del crecimiento.

Table 3. Mean length (TL, in cm)-at-age determined by otolith reading and using two methods for length-frequency analysis.
Tabla 3. Tallas medias (L.T., en cm) por edad determinadas a partir de los otolitos y dos métodos de análisis de frecuencia de tallas.

Method	Age groups 0	1	2	3
Otolith	10.6	13.2	16.3	16.8
Cassie's	10.1	14.2	16.5	18.5
MPA	10.9	13.9	16.0	17.9

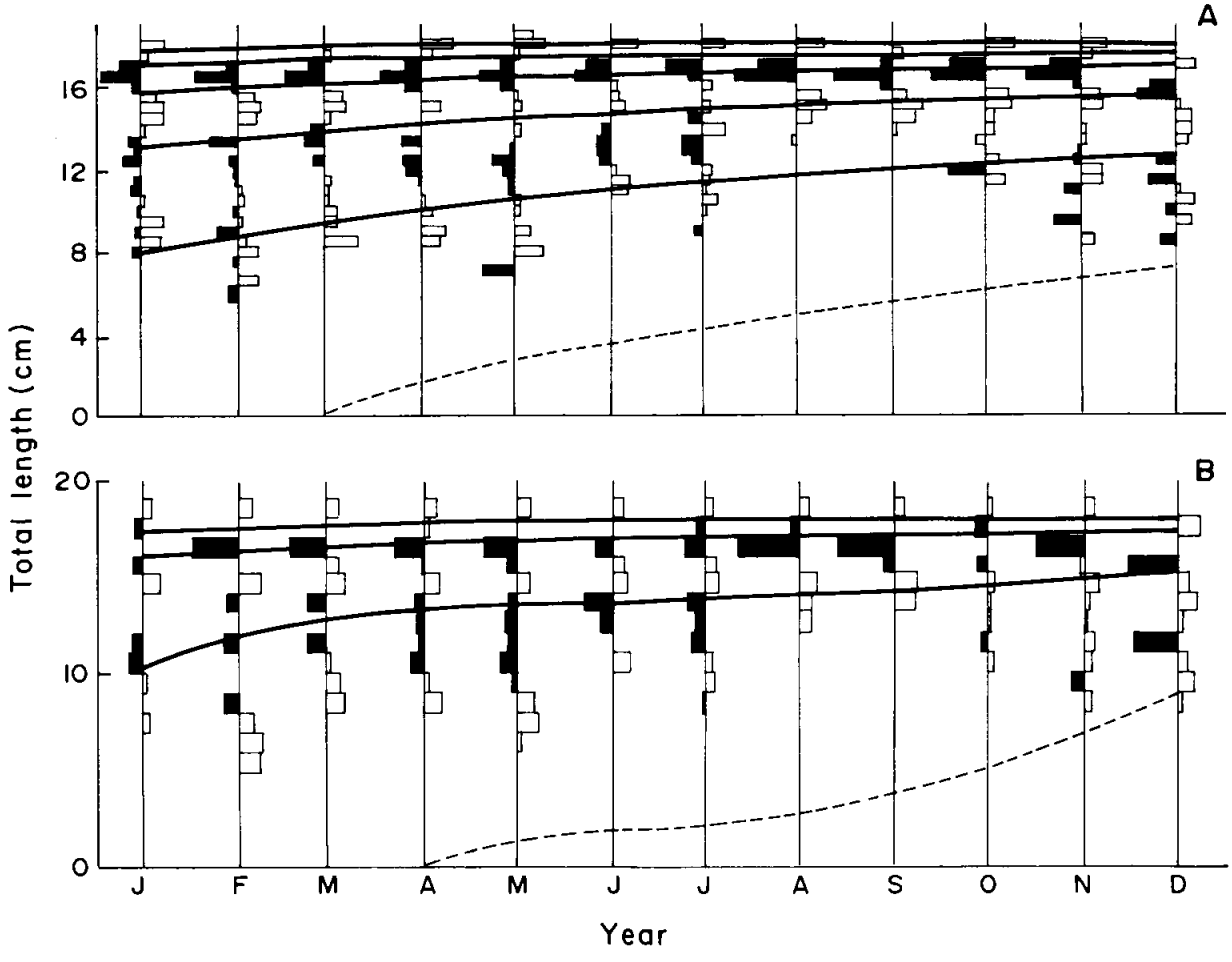

Fig. 4. Growth curves obtained with ELEFAN I. (A) Catch data. (B) Corrected length-frequencies.
Fig. 4. Curvas de crecimiento obtenidas con ELEFAN I. (A) Datos de captura. (B) Frecuencias de tallas corregidas.

Table 4. Growth increments of anchoveta, as derived using various methods.
Tabla 4. Incrementos de crecimiento de la anchoveta obtenidos por varios métodos.

No. of increment	Initial and end lengths of increments (TL, in cm) Initial	End	Times at beginning[a] and end of increments Mo./year	Mo./year	Source of set of growth increments
1	11.8	13.7	1/79	1/80	Set 1: Derived from data in Table 2, using MPA, following decomposition of mixtures of distributions using Bhattacharya's (1967) method, as implemented in the Compleat ELEFAN program (Gayanilo et al. 1988).[b]
2	13.7	16.9	1/80	1/81	
3	14.0	13.2	2/79	1/80	
4	13.2	16.8	2/80	1/81	
5	10.8	13.7	3/79	3/80	
6	13.7	16.9	3/80	3/81	
7	12.7	14.8	4/79	4/80	
8	14.8	16.7	4/80	4/81	
9	13.6	16.2	6/79	6/80	
10	16.2	17.3	6/80	6/81	
11	17.3	18.0	6/81	6/82	
12	14.9	16.8	9/79	9/80	
13	12.4	14.4	10/79	9/80	
14	10.6	13.2	1/79	1/80	Set 2: As obtained from the mean lengths of age groups in Table 3; abundant age age groups (1-2) used twice.
15	13.2	16.3	1/80	1/81	
16	13.2	16.3	1/80	1/81	
17	16.3	16.8	1/80	1/80	
18	9.5	12.5	1/79	1/80	
19	9.5	12.5	1/79	1/80	
20	9.5	13.5	1/79	1/80	
21	10.5	12.5	1/79	1/80	
22	11.5	15.5	1/79	1/80	Set 3: Derived from the length-at-age data in Table 1 using the method of Brey et al. (1988).
23	12.5	16.5	1/79	1/80	
24	12.5	16.5	1/79	1/80	
25	14.5	15.5	1/79	1/80	
26	15.5	16.5	1/79	1/80	

[a]Dates are (in part) arbitrary, only Δt values matter.
[b]See also Fig. 3.

Table 5. Example of a response surface of the joint goodness of fit index R_m[a] x 1,000, as derived by the ELEFAN V program of Gayanilo et al. (1988) from the length-frequency data in Table 1, corrected for incomplete recruitment and/or selection, and complemented by the growth increment data in Table 4 (3rd set).[b]
Tabla 5. Ejemplo de respuerta del índice de ajuste R_m[a] x 1,000, obtenido por el programa ELEFAN V de Gayanilo et al. (1988) a partir de los datos de frecuencia de tallas de la Tabla 1 corregidos para reclutamiento incompleto y selección, y/o de los incrementos de crecimiento de la Tabla 4 (3° grupo).[b]

K(year^{-1})	Asymptotic length (TL, cm) 16.5	16.7	16.9	17.1	17.3	17.5	17.7	17.9	18.1	18.3	18.5
1.50	425	494	509	532	536	547	**557**	486	448	411	409
1.44	446	461	501	524	536	**558**	**568**	517	479	419	399
1.38	420	442	494	509	552	**550**	**568**	519	486	436	401
1.32	421	440	461	501	533	528	524	**568**	519	473	411
1.26	446	435	440	462	503	493	528	539	511	480	456
1.20	450	420	431	458	463	503	513	498	539	499	452
1.14	417	446	435	431	452	453	494	495	494	518	467
1.08	423	449	428	435	439	455	437	490	495	460	492
1.02	414	438	449	444	429	444	443	437	**490**	444	455
0.96	418	422	456	430	449	428	425	441	429	428	435
0.90	408	413	446	456	428	440	421	415	422	423	403

[a]R_m = mean of R^2 between actual lengths and estimated lengths at the end of the growth increments and $R_n = 10^{ESP/ASP}/10$, as used to assess the goodness of fit of a growth curve to length-frequency data (see Gayanilo et al. 1988 for details). Bold values refer to values of R_m x 1,000 ≤ 500.

[b]These values of R_m were obtained with C = 0.42, WP = 0.37 and starting point set at SS = 1 and SL = 10.5 cm (see Gayanilo et al. 1988 for definitions).

Table 6. Growth parameters for the southern stock of the Peruvian anchoveta, as determined by means of different methods.
Tabla 6. Parámetros de crecimiento del stock sur de la anchoveta peruana determinados por diferentes métodos.

Data	Method/Program	Growth parameter estimates L_∞ (TL, cm)	K(year^{-1})	C	WP	ϕ'[a]	Goodness of fit index
Age-at-length data in Table 1	Fitting of VBGF (Gayanilo et al. 1988)	16.7[b]	1.82[b]	-	-	2.703	$r^2 = 0.79$
Length-frequency data[c] in Table 2	ELEFAN I, without adjustment of L/F data for incomplete recruitment and/or selection[c]	18.4	0.69	0.27	0.67	(2.370)	$R_n = 0.18$
Length-frequency data[c] in Table 2	ELEFAN I, with L/F data adjusted for incomplete recruitment and/or selection	18.0	1.30	0.80	0.51	2.624	$R_n = 0.47$
Length-frequency data in Table 2, plus growth increments from Table 4, Set 1	ELEFAN V, without adjustment of L/F data for incomplete recruitment and/or selection	17.1	0.84	0.84	0.84	(2.392)	$R_m = 0.20$
Length-frequency data in Table 2, plus growth increments from Table 4, Set 1	ELEFAN V, with L/F data adjusted for incomplete recruitment and/or selection	17.8	1.36	0.42	0.37	2.634	$R_m = 0.31$
Length-frequency data in Table 2, plus growth increments from Table 4, Set 2	ELEFAN V, without adjustment of L/F data for incomplete recruitment and/or selection	17.0	0.85	0.84	0.84	(2.397)	$R_m = 0.57$
Length-frequency data in Table 2, plus growth increments from Table 4, Set 2	ELEFAN V, with L/F data adjusted for incomplete recruitment and/or selection	17.2	1.75	0.42	0.57	2.711	$R_m = 0.74$
Length-frequency data in Table 2, plus growth increments from Table 4, Set 3	ELEFAN V, without adjustment of L/F data for incomplete recruitment and/or selection	17.4	1.16	0.84	0.84	(2.544)	$R_m = 0.32$
Length-frequency data in Table 2, plus growth increments from Table 4, Set 3[d]	ELEFAN V, with L/F data adjusted for incomplete recruitment and/or selection[d]	17.9	1.40	0.42	0.37	2.651	$R_m = 0.57$

[a] $\phi' = \log_{10}K+2\log_{10}L_\infty$ (TL, cm); values in brackets are too low for anchoveta, due to noncorrection of L/F data (see text).
[b] The estimate of t_0 obtained along with these values was 0.184 year.
[c] See also Fig. 4.
[d] See also Table 5.

Discussion

The mean length-at-age obtained from the otolith reading and the length-based methods were similar (Table 3). Cassie's method produced the more divergent means, probably due to the subjectivity of the selection of the inflection points, which were not very clear. The Bhattacharya method, as incorporated in the MPA routine of the Compleat ELEFAN package, provided better results.

The growth parameters determined by otolith reading and by the different programs for length-frequency analysis (ELEFAN I and ELEFAN V plus growth increment files) were rather variable. However, clear trends emerged, notably with regard to the effect of correcting the length-frequency data for incomplete recruitment and/or selection: K was consistently higher when the length-frequency data were corrected. The growth performance index $\phi' = \log_{10}K+2\log_{10}L_\infty$ (Pauly and Munro 1984; Moreau et al. 1986) for corrected L/F data was very close to the values reported for the northern/central stock of Peruvian anchoveta (Palomares et al. 1987, Fig. 15). Indeed, the mean of the 5 usable values in Table 6 is $\phi' = 2.665$, precisely the value estimated for the late 1970s by Palomares et al. (1987, Fig. 5B).

The ELEFAN I results were in the range of values reported for the northern/central stock, but lower than the growth parameters for this stock in 1979. However, the growth parameters obtained from the corrected length-frequency were closer to the values reported for the northern/central stock (see Table 6 and Palomares et al. 1987).

The results of the combined use of length-frequency analysis and growth increments suggested that the annual growth increments derived from otolith data (sets 2 and 3 in Table 4) gave a better fit than the increments obtained from MPA (set 1 in Table 4). The growth increments from otolith data weighted by abundance (set 2 in Table 4) gave a better fit than the more numerous, but shorter and more variable growth increments in set 3, where more weight is given to the interval between ages 0 and 1 than in the other two sets. This greater weight of the growth of the youngest fishes might be responsible for the higher K that was obtained. Nevertheless, when the corrected length-frequency data were used, this effect was compensated for (see Table 5).

The correction for recruitment and gear selection of the length-frequency data strongly affected the K growth parameter estimation. The estimates of K obtained after the correction were much closer to the value obtained from otolith reading than without the correction (Table 6). In some simulations, the ELEFAN I program was found to overestimate L_∞ and underestimate K (Rosenberg and Beddington 1987; Hampton and Majkowski 1987). This effect appears to be overcome in the case of the Peruvian anchoveta after the length-frequency data were corrected for incomplete recruitment and gear selection. The estimates of the seasonal growth parameters (C and WP) also improved when the length-frequencies were corrected and reached values closer to those of the northern/central stock (Palomares et al. 1987) and which also were in concordance with the environmental fluctuations (Bakun 1987).

This is the first growth study of the southern Peruvian anchoveta stock and one of the first applications of a method for simultaneous analysis of length and age data derived from Morgan (1987). It may be premature to propose which of the growth parameter sets in Table 6 are the most accurate. Nevertheless, the suitability of otoliths for Peruvian anchoveta age determination has been demonstrated. Here, the match of our otolith-based parameter estimates with those of Aguayo (1979) from northern Chile is particularly notable, given that anchoveta from southern Peru and northern Chile are presumed to belong to the same stock. Also, a marked improvement of the growth estimates following the correction of length-frequency data for incomplete recruitment and gear selection bias was made evident. However, it may be necessary to continue studies of this type, including otolith data from more landing areas, to have a reliable estimates of anchoveta growth parameters. Also, it would be advisable to jointly study the growth of the Chilean and southern Peruvian components of the southern anchoveta stock.

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References

Aguayo, H.M. 1979. Edad y crecimiento de la anchoveta (*Engraulis ringens*, Jenyns) del Norte de Chile (Arica-Iquique) Invest. Pesq. Santiago 23(1): 1-25 + 22 p of figures and tables.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bhattacharya, C.G. 1967. A simple method of resolution of a distribution into Gaussian components. Biometrics 23: 115-135.

Brey, T., M. Soriano and D. Pauly. 1988. Electronic length-frequency analysis: a revised and expanded user's guide to ELEFAN 0, 1 and 2 (2nd ed.). Ber. Inst. Meeresk. Univ. Kiel No. 177. 31 p.

Brothers, E.B. 1987. Methodological approaches to the examination of otoliths in aging studies, p. 319-330. *In* C. Summerfeldt and G.A. Hall (eds.) Age and growth of fish. Iowa University Press, Ames, Iowa.

Cassie, R.M. 1950. The analysis of polymodal frequency distributions by the probability paper method. N.Z. Sci. Rev. 8: 89-91.

Gaschütz, G., D. Pauly and N. David. 1980. A versatile BASIC program for fitting weight and seasonally oscillating length growth data. ICES C.M. 1980/D:6 Statistics Cttee. 14 p.

Gayanilo, F.C., Jr., M. Soriano and D. Pauly. 1988. A draft guide to the Compleat ELEFAN. ICLARM Software 2, 65 p. International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

George, K. and S.K. Banerji. 1964. Age and growth studies on the Indian mackerel *Rastrelliger kanagurta* with special reference to length-frequency data collected at Cochin. Indian J. Fish. 11(2): 621-638.

Hampton, J. and J. Majkowski. 1987. An examination of the reliability of the ELEFAN computer programs for length-based stock assessment, p. 203-216. *In* D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait.

Morales-Nin, B. 1988. Caution in the use of daily increments for ageing tropical fishes. Fishbyte 6(2): 5-6.

Moreau, J., C. Bambino and D. Pauly. 1986. Indices of overall growth performance of 100 tilapia (Cichlidae) populations, p. 201-206. *In* J. Maclean, L.B. Dizon and L.V. Hosillos (eds.) The First Asian Fisheries Forum. Asian Fisheries Society, Manila, Philippines.

Morgan, G.R. 1987. Incorporating age data into length-based stock assessment methods, p. 137-146. *In* D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait.

Palomares, M.L., P. Muck, J. Mendo, E. Chúman de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1982, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash.) 173: 1124-1167.

Pauly, D. 1986. On improving operation and use of the ELEFAN programs. Part III. Correcting length-frequency data for the effects of gear selection and/or incomplete recruitment. Fishbyte 4(9): 11-13.

Pauly, D. 1987. A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates, p. 7-34. *In* D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait.

Pauly, D. and G. Gaschütz. 1979. A simple method for fitting oscillating growth data, with a program for pocket calculator. ICES C.M. 1979/G: 24. Demersal Fish. Cttee. 26 p.

Pauly, D. and J.L. Munro. 1984. Once more on growth comparison in fish and invertebrate. Fishbyte 2(10): 21.

Pauly, D. and N. David. 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforsch. 28(4): 205-211.

Pauly, D. and I. Tsukayama. 1983. On the seasonal growth, monthly recruitment and monthly biomass of Peruvian anchoveta *(Engraulis ringens)* from 1961 to 1979, p. 987-1004. *In* G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. No. 291. Vol. 3.

Pauly, D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Rojas de Mendiola, B. 1971. Some observations on the feeding of the Peruvian anchoveta (*Engraulis ringens* J.) in two regions of Peruvian coast, p. 417-440. *In* J.D. Costlow (ed.) Fertility of the sea. Vol. 2. Gordon and Breach Sci. Publ., New York.

Rojas de Mendiola, B. and O. Gómez. 1981. Daily otolith rings in otoliths of larval anchovy (*Engraulis ringens*). Rapp. P.V. Réun. CIEM (178): 565-566.

Rosenberg, A.A. and J. Beddington. 1987. Monte Carlo testing of two methods for estimating growth from length-frequency data with general conditions for their applicability, p. 283-298. *In* D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait.

Santander, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru (4-14°S), p. 179-207. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Sparre, P. 1987. Computer programs for fish stock assessment: length-based fish stock assessment for Apple II computers. FAO Fish. Tech. Pap. 101. Suppl. 2. Rome. 218 p.

Tsukayama, I. 1966. El número de branquiespinas como caracter diferencial de sub-poblaciones de anchoveta (*Engraulis ringens*, J.) en las costas del Perú, p. 139-145. *In* I Seminario Latino-Americano Sóbre el Océano Pacifico Oriental. Universidad Mayor de San Marcos, Lima, Perú.

Villanueva, R. 1975. The Peruvian Eureka Programme. Paper presented at the FAO Technical Conference on Fish Finding, Purse Seining and Aimed Trawling, Rejkjavik, Iceland, 24-30 May 1975. 12 p.

New Estimates of Monthly Biomass, Recruitment and Related Statistics of Anchoveta *(Engraulis ringens)* off Peru (4-14°S), 1953-1985*

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Abstract

A length-structured version of Virtual Population Analysis, implemented through the ELEFAN III computer program, was used to estimate, on a monthly basis, anchoveta (*Engraulis ringens*) biomass, recruitment, as well as fishing and natural mortalities off Peru for the period 1953 to 1985. This analysis, pertaining to the northern/central stock of anchoveta, took into account the predation effects of mackerel, horse mackerel, hake, bonito, guano birds (three species) and pinnipeds (two species), and was calibrated using acoustic estimates of anchoveta biomass.

The resulting time series demonstrate the impact of El Niño events on anchoveta population dynamics, and allow separation of the effects of various anchoveta predators from that of the fishery.

Resumen

Se estimaron, en una base mensual, la biomasa, reclutamiento y la mortalidad natural y por pesca de la anchoveta peruana para el período 1953 a 1985, mediante el ánalisis de Población Virtual con estructuras por longitudes implementado en el programa ELEFAN III. Este análisis, llevado a cabo para el stock norte/central, consideró los efectos de predación de la caballa, jurel, merluza, bonito, aves guaneras (3 especies) y pinnipedos (2 especies) y fué calibrado usando estimaciones de biomasa obtenidas por medio de evaluaciones acústicas.

La serie de tiempo resultante demuestran el impacto de los eventos El Niño sobre la dinámica de la población de anchoveta y permite visualizar por separado el efecto de los predadores y de la pesquería.

Introduction

This contribution presents time series of anchoveta *(Engraulis ringens)* biomass recruitment and mortality on a time scale (one month) that is sufficiently small for capturing the rapid changes that characterize this resource. Monthly time series of various aspects of the population dynamics of anchoveta have been presented earlier (Palomares et al. 1987; Pauly et al. 1987a). This contribution aims to:

i) extend (to 1985) the previous time series, which covered the years 1953 to 1982;
ii) include in the analysis the predatory effects of horse mackerel (*Trachurus murphyi*), mackerel (*Scomber japonicus*) and hake (*Merluccius gayi*), which were not explicitly considered earlier; and thus,

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iii) reduce the uncertainty associated with the input values of baseline natural mortality (M_o), an important parameter of Virtual Population Analysis (VPA), when this is implemented such as to explicitly account for predation.

This contribution represents, as far as the estimation of anchoveta biomass (and related statistics) is concerned, the "third iteration" mentioned by Pauly and Tsukayama (1987). As was also the case with the previous iterations, the biomass estimates presented here do not question the validity of the available independent estimate of anchoveta biomass off Peru obtained through acoustics and other methods. Rather, these were used to calibrate our VPA's, i.e., to estimate values of baseline natural mortality (M_o) which made the VPA results compatible with the independent biomass estimates.

Materials

The data used for this analysis largely overlap with those used in Pauly et al. (1987a). However, more information was available at the time this analysis was performed. Among other things, we used Tables 1 to 5, covering the period 1983 to 1987, in addition to the catch and catch composition data from Tables 1 to 30 of Tsukayama and Palomares (1987), covering the period 1953 to 1982. As in the previous analysis, all monthly nominal catches were multiplied with a factor of 1.2 to account for unrecorded catches (Castillo and Mendo 1987).

Total monthly withdrawals from the anchoveta population were computed as the sum of anchoveta consumption by the predators explicitly accounted for, plus the catch taken by the fishery (Table 6). In addition to the predator groups considered in Pauly et al. (1987a), i.e., cormorants, boobies and pelicans (from Muck and Pauly 1987); bonito (from Pauly et al. 1987b); sea lions and fur seals (from Muck and Fuentes 1987), the anchoveta consumption estimates of mackerel and horse mackerel (from Muck and Sanchez 1987), and hake (from Muck et al., this

Table 1. Monthly catch (in t x 10^3), per cent catch composition and condition factor (c.f.) of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1983.
Tabla 1. Capturas mensuales (en t x 1,000), composición en porcentaje y factor de condición (c.f.) de la anchoveta peruana (E. ringens, *stock norte/central, 4-14°S) basado en datos colectados por personal de IMARPE en 1983.*

Midlength (TL; cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
5.25												
6.25												
7.25												
8.25												
9.25												
10.25		0.06										
11.25		0.42										
12.25	7.24	1.59	4.5									
13.25	14.04	13.01	15.02									
14.25	18.81	21.36	17.32									
15.25	27.33	27.98	27.75									
16.25	18.00	23.04	19.62									
17.25	10.90	9.96	11.58									
18.25	3.71	2.4	4.02									
19.25		0.19	0.19									
20.25												
Catch	87,692	19,991	693	0	0	0	0	0	0	0	0	0
c.f.[a]	1.029	0.690	0.690	(0.598)	(0.633)	(0.642)	(0.666)	(0.673)	(0.665)	(0.652)	(0.714)	(0.635)

[a]Values in parentheses estimated from SST data in Table 6 of Brainard and McLain (1987) and SST *vs.* c.f. relationship in Palomares et al. (1987).

Table 2. Monthly catch (in t x 10^3), per cent catch composition and condition factor (c.f.) of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1984.
Tabla 2. Capturas mensuales (en t x 1,000), composición en porcentaje y factor de condición (c.f.) de la anchoveta peruana (E. ringens, *stock norte/central, 4-14°S) basado en datos colectados por personal de IMARPE en 1984.*

Midlength (TL; cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
5.25												
6.25					0.26							
7.25					7.96							
8.25					22.98					0.03		
9.25					11.67	2.39				0.03		
10.25					9.55	16.10	3.88			0.05		5.13
11.25	5.17				1.62	40.84	3.88		0.06	0.30		59.93
12.25	6.68				0.88	31.31	19.27		1.45	0.80	0.03	31.95
13.25	8.45				7.35	6.56	46.83		6.94	2.61	0.43	1.19
14.25	10.51		83.34		21.59	0.54	26.14		30.66	23.00	5.29	0.76
15.25	12.88		16.67		12.21	1.03			48.54	46.88	45.03	0.54
16.25	15.58				36.68	1.12			11.72	24.83	44.47	0.51
17.25	18.65				0.27	0.13			0.61	1.35	4.52	
18.25	22.08								0.06	0.13	0.33	
19.25												
Catch	0	0	11	0	1,265	907	26	0	6,911	9,069	4,339	836
c.f.[a]	(0.616)	(0.605)	0.758	(0.620)	1.079	0.719	0.618	(0.674)	0.849	0.827	0.841	0.723

[a]Values in parentheses estimated from SST data in Table 6 of Brainard and McLain (1987) and SST *vs.* c.f. relationship in Palomares et al. (1987).

Table 3. Monthly catch (in t x 10^3), per cent catch composition and condition factor (c.f.) of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1985.
Tabla 3. Capturas mensuales (en t x 1,000), composición en porcentaje y factor de condición (c.f.) de la anchoveta peruana (E. ringens, *stock norte/central, 4-14°S) basado en datos colectados por personal de IMARPE en 1985.*

Midlength (TL; cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
8.25	0.06	0.01	0.03									
9.25	0.40	0.06	0.91	0.07	0.07	0.01						
10.25	0.93	0.24	3.39	1.35	1.35	0.79	0.20					
11.25	4.30	4.76	3.91	10.77	10.77	9.91	4.24					
12.25	21.42	22.17	8.14	13.01	13.01	28.92	18.96	0.51	0.06	0.05	0.02	0.08
13.25	38.47	33.00	38.21	20.29	20.29	34.23	29.75	9.98	3.29	3.86	2.80	2.58
14.25	20.29	23.03	39.21	26.62	26.62	20.31	25.39	37.33	24.86	36.21	25.63	29.76
15.25	6.10	9.37	4.43	20.40	20.40	4.47	14.23	38.29	40.16	42.11	44.51	41.71
16.25	6.59	6.16	1.13	4.39	4.39	0.83	5.34	11.63	23.31	14.34	22.74	21.40
17.25	1.44	1.19	0.60	2.81	2.81	0.51	1.77	2.07	6.73	2.94	3.93	4.20
18.25			0.03	0.27	0.27	0.04	0.13	0.19	1.52	0.51	0.37	0.26
19.25								0.01	0.05	0.02		
Catch	14,894	63,875	20,329	0	0	78,959	114,067	90,042	13,666	176,416	154,852	98,657
c.f.	0.716	0.708	0.746	(0.718)[a]	(0.790)[a]	0.662	0.475	0.713	0.713	0.703	0.714	0.669

[a]Interpolated values.

Table 4. Monthly catch (in t x 10^3), per cent catch composition and condition factor (c.f.) of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1986.
*Tabla 4. Capturas mensuales (en t x 1000), composición en porcentaje y factor de condición (c.f.) de la anchoveta peruana (*E. ringens, *stock norte/central, 4-14°S) basado en datos colectados por personal de IMARPE en 1986.*

Midlength (TL; cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
7.25											0.05	
8.25											0.07	0.11
9.25											0.03	1.41
10.25											0.04	3.10
11.25											0.03	3.36
12.25			0.05								0.01	1.01
13.25	0.54	0.56	0.60	0.06	0.03	0.01	0.04			0.01		0.06
14.25	18.05	16.96	10.56	4.23	2.33	2.29	3.17	1.29	0.17	0.08		0.10
15.25	52.05	50.13	46.25	35.16	31.29	29.54	34.25	27.33	8.39	7.67	3.94	3.70
16.25	25.78	28.96	37.78	47.84	51.68	47.58	47.51	52.16	44.63	46.1	40.64	38.67
17.25	3.26	3.32	4.73	12.07	14.09	17.41	14.16	18.07	40.65	40.27	47.55	42.08
18.25	0.31	0.10	0.05	0.63	0.56	3.19	0.88	1.14	6.13	5.81	7.56	6.30
19.25				0.03	0.01		0.01		0.03	0.08	0.09	0.11
Catch	181,025	167,004	138,447	275,645	350,026	221,780	388,388	181,822	95,443[a]	346,733[a]	429,086	285,046
c.f.	0.706	0.317	0.764	0.731	0.745	0.683	0.706	0.686	0.680	0.688	0.705	0.669

[a]Northern subarea only.

Table 5. Monthly catch (in t x 10^3), per cent catch composition and condition factor (c.f.) of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1987.
*Tabla 5. Capturas mensuales (en t x 1,000), composición en porcentaje y factor de condición (c.f.) de la anchoveta peruana (*E. ringens, *stock norte/central, 4-14°S) basado en datos colectados por personal de IMARPE en 1987.*

Midlength (TL; cm)	Jan	Feb	Mar	Apr	May	Jun	Jul
7.25		0.06	0.03				
8.25	0.10	0.34	0.20	0.01			
9.25	1.21	0.37	0.55	0.19	0.03	0.03	0.01
10.25	4.31	0.91	1.27	0.94	0.95	0.35	0.85
11.25	4.05	4.72	1.38	0.82	0.80	1.14	6.78
12.25	2.98	11.64	2.17	0.96	0.59	1.08	3.81
13.25	0.65	6.46	2.76	1.72	0.88	0.73	1.79
14.25	0.25	1.36	1.45	1.05	1.07	0.88	4.79
15.25	3.12	3.28	5.26	4.34	15.69	2.55	4.20
16.25	32.41	30.89	40.06	40.13	56.00	29.88	20.66
17.25	42.92	34.86	39.33	43.39	22.89	52.67	46.63
18.25	7.86	5.03	5.50	6.32	1.10	10.51	10.35
19.25	0.14	0.06	0.06	0.09		0.18	0.13
Catch	297,252	227,712	206,730	179,324	162,123	128,912	68,380
c.f.	0.956	0.618	0.583	0.625	0.689	0.616	0.632

Table 6. Total monthly withdrawals (in tonnes) of anchoveta *(Engraulis ringens)* off Peru (4-14°S), 1953-1982. The fishery catches are nominal catch x 1.2; the anchoveta predators considered are horse mackerels, bonitos, mackerels, hakes, cormorants, boobies, pelicans, fur seals and sea lions.

Tabla 6. Remoción total mensual (en toneladas) de anchoveta (Engraulis ringens) *frente al Perú (4-14°S), 1953-1982. Las capturas de la pesquería son capturas nominales x 1.2; los predadores de anchoveta considerados son jurel, bonito, caballa, merluza, guanay, piquero, pelícano, lobo fino y lobo chusco.*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	825,792	1,072,915	1,186,318	1,067,930	836,488	709,967	650,404	570,244	615,045	654,029	713,487	707,991
1954	736,209	821,801	746,619	694,627	668,921	645,430	601,546	477,193	530,968	539,766	649,731	731,855
1955	988,469	890,593	690,993	776,348	688,842	715,316	649,647	587,985	623,807	556,878	630,384	566,006
1956	711,910	882,715	951,986	839,926	768,389	765,215	718,719	613,748	591,626	601,781	629,876	544,707
1957	704,513	1,145,595	1,121,876	1,087,444	1,128,893	1,025,455	865,765	668,789	624,876	715,647	750,074	926,959
1958	1,118,527	1,161,427	1,135,944	922,152	783,434	703,347	620,305	575,577	595,014	646,443	694,920	579,613
1959	885,506	1,095,688	1,081,000	1,001,509	872,124	768,844	680,423	597,914	632,035	748,284	943,484	931,112
1960	1,057,142	1,073,039	1,030,897	817,823	707,982	845,860	665,600	639,292	664,652	717,887	884,518	1,004,675
1961	1,168,485	1,286,119	1,027,421	1,048,639	1,090,453	931,878	766,058	628,438	715,093	900,597	1,111,755	1,079,428
1962	1,142,568	1,136,605	1,084,660	1,124,940	1,267,573	1,020,028	882,416	784,018	842,735	982,643	1,311,027	1,304,075
1963	1,345,736	917,011	1,371,533	1,335,938	1,320,676	944,821	768,580	725,337	772,972	924,277	1,160,852	1,313,983
1964	1,736,191	1,451,241	1,722,931	1,453,814	1,147,499	873,492	824,960	788,922	671,556	1,121,027	1,360,506	1,403,321
1965	1,634,799	1,406,029	1,889,431	1,738,490	1,526,724	1,239,930	705,963	619,880	619,062	739,460	1,217,483	1,724,949
1966	2,108,870	1,820,584	1,803,065	1,566,259	1,445,641	500,575	467,057	457,040	977,800	1,317,426	465,949	1,393,149
1967	2,132,128	1,319,437	1,578,827	1,774,488	1,593,738	585,881	446,846	411,721	646,675	1,487,237	1,610,151	1,782,979
1968	2,014,350	1,443,427	1,356,605	1,534,794	1,395,790	381,045	400,837	422,222	1,686,059	1,659,054	1,386,920	1,291,634
1969	1,842,948	658,394	2,565,124	2,073,777	1,683,409	706,069	501,760	500,734	973,974	971,377	874,870	2,331,660
1970	2,671,681	1,735,979	1,774,977	2,574,871	1,452,261	589,097	484,631	472,545	1,649,159	1,769,176	1,475,093	1,150,553
1971	592,382	681,036	3,107,920	2,213,205	1,272,190	663,789	569,688	566,269	1,627,966	1,704,829	1,557,603	1,643,667
1972	635,019	835,215	2,569,167	2,138,103	1,024,547	815,770	539,086	437,416	327,779	378,466	419,146	552,076
1973	807,698	1,030,097	1,554,825	717,164	315,292	262,364	239,135	208,637	245,256	247,312	321,169	259,926
1974	303,602	369,590	895,124	1,295,566	895,902	461,777	369,151	335,729	337,252	935,602	905,044	395,543
1975	586,136	802,060	1,587,162	1,409,670	1,033,478	387,792	353,905	311,313	364,466	405,657	380,340	414,789
1976	769,163	960,260	1,279,830	1,297,294	1,024,264	1,173,557	694,150	482,145	340,740	397,048	717,567	724,577
1977	541,429	270,448	301,930	587,632	403,019	263,517	253,406	243,993	247,148	261,224	295,894	298,250
1978	338,841	481,089	411,555	411,391	334,055	293,744	230,341	148,032	144,757	161,731	198,212	345,996
1979	229,936	242,076	497,954	822,228	177,902	147,158	126,104	125,559	105,885	172,324	113,345	37,194
1980	108,740	109,587	129,529	129,600	241,712	144,648	107,183	96,116	105,984	115,985	146,397	182,580
1981	154,775	175,154	134,644	141,936	157,429	124,706	52,880	52,566	42,307	87,563	81,968	141,819
1982	104,597	164,257	251,417	270,384	293,452	261,435	343,821	44,199	57,276	11,224	240,192	331,198

vol.) were also included. These contributions contain anchoveta length-frequency data from stomach contents showing that the predators in question consume anchoveta of roughly the same size composition as is taken by the fishery, thus allowing pooling of catch and consumption data. Tables 1 to 5 (and Tables 1 to 30 of Tsukayama and Palomares 1987) were raised to total withdrawals as follows:

$$RF_{(1)} = \text{withdrawals}/W_{s(i)} \qquad ...1)$$

where RF is the raising factor for each month (i) and $W_{s(1)}$ is the weight of the % catch composition data in month (i). The values of $W_{s(i)}$ were computed as

$$W_{s(i)} = \sum_{j=1}^{n} f_{ij} W_{ij} \qquad ...2)$$

where W_{ij} is the mean weight of fish in class j of sample i, n the total number of length classes in that sample, and f_{ij} the % frequency of class j in sample i. The mean weight of the fish in each length class interval was obtained via length-weight relationships of the form:

$$W = a_i L^b \qquad ...3)$$

from

$$W = 1/(L_{j2}-L_{j1})\ a_i/(b+1)\ [L_{j2}b+1 - L_{j1}b+1] \qquad ...4)$$

where L_{j1} and L_{j2} are the lower and upper limits of class (j), and which provides an unbiased estimate of the mean weight of fish in a given length class (Beyer 1987). The value of b used in equation (4) was set equal to 3 and the appropriate values of a = c.f./100 (see Tables 1-5 for c.f. values for 1983-1987. Equations (1) to (4) were applied 403 times, for every month from January 1953 to July 1987, i.e., to the data in Tables 1 to 30 of Tsukayama and Palomares (1987), to the data in Tables 1 to 5, and to the samples interpolated to fill in gaps.

Missing % length-composition data were linearly interpolated between adjacent months for all years with data gaps except for 1953 and 1983 for which data for the corresponding months of 1955 and 1984, respectively, were inserted. In a few cases, minimum catch estimates, set at 1 tonne, were inserted in the catch-at-length matrix to prevent underflow and/or division by zero errors. We expect these manipulations to have little impact on final results - at least when compared with the large impact of the parameter M_O, of which only approximate values could be obtained (see below).

Methods
(adapted from Pauly et al. 1987a)

Brief Description of Length-Structured VPA

Beverton and Holt (1957) showed that the catch (C_i) from a population during a unit time period (i) is equal to the product of the population size at the beginning of the time period (N_i) times the fraction of the deaths caused by fishing, times the fraction of total deaths, or:

$$C_i = \frac{F_i}{Z_i} (1 - e^{-Z_i}) N_i \qquad ...5)$$

where F_i is the fishing mortality in the ith period, M is the natural mortality, generally assumed constant for all period, and $Z_i = F_i + M$.

The version of Beverton and Holt's catch equation which has become most widely used for stock assessment purposes, however, is:

$$\frac{N_{i+1}}{C_i} = \frac{Z_i \cdot e^{-Z_i}}{F_i\,(1 - e^{-Z_i})} \qquad ...6)$$

also written

$$\frac{C_i}{N_{i+1}} = \frac{F_i}{Z_i}\,(e^{-Z_i} - 1) \qquad ...7)$$

which is the equation in Gulland's (1965) VPA and which can be derived from equation (5) by substituting for N_i the relationship:

$$N_i = N_{i+1} e Z_i \qquad ...8)$$

Given values of C_i and an estimate of M (here: "M_o"), equation (7) can be used to estimate (retroactively) the size of past cohorts (i.e., of groups of fish born at the same time and exposed to the same mortalities throughout their lives), given an estimate of N_{i+1} from which to start the computation. Such estimate of N_{i+1} (expressing the last population size a cohort had before it went extinct) are usually called "terminal populations" (N_t). Values of N_t can be obtained from:

$$N_t = C_t/F_t \qquad ...9)$$

where C_t is the terminal catch (i.e., the last catch taken from a cohort before it went extinct) and F_t is the terminal fishing mortality, i.e., the fishing pressure (here inclusive of predation) that generated C_t (Mesnil 1980; Pauly 1984).

The feature of VPA that is most important in the context of this contribution is that, given high withdrawal estimates of population size obtained by repeated application of equations (6) or (7) tend to rapidly converge toward their true value, and hence, usually provide, given reasonable estimates of M, very reliable estimates of recruitment (Pope 1972; Pauly 1984). Moreover, the speed of convergence from the guessed values of N_t (i.e., values of N_t based on guessed values of F_t) toward accurate values of N_i is a function of the ratio of F to M. That is, the higher the proportion of the cohort is which ends up being withdrawn by the fishery and eaten by horse mackerel, mackerel, hake, bonito, birds and seals, the more reliable the population estimates will be. This is the reason why we have accounted explicitly here for the anchoveta consumed by these predators, and thus left M_o low, rather than replace predation by a higher, constant estimate of M.

Three forms of VPA, all included in the ELEFAN III program, may be distinguished (Pauly and Tsukayama 1983; Gayanilo et al. 1988):

i) VPA I, which is the version originally proposed by Gulland (1965) and which Pope (1972) reformulated as "Cohort Analysis";
ii) VPA II, the VPA equivalent of Jones' (1981) "Length Cohort Analysis" (see also Jones and van Zalinge 1981; Pauly 1984; Pauly and Morgan 1987); and
iii) VPA III, which combines features of (i) and (ii) and which is documented in Pauly and Tsukayama (1983), in Pope et al. (p. 386-390) in Morgan and Pauly (1987) and in Gayanilo et al. (1988).

VPA III is a version of VPA I performed on "cohorts" obtained by superimposing growth curves, drawn at monthly intervals, onto a set of catch-at-length data, the catch pertaining to each "cohort" and month being simply that part of the monthly catches contained between two adjacent growth curves (see Fig. 1).

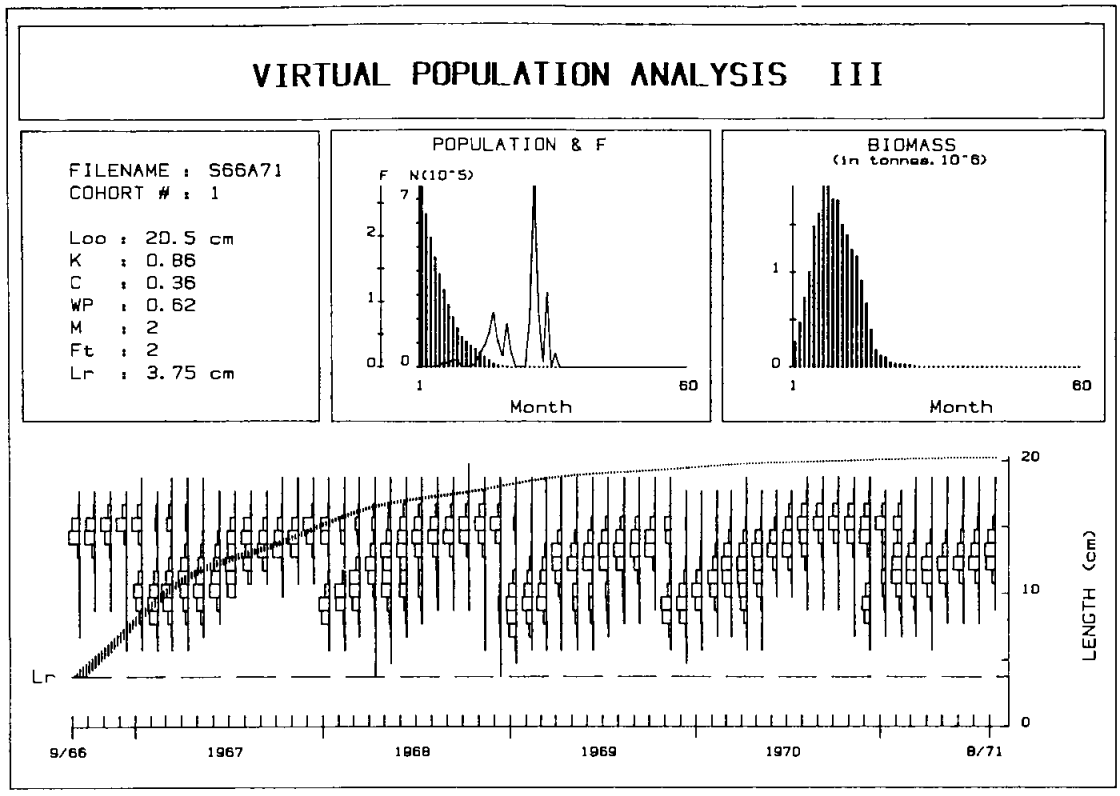

Fig. 1. Facsimile of an ELEFAN III output (via plotter) showing monthly catch-at-length data (not to scale) and one of the many monthly cohorts which can be superimposed on these data. The upper two panels show the population and fishing mortality estimate pertaining to this cohort, along with its biomass (rightmost panel). The population estimate pertaining to month 1 is an expression of recruitment of anchoveta of length L_r = 3.75-4.75 cm (from Pauly et al. 1987a).

Fig. 1. Ejemplo de los resultados obtenidos con el ELEFAN III (via plotter) que muestra datos mensuales de la composición de la captura por longitudes (sin escala) y uno de los tantos cohortes que pueden ser sobrepuestos en esos datos. Los dos paneles de arriba muestran las estimaciones de la población y la mortalidad por pesca de esta cohorte junto a su biomasa (panel de la derecha). La población estimada correspondiente al mes 1 es una expresión del reclutamiento de la anchoveta de longitud L_r = 3.75-4.75 cm (de Pauly et al. 1987a).

For such cohorts to really consist of fish recruited at the same time, the growth curves used for "slicing up" a cohort must be obviously as close to the true growth curve of that cohort as possible. This, among other things, makes it imperative that a seasonally oscillating growth curve be used, since, as shown in Pauly and Ingles (1981), Pauly (1982) and Longhurst and Pauly (1987), virtually all natural fish stocks, including those occurring in tropical waters, display seasonally oscillating growth (see also Palomares et al. 1987).

In reality, not all fish of a given cohort have the same growth parameters, however, and it can be expected that some fish will "leave their cohort" because they grow either faster or slower than predicted by the mean cohort growth curve. Such differences in growth rate should here have the effect of artificially increasing the autocorrelation between estimates of recruitment (see Mendelssohn and Mendo 1987).

The growth curves used here to "slice cohorts" were based on the seasonally oscillating version of the von Bertalanffy Growth Function (VBGF) developed by Pauly and Gaschütz (1979), i.e.,

$$L_t = L_\infty(1-\exp(-[[K(t-t_0)] = [KC/2\pi\sin 2\pi(t-t_s)]]) \qquad ...10)$$

where L_t is the length at age t, L_∞ the asymptotic length, K a growth constant, t_0 the "age" at which length is zero if the fish always grew according to the equation, C is a dimensionless constant expressing the amplitude of the growth oscillations and t_s is the time (with respect to t = 0) at the beginning of a sinusoidal growth oscillation of a one-year period.

For practical purposes, the estimation of t_s was replaced by the estimation of a Winter Point (WP), defined as:

$$t_s + 0.5 = WP \qquad ...11)$$

which expresses (as a fraction of the year) the time during which growth is slowest. It should be mentioned here that the ELEFAN programs, being based on length-frequency data (rather than length-at-age data) do not allow for the estimation, nor require estimates of t_o, hence of *absolute* ages; all "ages" used internally by the programs are *relative* ages, expressed in relation to an arbitrary birthdate that is set internally and not output by the program.

For this reason, our estimates of growth parameters, biomass, recruitment, etc. are not affected by Somers' (1988) observation that equation (10) produces slightly biased estimates of t_0 (when applied to *age*-at-length data).

The VPA III routines of ELEFAN III were applied to the available catch-at-length data, using for 1953 to 1982 the growth parameters in Table 3 of Palomares et al. (1987), new growth parameter estimates based on Tables 1 to 5 and on the ELEFAN I program (Pauly and David 1981; Gayanilo et al. 1988) for the years 1983 to 1987. The year-to-year differences in the values of these growth parameters caused a slight overlap of some "cohorts" (i.e, some of the catch data were used twice), and small gaps (i.e., some of the catch data were not included in any cohort). This source of error could have been avoided by using the same growth parameters throughout. This, however, would have caused a large bias, given the strong positive trend in anchoveta growth performance documented in Palomares et al. (1987).

Estimation of Monthly Recruitment and Biomass

Monthly population estimates per length class were obtained by regrouping monthly values of N_i obtained on a cohort basis into regular class intervals (the same intervals as those in which the catch data were originally grouped). The population estimates (in numbers) of the smallest class considered here (3.75 to 4.75 cm) are here defined as "recruitment" (of fish with mean length 4.25 cm).

The population estimates (in numbers), by length class, were then multiplied, for each month and length class separately by the appropriate mean weight values (see equation 4) to obtain monthly population biomass by length class (Fig. 2).

The analyses for 1953 to 1982 were run with "F_t" = 5 year^{-1}, while those for 1983-1987 were run with "F_t" = 2 year^{-1}, because predation was not included as part of fishing "mortality" for the latter period. It is recalled that these values (a) pertain to $Z-M_o$ (i.e., to the sum of true fishing mortality plus all sources of natural mortality represented by distinct predators and (b) that values of F_t have little impact on final results, especially on recruitment estimates.

Estimation of Natural and Fishing Mortalities

The natural mortality (M_p) exerted by any given predator (p) with anchoveta consumption $C_{p(i)}$ was estimated, for each month (i) from

$$M_{p(i)} = \text{anchoveta consumption } (C_{p(i)})/\text{anchoveta biomass (i)} \qquad ...12)$$

Similarly, fishing mortality (F) was estimated from

$$F_i = \text{anchoveta fishery catch (i)/anchoveta biomass (i)} \qquad ...13)$$

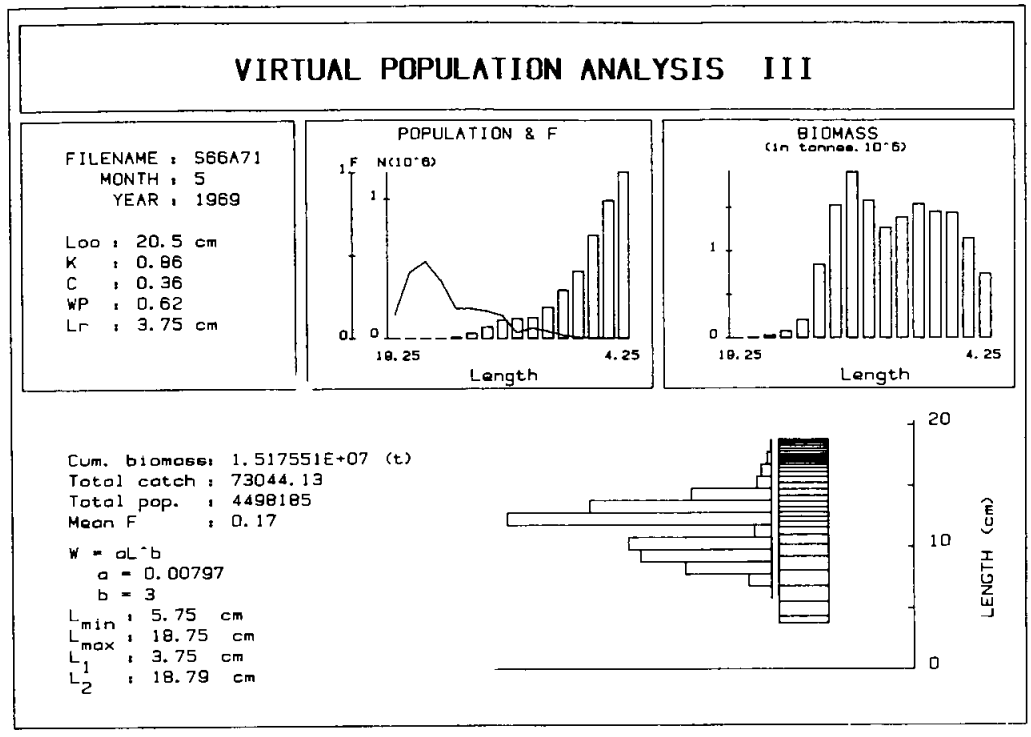

Fig. 2. Facsimile of an ELEFAN III output (via plotter) showing summary of result of a VPA III pertaining to a given month (here May 1969), and showing the catch data (lower panel, right, histograms) the cohorts "passing through" that month (box with narrowing lines), the size structure of the population (upper boxes, center and right), as well as summary statistics (lower panel, left) (from Pauly et al. 1987a).

Fig. 2. Ejemplo de los resultados obtenidos con el ELEFAN III (via plotter) mostrando un resumen de los resultados del VPA III correspondientes a un mes dado (aquí Mayo 1969), y los datos de captura (panel inferior de la derecha, histogramas) del cohorte que está "pasando a través" de ese mes (cuadro con líneas que se juntan), la estructura por tamaños de la población (cuadros de arriba, centro y derecha), así como un resumen estadístico (panel de abajo, izquierda) (de Pauly et al. 1987a).

Thus, all estimates of mortality presented here pertain to weights, not numbers. From these data, total mortality (Z) can be estimated from:

$$Z_i = F_i + M_o + \sum_{m=1}^{5} p_i \qquad ...14)$$

where m is the number of predator groups considered here, i.e., horse mackerel and mackerel, hake, bonito, birds and seals.

Results and Discussion

Estimate of Growth Parameters for the Years 1983 to 1987

The length-frequency data in Tables 1 to 5 had too many gaps to allow estimation of growth parameters for different cohorts or years. Therefore, we applied the ELEFAN I program to all data in Tables 1 to 5. This resulted in the following estimates: asymptotic length $L_\infty = 20.3$ cm (TL); growth constant $K = 0.8$ year^{-1}; amplitude of seasonal growth oscillation $C = 0.27$ and Winter Point (i.e., time of the year with lowest growth rate) $WP = 0.62$.

These values resemble those estimated by Palomares et al (1987). However, the growth performance index $\phi' = \log_{10} K + 2\log_{10}L_\infty$ (Pauly 1979; Pauly and Munro 1984) for this period was 2.518, i.e., lower than estimated for the late 1970s and early 1980s. The new estimate of ϕ' is still higher, however, than the values estimated for the 1950s, thus confirming, overall, the trend expressed by Fig. 3.

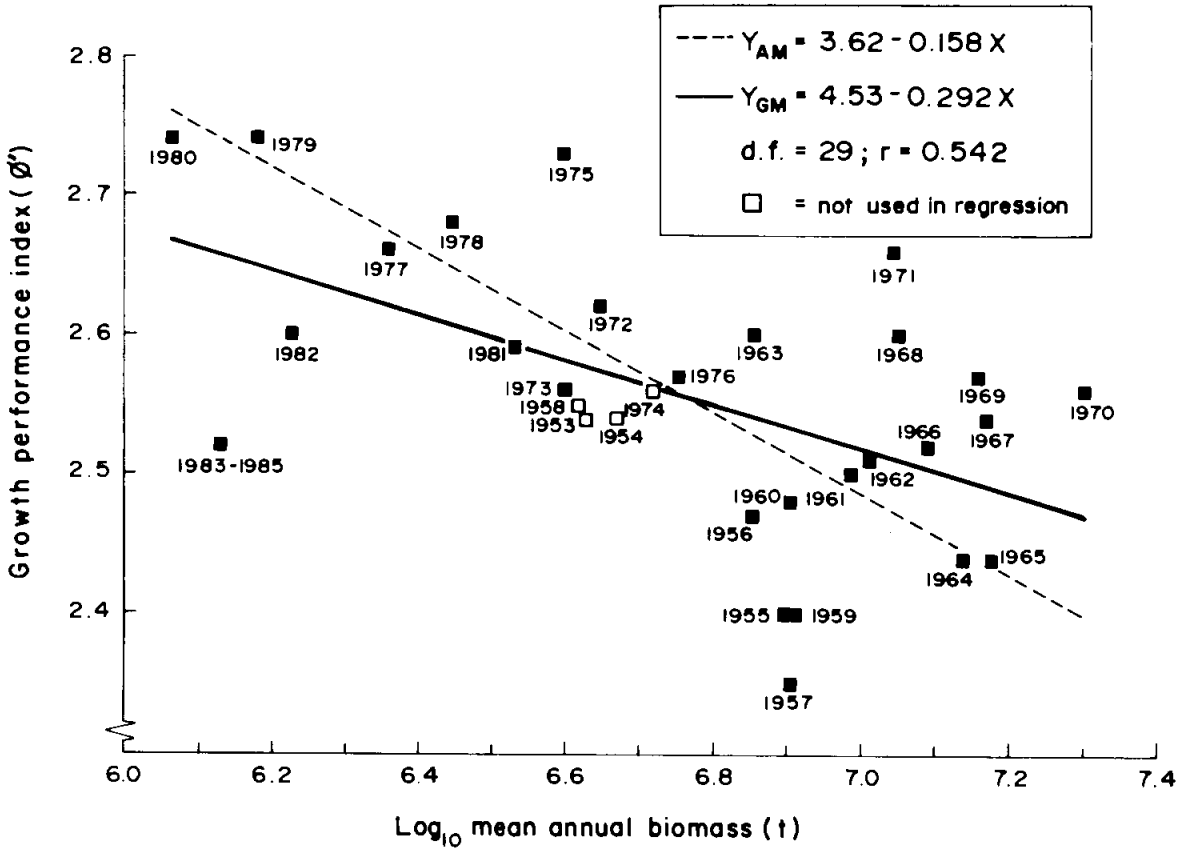

Fig. 3. Relationship between the growth performance index of anchoveta ($\phi' = \log_{10}K + 2\log_{10}L_\infty$; K in year^{-1}; L_∞ in cm T.L.) and mean anchoveta biomass off Peru (4-14°S), 1953 to 1985 (this contribution). The ϕ' values are from Palomares et al. (1987) and the present contribution. Note clear evidence of density-dependent growth of anchoveta.

Fig. 3. Relación entre el indice de eficacia en crecimiento de la anchoveta ($\phi' = \log_{10} K + 2 \log_{10} L_\infty$; K año^{-1}; L_∞ en cm L.T.) y la biomasa promedio de anchoveta (4-14°S) 1953 a 1985 (ésta contribución). Los valores de ϕ'son de Palomares et al. (1987) y de la presente contribución. Nótese la clara evidencia de la densodependencia del crecimiento de la anchoveta.

Estimates of M_o and Their Implication

Table 7 and Fig. 4 document the values of M_o obtained iteratively, i.e., by changing the input value of M_o for a given month until the biomass estimated by VPA matched the independent biomass estimates in Table 7.

As might be seen, the estimated values of M_o are extremely variable. Thus, our extrapolation of $M_o = 0.6$ year^{-1} for the period 1953 to 1963 is tentative. On the other hand, the overall level of M_o is lower, by a factor of about three, than the level of M_o in Pauly et al. (1987a). This is due to the explicit consideration of the predation effect of horse mackerel, mackerel and hake, whose anchoveta consumption is now included in the total withdrawals (Table 6).

Indeed, if one assumes that the independent biomass estimates are accurate, then the drop to zero of the M_o values in the early 1970s suggests that total withdrawals were overestimated for that period.

A similar decline was demonstrated by Pauly et al. (1987a) for the early 1970s, and shown to parallel independent (tagging) estimates of natural mortality. The explicit consideration here

the effect of new predators - especially horse mackerel - has now further reduced our M_o estimates. Our VPA biomass estimates are, for the early 1970s, lower than the independent estimate (see Fig. 4) suggesting that, for that period, M_o should have been negative, or more reasonably, that the withdrawals and the observed biomasses are mutually incompatible. One way to correct for this would be to identify (in a fourth iteration) a mechanism leading to reduced estimates of consumption by the various anchoveta predators during the period in question.

Table 7. Independent estimates of anchoveta biomass off Peru (4-14°S) and estimated values of baseline natural mortality (M_O) using VPA III (see also Fig. 4).
Tabla 7. Estimaciones independientes de biomasa de anchoveta (4-14°S) y valores estimados de la línea base de mortalidad (M_O) usando el VPA III (ver también Fig. 4).

Month/ year	Independent biomass estimate ($t \times 10^6$)[a]	Source of biomass estimates	VPA III estimates of M_O ($year^{-1}$)
Jan '64	14.20		0.84
Jan '65	11.20		0.25
Jan '66	13.30		1.04
Jan '67	13.80		1.08
Jan '68	13.30	Fig. 1 and text	1.41
Jan '69	12.50	IMARPE (1974a)	1.67
Jan '70	18.30		1.59
Jan '71	15.40		2.19
Mar '72	3.00		<0.01
Sep '72	2.00		<0.01
Jan '73	3.16		<0.01
Feb '73	3.30[b]		<0.01
Sep '73	3.09		<0.01
Nov '73	4.48	IMARPE (1974b)	0.11
Feb '74	3.39		<0.01
May '74	2.19		<0.01
Aug '74	3.92		<0.01
Sep '74	3.09		<0.01
Nov '74	3.25	IMARPE (1975)	<0.01
Feb '75	4.32		<0.01
Aug '75	3.39		0.66
Sep '75	4.27		1.35
Jan '76	7.41		0.89
Aug '76	4.62	Johannesson and	1.20
Feb '77	1.89	Vilchez (1981)	0.08
Jul '77	1.39		0.93
Jun '78	3.78		2.59
Nov '78	2.02		1.00
Apr '79	2.15		2.25
Jl/A '84	0.83	Vilchez et al. (1988)	0.99
Apr '85	4.94		1.12
May '86	3.18	IMARPE (1986)	0.14
Nov '86	1.80	Vilchez et al. (1988)	<0.01
Au/S '87	0.70		-
Jun '88	3.77	IMARPE (1988)	-

[a]All values were adjusted through linear inter- and extrapolations to pertain only to the region between 4 and 14°S.

[b]See also Johannesson and Robles (1977).

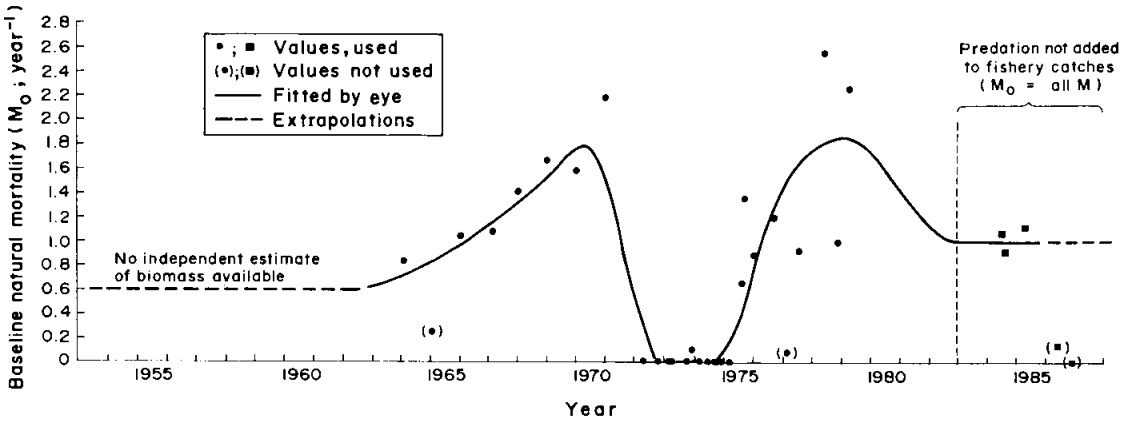

Fig. 4. Estimates of baseline natural mortality (M_0), as required to reproduce independent estimates of anchoveta biomass in Table 7, using the VPA III routine of the ELEFAN III program. Note forward and backward extrapolations, and that high withdrawals, from 1972 to early 1975, precluded reproduction of independent biomass estimates using positive values of M_0 (see text).

Fig. 4. Estimaciones de la línea base de mortalidad natural (M_0) requeridas para reproducir estimaciones independientes de biomasa de anchoveta en la Tabla 7, usando la rutina del VPA del programa ELEFAN III. Nótese las extrapolaciones hacia adelante y hacia atrás y que las altas remociones, de 1972 y comienzos de 1975, imposibilitan la reproducción de estimaciones independientes de biomasa usando valores positivos de M_0 (ver texto).

Estimates of Anchoveta Biomass and Recruitment, 1953 to 1985

Table 8 and Fig. 5 present our biomass estimates. Table 8 presents the data on a monthly basis, while Fig. 5, recalls them as smoothed series, emphasizing the interannual changes.

As might be seen, this time series quite faithfully reflects the known dynamics of the stock, inclusive of rapid decreases associated with El Niño events. This also applies to the early period for which no independent biomass estimates are available (1953 to 1963) and whose overall level of biomass may be higher (or lower, depending on M_0) than indicated. The biomass estimates for the early 1970s are, as discussed above, slightly too high. This improves, however, in the late 1970s and early 1980s, and indeed the near total collapse following the strong 1982-1983 El Niño event is rather well reproduced.

We have abstained from presenting in table form the length composition of the biomass estimates summarized in Table 8 and Fig. 5, but these are available on 5-1/4' MSDOS diskettes, along with our inputs and other data (see Appendix I).

Fig. 6 presents our estimates of anchoveta recruitment[a] for the period 1953 to 1985. As might be seen, these time series resemble those of biomass, which is not surprising for a resource in which 0.5 to 1.5 year old fish constitute the bulk of the biomass.

Two important features of this time series match those reported earlier by Pauly et al. (1987a), i.e.,

i) the increased within-year variability of recruitment from the late 1950s to the late 1960s, probably an effect of the increasing fishing pressure; and
ii) the fact that the recruitment collapse of 1971 appears to have occurred *before* the onset of the 1972-1973 El Niño event, as also observed by Mendelssohn and Mendo (1987).

Item (ii) implies that the El Niño event of 1972-1973 (at least as conventionally defined, i.e., as temperature anomaly) cannot have been the cause for the collapse of the fishery.

Natural and Fishing Mortality of Anchoveta, 1953 to 1985

Fig. 7 presents our estimates of predator-specific M values, our estimates of total M, of F and of Z = M + F. As might be seen, horse mackerel is by far the most important predator of anchoveta, followed (in the 1950s at least) by cormorants, bonito, mackerel and hake.

[a]Editors' note: These estimates are also documented in Table 2 of Appendix I.

Table 8. VPA III estimates of anchoveta biomass off Peru (4-14°S), January 1953 to August 1985 (in tonnes).
Tabla 8. Estimaciones de biomasa de anchoveta frente al Perú (4-14°S) mediante el VPA III, Enero 1953 a Agosto 1985 (en toneladas).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	5,273,333	5,332,432	5,068,356	4,732,896	4,437,194	4,229,566	4,032,404	3,893,989	3,301,880	3,343,782	3,449,599	3,615,853
1954	4,515,320	4,719,681	4,823,731	4,924,143	4,917,512	4,810,300	4,544,498	4,440,413	4,508,864	4,559,097	4,698,249	4,752,512
1955	7,795,231	8,059,812	8,342,795	8,335,965	8,263,994	7,965,718	7,562,810	7,332,870	7,365,702	7,495,989	7,805,237	8,151,112
1956	7,089,264	7,206,608	7,265,571	7,439,651	7,366,700	7,343,874	7,149,830	6,966,351	6,753,963	6,744,946	6,901,314	7,147,365
1957	9,252,552	9,125,360	9,092,212	8,957,621	8,412,497	7,953,915	7,478,838	7,209,598	7,224,006	7,205,715	7,293,950	7,149,962
1958	5,070,142	4,892,199	4,795,686	4,573,515	4,491,117	4,312,200	4,083,549	3,727,062	3,565,956	3,475,082	3,452,610	3,526,188
1959	5,961,980	6,306,387	6,831,662	7,427,582	8,011,048	8,429,620	8,734,230	8,882,412	8,999,017	9,175,769	9,423,735	9,640,071
1960	6,666,056	7,142,783	7,597,619	7,980,020	8,314,255	8,398,191	8,184,005	8,040,322	8,024,638	8,206,459	8,576,082	8,903,001
1961	9,507,219	9,583,872	10,075,863	10,404,831	10,132,890	9,434,414	8,733,692	8,902,026	9,543,712	9,906,323	9,947,812	9,883,355
1962	10,051,414	10,061,623	10,941,309	11,120,378	10,850,292	10,083,781	9,818,269	9,871,519	10,105,850	10,094,572	10,213,415	9,812,666
1963	7,832,765	7,535,953	7,800,681	7,921,076	7,518,253	4,736,437	6,058,325	5,847,840	6,112,957	7,335,947	8,159,838	9,065,109
1964	13,229,833	13,210,993	14,062,682	14,369,568	15,096,616	14,771,587	14,739,721	14,836,930	14,104,511	14,171,854	10,639,644	11,377,494
1965	14,812,507	12,377,234	14,127,285	13,874,998	13,475,350	13,215,424	14,284,232	14,656,564	14,935,035	17,025,442	18,297,366	19,025,254
1966	12,916,518	13,208,795	12,438,383	12,738,976	12,721,971	10,925,868	11,152,847	11,480,069	11,690,221	12,324,594	12,327,534	13,329,965
1967	14,243,137	12,827,012	14,276,425	14,109,462	13,741,492	14,664,788	14,069,646	14,739,803	14,932,144	16,447,987	16,260,340	16,667,207
1968	12,766,037	12,198,458	12,320,137	12,846,767	11,453,907	10,709,782	10,719,875	10,830,087	10,363,791	9,642,320	10,201,184	10,735,116
1969	11,821,083	11,931,786	12,462,217	12,268,131	13,959,746	11,824,101	13,257,479	14,557,659	15,752,115	16,166,783	18,724,670	20,030,972
1970	20,388,480	21,218,716	22,783,714	21,079,576	20,434,284	19,123,574	19,074,822	18,536,920	18,815,296	18,833,030	18,920,386	20,664,156
1971	10,922,469	13,043,405	14,308,998	12,028,685	10,836,496	10,231,702	11,013,697	10,907,770	10,469,347	10,087,245	9,691,741	8,683,223
1972	8,043,960	7,969,600	8,068,886	5,313,904	3,753,378	3,146,167	2,626,106	2,442,102	2,418,136	2,597,167	2,889,928	3,915,887
1973	4,170,048	4,153,528	4,489,177	3,354,402	2,985,354	3,210,263	5,288,675	3,530,712	3,754,857	3,981,788	4,252,518	4,607,763
1974	4,936,110	5,270,781	6,035,931	5,502,677	4,800,321	4,449,409	4,640,200	4,879,067	5,126,927	5,774,150	5,789,662	5,429,115
1975	4,650,409	5,455,392	5,511,036	4,803,395	3,903,044	3,228,646	3,163,909	3,138,126	3,127,783	3,332,876	3,355,898	3,775,461
1976	7,092,915	7,415,232	8,020,737	6,544,905	6,096,795	5,131,526	4,315,163	4,693,030	4,681,332	4,519,576	4,932,656	4,560,410
1977	2,760,918	3,025,668	2,949,233	2,736,841	2,229,920	1,879,846	1,698,077	1,604,278	1,640,095	1,854,590	2,265,478	2,624,053
1978	2,674,240	2,374,089	3,060,656	2,928,502	2,890,239	2,489,025	2,636,846	3,074,006	2,751,110	2,709,076	2,769,031	2,883,141
1979	2,220,062	2,345,230	2,279,710	1,921,915	1,424,376	1,403,859	1,341,497	1,261,441	1,167,837	933,541	834,357	940,000
1980	1,078,731	1,195,093	1,337,266	1,023,803	1,366,529	1,146,462	1,307,882	1,262,657	1,084,800	1,021,143	970,076	1,040,570
1981	3,406,370	3,527,701	3,676,925	3,671,599	3,707,965	3,375,280	3,588,441	3,421,931	3,263,902	3,096,604	2,964,266	3,182,371
1982	2,820,826	2,695,177	2,761,440	2,399,998	2,328,817	1,626,237	1,651,296	1,004,998	929,512	828,566	673,280	412,053
1983	120,765	24,151	6,279	7,145	17,543	21,935	26,560	32,402	39,541	47,995	59,746	77,152
1984	106,408	151,009	269,524	304,091	868,126	721,067	742,965	949,138	1,052,128	1,546,609	1,959,610	2,134,431
1985	2,632,144	3,198,372	3,939,355	4,152,693	4,574,965	4,632,388	3,384,967	5,035,334	-	-	-	-

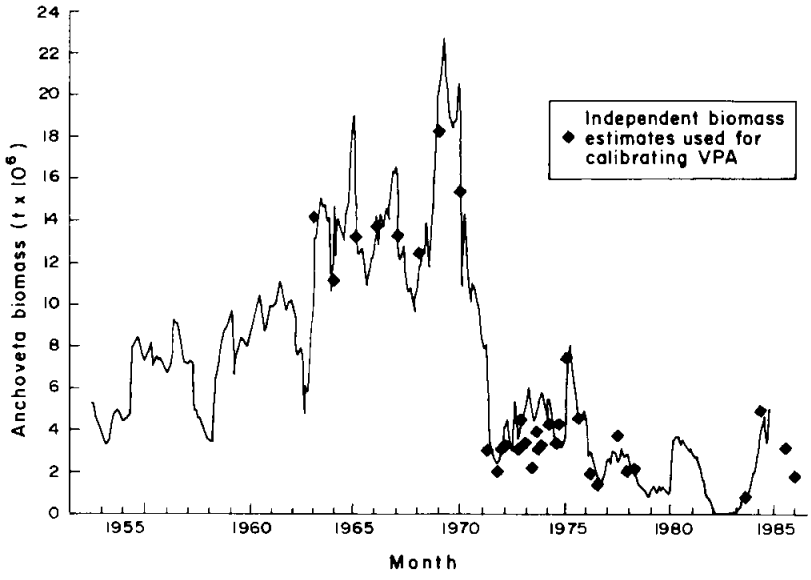

Fig. 5. Biomass estimates of Peruvian anchoveta, 4-14°S, 1953-1985 (obtained through the VPA III routine of the ELEFAN III program, see text) and showing independent biomass estimates used to calibrate VPA.

Fig. 5. Estimaciones de biomasa de la anchoveta peruana 4-14°S, 1953-1985 (obtenida mediante la rutina del VPA III del programa ELEFAN III, ver texto) y estimaciones de biomasa independientes usadas para calibrar el VPA.

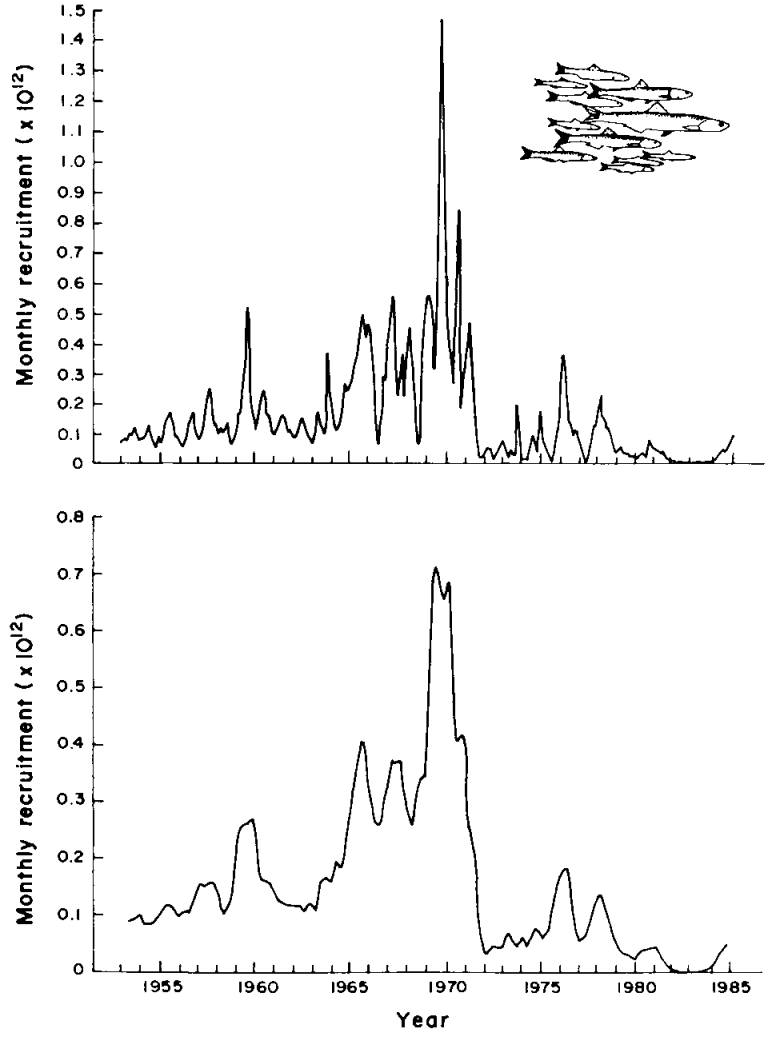

Fig. 6. Time series of recruitment (of fish ranging from 3.75 to 4.75 cm, slightly less than 3 months old) into the anchoveta stock, January 1953 to December 1985. *Above:* monthly recruitment showing increasing variability, from the late 1950s to 1970, probably due to increasing fishing pressure and leading to recruitment collapse in early 1971, prior to the onset of the 1972-1973 El Niño. *Below:* smoothed data (using a 12-month running average), showing that the 1960s, which saw the buildup of the fishery, may have been a period of exceptionally and steadily high recruitment.

Fig. 6. Serie temporal de reclutamiento (de peces en un rango de 3.75-4.75 cm, algo menos de tres meses de edad) al stock de anchoveta, Enero 1953 a Diciembre 1985. Arriba: reclutamiento mensual mostrando un incremento en la variabilidad, de fines de la década del 1950 a 1970, probablemente debido al incremento de la presión pesquera y que condujo al colapso del reclutamiento a comienzos de 1971, antes de la aparición del fenómeno de El Niño 1972-1973. Abajo: datos suavizados (usando promedio corrido de 12 meses), mostrando que la década del 1960, que marcó el surgimiento de la pesquería, puede haber sido un período de reclutamiento excepcionalmente alto y constante.

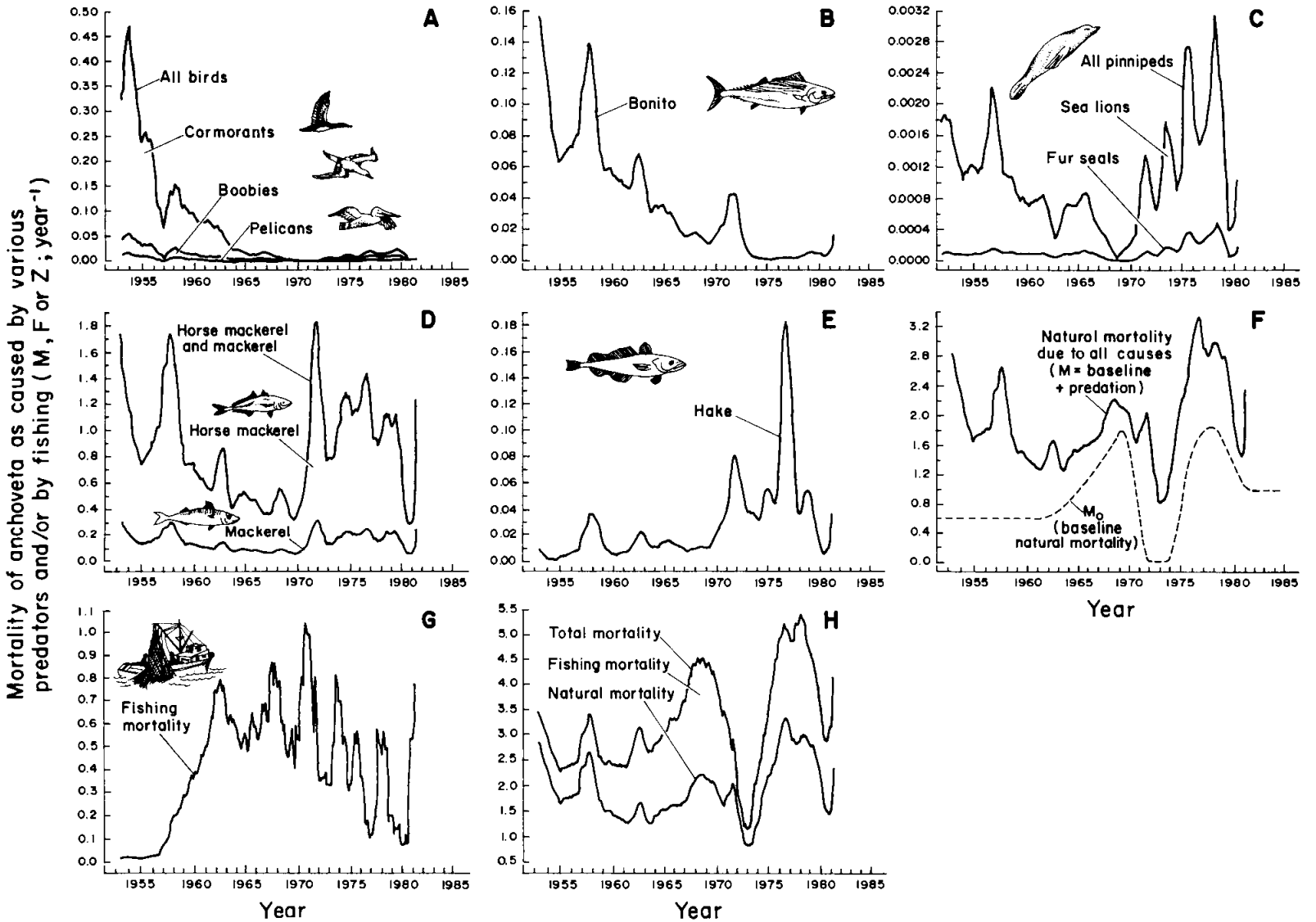

Fig. 7. Estimates of natural mortality due to various predators (A-E), all causes (F), and estimates of fishing (G) and total mortality (H) of Peruvian anchoveta. Data values smoothed over 13 months to emphasize interannual variations. Note different scales, and comparatively large impact of horse mackerel.

Fig. 7. Estimaciones de la mortalidad natural debido a varios predadores (A-E), a todas las causas (F) y estimaciones de mortalidad por pesca (G) y mortalidad total (H) de la anchoveta peruana. Los datos han sido suavizados con promedios corridos de 13 meses para enfatizar las variaciones interanuales. Nótese las escalas diferentes y comparativamente, el gran impacto del jurel.

The least important predators were, on the other hand, hake and pinnipeds (at least as far as the stretch of Peruvian coast comprised between 4 and 14°S is concerned). This is not surprising, as the bulk of Peruvian hake and pinnipeds are generally concentrated north and south of 4 - 14°S, respectively.

Overall, natural mortality (baseline + predator-induced) shows no long-term trend, averaging 1.9 $year^{-1}$ from 1953 to 1985, i.e., about two times the value of the growth parameter K, which was estimated by Palomares et al. (1987) to range from 0.6 to 1.3 $year^{-1}$, with a mean of 0.9. Thus, M/K is in anchoveta of the order of 2 as is often the case in small fishes (Beverton and Holt 1959; Pauly 1980). The overall consistency of M, and its relationship with K, suggest that our values of M_o are probably not too far off the mark.

Obviously, one could also emphasize the *variability* of M, which ranged from 0.8 $year^{-1}$ in the mid 1970s to about 3 $year^{-1}$ in the late 1970s. We cannot at present explain these changes; they may be real, or they may have to do with erroneous withdrawal estimates (especially with regard to the predation estimates by horse mackerel) or with biases in the acoustic estimate, due e.g. to post-collapse changes in the schooling patterns of anchoveta.

Overall, we feel we have achieved the aims of the third iteration, i.e., to derive new estimates of anchoveta biomass and recruitment while simultaneously accounting for all of its important predators. We leave the refinement of our analyses to a "fourth iteration", which would have to address the problems alluded to above, pertaining to the dip of natural mortality in the early 1970s.

References

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II. Vol. 19. 533 p.

Beyer, J. 1987. On length-weight relationships. Part I. Computing the mean weight of the fish in a given length class. Fishbyte 5(1): 12-14.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984, p. 14-45. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Castillo, S. and J. Mendo. 1987. Estimation of unregistered Peruvian anchoveta *(Engraulis ringens)* in official catch statistics, 1951 to 1982, p. 109-116. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Gayanilo, F.C. Jr., M. Soriano and D. Pauly. 1988. A draft guide to the Compleat ELEFAN. ICLARM Software 2, 65, p. International Center for Living Aquatic Resources Management (CLARM), Manila, Philippines.

Gulland, J.A. 1965. Estimation of mortality rates. Annex to Rep. Arctic Fish. Working Group. I.C.E.S. C.M. 1965(3). 9 p.

IMARPE. 1974a. Report of the Fourth Session of the Panel of Experts on Stock Assessment on Peruvian Anchoveta. Bol. Inst. Mar Perú-Callao 2(10): 604-723.

IMARPE. 1974b. Operacion Eureka XXXI, 3-4 de Septiembre de 1974. Informe Inst. Mar Perú-Callao (168). 62 p.

IMARPE. 1975. Operacion Eureka XXXII, 14-15 Febrero 1975. Informe Inst. Mar Perú-Callao (177). 55 p.

IMARPE. 1986. Informe del crucero BIC SNP-1 8604-05 y Diagnóstico de la situación de los Recursos pelágicos a Mayo 1986. Ser. Inf. Esp. Inst. Mar Peru-Callao (193). 23 p. + Anexos.

IMARPE. 1988. Informe del crucero de Evaluación acustica BIC/SNP-1, BIC/Humboldt 8805-07 y Diagnóstico de la situación de los recursos pelágicos a Julio 1988. Ser. Inf. Esp. Inst. Mar Perú-Callao (194). 19 p. + Anexos.

Johannesson, K. and A.N. Robles. 1977. Echo surveys of Peruvian anchoveta. Rapp. P.-V. Réun. CIEM 170: 237-244.

Johannesson, K. and R. Vilchez. 1981. Application and some results of echo-integrating methods in monitoring Peruvian anchovy resources, p. 765-816. *In* J.B. Suomala (ed.) Meeting on Hydroacoustical Methods for the Estimation of Marine Fish Population. Vol. II. Part II: Contributed Papers, Discussions and Comments. Charles Stark Draper Laboratory, Cambridge, Massachusetts.

Jones, R. 1981. The use of length composition data in fish stock assessment (with notes on VPA and Cohort Analysis). FAO Fish. Circ. 734. 55 p.

Jones, R. and N. van Zalinge. 1981. Estimates of mortality rates and population size for shrimp in Kuwait waters. Kuwait Bull. Mar. Sci. 2: 273-288.

Longhurst, A.R. and D. Pauly. 1987. Ecology of tropical oceans. Academic Press, San Diego.

Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Mesnil, B. 1980. Theorie et pratique de l'analyse des cohortes. Rev. Trav. Inst. Pêches Marit. 44(2): 119-155.

Morgan, G.R. and D. Pauly. 1987. Analysis of length-frequency data: some available programs and user's instructions, p. 373-362. *In* D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait.

Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and G. Sanchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Palomares, M.L., P. Muck, J. Mendo, E. Chúman de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1982, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Ber. Inst. Meereskd. Univ. Kiel No. 63. 156 p.

Pauly, D. 1980. A BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforsch. 28(4): 205-211.

Pauly, D. 1982. Studying single-species dynamics in a multispecies context, p. 33-70. *In* D. Pauly and G.I. Murphy (eds.) Theory and management of tropical fishes. ICLARM Conference Proceedings 9, 360 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Commonwealth Scientific and Industrial Research Organization, Division of Fisheries Research, Cronulla, Australia.

Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews 8, 325 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D. and N. David. 1981. ELEFAN I, a BASIC Program for the objective extraction of growth parameters from length-frequency data. Meeresforsch. 28: 205-211.

Pauly, D. and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculator. I.C.E.S. C.M. 1979/G:24 Demersal Fish Cttee. 26 p.

Pauly, D. and J. Ingles. 1981. Aspects of the growth and mortality of exploited coral reef fishes, p. 89-98. *In* E. Gomez, C.E. Birkeland, R.W. Buddemeyer, R.E. Johannes, J.A. Marsh, Jr. and R.T. Tsuda (eds.) Proceedings of the Fourth International Coral Reef Symposium, Manila, Philippines. Vol. 1. 725 p.

Pauly D. and G.R. Morgan. 1987. Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait.

Pauly, D. and J.L. Munro. 1984. Once more on growth comparison in fish and invertebrates. Fishbyte 2(1): 21.

Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987a. VPA estimates of monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama. 1983. On the seasonal growth, monthly recruitment and monthly biomass of the Peruvian anchoveta from 1961 to 1979, p. 987-1004. *In* G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, 18-29 April 1983. FAO Fish Rep. No. 291. Vol. 3.

Pauly, D., A.Ch. Vildoso, J. Mejiá, M. Samamé and M.L. Palomares. 1987b. Population dynamics and estimated anchoveta consumption of bonito *(Sarda chiliensis)* off Peru, 1953 to 1982, p. 248-267. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. ICNAR Res. Bull. 9: 65-74.

Somers, I.F. 1988. On a seasonally oscillating growth function. Fishbyte 6(1): 8-11.

Tsukayama, I. and M.L. Palomares. 1987. Monthly catch and catch composition of Peruvian anchoveta *(Engraulis ringens)* (northern-central stock, 4-14°S), 1953 to 1982, p. 89-108. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Vilchez, R., P. Muck and A. Gonzales. 1988. Variaciones en la biomasa y en la distribución de los principales recursos pelágicos del Perú entre 1983 y 1987, p. 255-264. *In* H. Salzwedel and A. Landa (eds.) Recursos y Dinámica del Ecosistema de Afloramiento Peruano. Bol. Inst. Mar Perú-Callao, Vol. extraordinario.

Changes in the Catchability Coefficient in the Peruvian Anchoveta *(Engraulis ringens)* Fishery

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CSIRKE, J. 1989. Changes in the catchability coefficient in the Peruvian anchoveta *(Engraulis ringens)* fishery, p. 207-219. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Monthly changes in the catchability coefficient in the Peruvian anchoveta *(Engraulis ringens)* fishery are analyzed for the years 1960 through 1982. A clear seasonality in the fluctuation of monthly catchability is found from 1960 through 1971, with higher mean values during the austral summer and lower values in winter. After 1972, catchability increased dramatically and the seasonal pattern changed, becoming higher during mid-spring and fall. It is shown that there is a strong density dependence in these fluctuations. The estimated catchability coefficient (q) was found to be inversely related to population size (B), fitting the power function $q = a \cdot B^b$, with a slope $b = -0.97$. The implications of this depensatory mechanism are discussed and reference is made to some indications of a possible change of state in the Peruvian anchoveta ecosystem, which may have switched the population to a path with a much lower maximum equilibrium level after the fishery collapsed in 1972.

Resumen

Se analizan los cambios mensuales del coeficiente de capturabilidad en la pesquería de la anchoveta peruana *(Engraulis ringens)* en los años 1960 a 1982. Se encuentra una clara estacionalidad en las fluctuaciones de la capturabilidad por meses entre 1960 y 1971, con valores promedios mayores durante el verano austral y valores menores en invierno. Después de 1972 la capturabilidad aumentó dramáticamente y cambió el patrón estacional, haciéndose mayor a mediados de primavera y en otoño. Se muestra que hay una fuerte dependencia de la densidad en estás fluctuaciones. Se encontró que los estimados del coeficiente de capturabilidad (q) están inversamente relacionados con el tamaño de la población (B), ajustándose a la función $q = a \cdot B^b$ con una pendiente $b = -0.97$. Se discuten las implicancias de este mecanismo depensatorio y se hace referencia a algunos indicios de un posible cambio de estado en el ecosistema de la anchoveta peruana, la cual, después del colapso de la pesquería en 1972, habría pasado a un nuevo curso poblacional con un nivel de equilibrio máximo mucho menor.

Introduction

When dealing with the variability and collapse of fish stocks and fisheries, the specialized literature frequently points out the high incidence of collapse amongst small shoaling pelagic fisheries and the features common to these stocks that may explain their high vulnerability to unrestrained fishing (see, for example, Saville 1980; Sharp and Csirke 1983; Beverton et al. 1984; Csirke 1988). One of these features identified to contribute to the higher risk of collapse of these fish stocks and their related fisheries is the density dependence of the catchability coefficient.

Higher catchability with decreasing stock sizes have been reported in several pelagic stocks that have collapsed, such as, for instance, the California sardine (Fox 1974; MacCall 1976), the

Atlantic menhaden (Schaaf 1975, 1980), the Norwegian spring-spawning herring (Ulltang 1976, 1980) and the South African sardine (Shelton and Armstrong 1983). The existence of a similar type of relationship was also suspected on the Peruvian anchoveta that collapsed in the early 1970s, but no clear evidence to this respect was reported until now.

Besides affecting recruitment, the 1972-73 "El Niño" event confined the already reduced anchoveta stock to a much smaller area, which caused an increase in the catchability coefficient that allowed the fleet to obtain higher catch rates even while fishing on a decimated stock (Csirke 1980). Although it occurred at a low abundance level, this did not provide enough evidence of a causal depensatory relationship between catchability coefficient and stock size because at that time the change in catchability was mostly associated with a major environmental factor.

The increased catchability was particularly notorious late in 1971 and early 1972, during the onset of the "El Niño" event. The sequence of events that followed are well known, the fishery collapsed, and fisheries scientists and administrators now tend to agree that the collapse was caused by a combination of both fishery-related and natural factors (i.e., "El Niño"-related adverse environmental conditions, see e.g., Muck, this vol.). Some discussion still goes on, however, on which of these factors are to be blamed the most, to what extent the collapse was avoidable, and if so, what needed to be done and when. Hopefully, knowing more about the behavior of the catchability coefficient may contribute to elucidate some of these questions.

The IMARPE-based international multidisciplinary project that led to the publication of the book edited by Pauly and Tsukayama (1987), provided both the stimulus and the additional sets of data and information needed to analyze the seasonal and year-to-year fluctuations of the catchability coefficient, and to explore further the hypothesis that in the Peruvian anchoveta fishery the catchability coefficient increased as stock size decreased.

Material and Methods

The anchoveta stock referred to here is the one that occurs off northern-central Peru, from the northern end of the species distribution range, at 4°30'S (Jordán 1971), to approximately 14°S. Before collapsing in the early 1970s, the stock in this area accounted for around 80% of the world catches of this species. Tagging, morphometric and other biological studies tend to support the idea that the anchoveta in this area belongs to a same unit stock, and indicated that it has similar and relatively uniform characteristics and mixes little with the anchoveta found further south, off southern Peru and northern Chile.

The analyses in this paper are based on monthly data and estimates from 1960 to 1982, thus covering the most important years in the history of this fishery. Prior to 1960 the fishery was still in an early development phase, total catches represented a fairly small fraction of the total stock and fishing effort data are not readily available for those years. No comparable set of data is at the moment available for the more recent years. Another, much stronger "El Niño" event occurred in 1983-1984, which had a severe impact on the anchoveta stock and called for more drastic regulations and changes in the fishing fleet, gears and fishing operations, all aimed at reducing pressure on the depleted anchoveta stock and improving exploitation of sardines and other small pelagics which had increased in the mean time. This apparently made the collection of reliable anchoveta fishing effort statistics far more difficult besides making it less comparable with previous years.

Total catches by month for 1960-1982 (Table 1) were reported by Tsukayama and Palomares (1987). For the same stock Pauly et al. (1987) estimated the total biomass by size group at the beginning of each month, using a newly developed version of length-structured virtual population analysis (VPA). The mean biomass of the exploited stock for each month (Table 2) was calculated taking the bimonthly average of the VPA biomass estimates of fish larger than or equal to 7.75 cm (mid-length at 8.25 cm in Pauly et al. (1987)).

This stock is only exploited by Peruvian purse seiners, called "bolicheras", and the estimated monthly total fishing effort directed to the anchoveta stock by this fleet is presented in Table 3. The fishing effort estimates are those produced for, and used by, the Panels of Experts on Peruvian Anchoveta until 1973 (IMARPE 1970, 1972, 1973, 1974), which have been updated

Table 1. Nominal catch ($t \cdot 10^3$) of Peruvian anchoveta *(Engraulis ringens)* between 4° and 14° South, by month and by year from 1960 to 1982 (from Tsukayama and Palomares 1987).
Tabla 1. Captura nominal ($t \cdot 10^3$) de anchoveta peruana (Engraulis ringens) *entre los 4° y 14° Sur, por mes y por año entre 1960 y 1982 (de Tsukayama y Palomares 1987).*

Year	J	F	M	A	M	J	J	A	S	O	N	D
1960	303	292	279	182	137	258	138	117	158	223	348	397
1961	447	379	283	364	439	343	233	183	208	375	571	591
1962	432	404	450	549	647	432	351	275	324	498	800	832
1963	780	229	629	701	652	346	191	178	232	388	624	733
1964	1,026	691	996	865	657	437	417	226	237	662	895	968
1965	1,037	634	1,019	760	650	486	11	0	65	199	629	1,146
1966	1,310	972	1,092	960	899	0	0	0	561	865	7	958
1967	1,506	570	876	1,210	1,082	126	0	0	232	1,109	1,238	1,365
1968	1,469	900	744	1,079	952	0	0	0	1,246	1,242	939	880
1969	1,226	0	1,762	1,252	790	0	0	0	482	470	373	1,802
1970	1,998	986	995	1,900	830	41	10	0	1,178	1,267	995	731
1971	0	0	2,366	1,453	636	92	0	0	1,118	1,229	1,066	1,224
1972	8	1	1,653	1,359	342	145	0	0	0	0	0	14
1973	0	0	1,193	357	0	0	0	3	20	13	36	0
1974	0	0	497	869	481	0	0	0	34	623	534	0
1975	174	305	823	799	536	12	0	0	0	8	0	9
1976	263	51	348	573	318	515	144	0	0	78	390	353
1977	184	0	1	265	130	0	0	0	0	0	0	0
1978	0	50	0	81	84	91	46	0	1	0	20	207
1979	0	0	258	603	0	0	0	0	0	66	27	0
1980	0	0	0	0	123	27	0	0	0	0	0	45
1981	0	0	0	28	53	51	0	0	0	25	9	118
1982	0	49	146	185	208	196	279	0	3	16	54	72

Table 2. Estimated mean biomass ($t \cdot 10^3$) of Peruvian anchoveta *(Engraulis ringens)* larger than or equal to 7.75 cm between 4° and 14° South, by month and by year from 1960 to 1982 (from Pauly et al. 1987).
Tabla 2. Biomasa promedia estimada ($t \cdot 10^3$) de anchoveta peruana (Engraulis ringens) *mayor de o igual a 7.75 cm entre los 4° y 14° Sur, por mes y por año entre 1960 y 1982 (de Pauly et al. 1987).*

Year	J	F	M	A	M	J	J	A	S	O	N	D
1960	6,129	7,095	8,213	9,237	10,017	10,433	10,479	10,331	10,195	10,254	10,451	10,546
1961	10,891	12,185	13,921	15,066	15,291	14,848	14,617	14,966	15,088	14,562	13,830	13,408
1962	13,453	14,309	15,171	15,035	14,134	13,133	12,577	12,253	11,818	11,277	10,623	9,495
1963	8,733	9,106	10,032	10,577	8,885	8,658	10,045	10,068	10,996	12,138	13,026	13,173
1964	13,182	14,364	12,625	13,104	15,564	14,546	13,623	12,514	11,464	10,819	9,970	8,790
1965	7,649	7,424	7,741	7,768	7,847	8,377	9,164	9,735	10,997	12,880	14,881	14,747
1966	14,046	14,488	14,699	14,892	13,531	12,217	12,037	11,662	11,424	11,252	11,484	12,610
1967	13,208	14,685	16,709	17,153	17,747	17,702	17,090	16,704	16,692	16,595	16,153	15,484
1968	14,464	14,201	14,520	13,797	12,119	11,232	10,831	10,130	8,905	8,018	7,833	7,631
1969	7,542	8,169	8,407	8,621	8,606	8,834	10,295	11,535	12,224	13,453	15,172	15,008
1970	14,137	14,568	14,364	12,717	11,144	10,579	10,712	11,054	11,034	10,686	11,389	12,033
1971	13,474	16,275	16,516	15,167	14,341	14,259	14,244	13,062	11,571	10,156	8,454	6,377
1972	5,205	5,143	3,946	2,038	1,280	1,253	1,421	1,505	1,598	1,910	2,547	2,822
1973	2,896	3,672	3,595	2,620	2,333	2,600	2,807	2,751	2,674	2,821	3,043	3,289
1974	3,555	4,037	4,077	3,266	2,558	2,516	2,757	3,272	3,839	3,703	3,074	2,912
1975	3,101	2,934	2,620	2,214	1,607	1,279	1,293	1,966	2,673	2,693	2,820	3,065
1976	3,355	4,040	4,269	5,020	5,472	4,375	3,856	3,699	3,179	2,722	2,255	1,471
1977	975	882	839	635	365	313	378	438	507	647	909	1,283
1978	1,626	2,375	3,179	3,543	3,561	3,540	3,892	3,741	3,193	2,925	2,776	2,546
1979	2,356	2,186	1,763	1,170	867	873	836	788	686	578	597	667
1980	740	847	818	937	1,091	1,176	1,377	1,488	1,652	1,972	2,682	3,250
1981	4,072	5,844	7,694	9,180	9,581	9,562	9,336	8,421	7,496	6,689	6,407	5,711
1982	4,747	4,482	4,050	3,477	2,659	1,918	1,347	803	621	461	314	241

Table 3. Total fishing effort (GRT · trip^{-1} · 10^{3}) directed toward Peruvian anchoveta *(Engraulis ringens)* between 4° and 14° South, by month and by year from 1960 to 1982 (from IMARPE, unpublished data)[a].
Tabla 3. Esfuerzo total de pesca (TRB · viaje^{-1} · 10^{3}) dirijido a la anchoveta peruana (Engraulis ringens) entre los 4° y 14° Sur, por mes y por año entre 1960 y 1982 (de IMARPE, datos no publicados)[a].

Year	J	F	M	A	M	J	J	A	S	O	N	D
1960	(662.6)	(635.8)	(604.8)	(393.2)	(295.2)	(555.3)	(297.0)	(251.9)	514.7	577.7	535.4	565.5
1961	591.2	585.1	584.9	647.3	673.9	628.4	541.7	589.0	554.9	671.7	715.6	711.0
1962	696.5	672.4	770.6	775.0	864.8	664.7	725.0	741.4	689.8	1,025.6	1,065.6	1,046.0
1963	1,222.6	374.8	1,091.5	1,253.7	1,244.4	1,082.9	1,090.7	1,337.1	1,114.6	1,217.6	1,689.6	1,777.7
1964	1,721.4	1,462.1	1,634.8	1,535.6	1,507.3	1,530.1	1,239.6	1,000.1	1,031.0	1,566.5	1,472.4	1,727.9
1965	1,701.0	1,170.9	2,059.0	1,751.4	1,756.9	1,493.3	473.7	0.0	951.5	1,333.0	1,911.5	2,126.6
1966	2,131.5	2,180.7	2,059.2	2,400.0	1,757.6	0.0	0.0	0.0	1,426.8	2,064.5	15.2	1,388.0
1967	2,553.2	1,126.2	1,129.4	1,891.7	2,056.3	718.2	0.0	0.0	428.6	2,092.3	2,236.7	1,917.1
1968	1,935.9	1,211.6	954.2	2,029.2	2,054.7	0.0	0.0	0.0	2,293.7	2,192.5	1,728.3	1,647.0
1969	2,328.4	0.0	2,175.4	2,307.4	2,259.3	0.0	0.0	0.0	2,121.6	2,073.4	1,099.9	2,927.8
1970	2,495.2	1,249.2	1,326.2	2,758.7	1,109.2	73.1	40.2	0.0	2,530.3	2,802.7	2,364.1	2,073.9
1971	0.0	0.0	2,820.9	1,499.7	651.7	98.4	0.0	0.0	1,821.3	1,729.2	1,147.0	1,346.2
1972	9.2	1.3	1,978.4	2,714.4	1,903.1	1,059.8	0.0	0.0	0.0	0.0	0.0	32.7
1973	0.0	0.0	1,718.8	1,221.2	0.0	0.0	0.0	(6.7)	(44.8)	(29.1)	(80.4)	0.0
1974	0.0	0.0	858.0	1,125.6	640.7	0.0	0.0	0.0	76.8	1,393.8	1,767.8	0.0
1975	394.4	710.6	1,349.8	1,389.3	1,023.7	41.0	0.0	0.0	0.0	118.6	0.0	43.3
1976	736.4	187.0	662.7	1,266.9	824.6	1,373.3	524.4	0.0	0.0	240.2	935.6	1,085.3
1977	(425.2)	0.0	(2.3)	(620.3)	(309.4)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1978	0.0	88.9	0.0	114.0	72.2	136.8	78.3	0.0	(2.2)	0.0	(44.8)	(464.8)
1979	0.0	0.0	394.4	719.0	0.0	0.0	0.0	0.0	0.0	121.6	40.3	0.0
1980	0.0	0.0	0.0	0.0	196.1	35.0	0.0	0.0	0.0	0.0	0.0	73.0
1981	0.0	0.0	0.0	38.8	66.9	61.6	0.0	0.0	0.0	56.2	13.7	177.8
1982	0.0	92.7	123.1	247.0	328.3	275.9	394.4	0.0	11.4	(37.8)	(129.1)	(173.5)

[a]Values in parentheses are theoretical estimates made on the basis of values of q estimated from equation (3), see text, and fishing mortality for that month (from Table 4).

Table 4. Fishing mortality (F; month^{-1}) of the Peruvian anchoveta *(Engraulis ringens)* between 4° and 14° South, by month and by year from 1960 to 1982[a].
Tabla 4. Mortalidad por pesca (F; mes^{-1}) de la anchoveta peruana (Engraulis ringens) *entre los 4° y 14° Sur, por mes y por año entre 1960 y 1982.*

Year	J	F	M	A	M	J	J	A	S	O	N	D
1960	0.0494	0.0412	0.0340	0.0197	0.0137	0.0247	0.0132	0.0113	0.0155	0.0217	0.0333	0.0376
1961	0.0410	0.0311	0.0203	0.0242	0.0287	0.0231	0.0159	0.0122	0.0138	0.0258	0.0413	0.0441
1962	0.0321	0.0282	0.0297	0.0365	0.0458	0.0329	0.0279	0.0224	0.0274	0.0442	0.0753	0.0876
1963	0.0893	0.0251	0.0627	0.0663	0.0734	0.0400	0.0190	0.0177	0.0211	0.0320	0.0479	0.0556
1964	0.0778	0.0481	0.0789	0.0660	0.0422	0.0300	0.0306	0.0181	0.0207	0.0612	0.0898	0.1101
1965	0.1356	0.0854	0.1316	0.0978	0.0828	0.0580	0.0012	0.0000	0.0059	0.0155	0.0423	0.0777
1966	0.0933	0.0671	0.0743	0.0645	0.0664	0.0000	0.0000	0.0000	0.0491	0.0769	0.0006	0.0760
1967	0.1140	0.0388	0.0524	0.0705	0.0610	0.0071	0.0000	0.0000	0.0139	0.0668	0.0766	0.0882
1968	0.1016	0.0634	0.0512	0.0782	0.0786	0.0000	0.0000	0.0000	0.1399	0.1549	0.1199	0.1153
1969	0.1625	0.0000	0.2096	0.1452	0.0918	0.0000	0.0000	0.0000	0.0394	0.0349	0.0246	0.1201
1970	0.1413	0.0677	0.0693	0.1494	0.0745	0.0039	0.0009	0.0000	0.1068	0.1186	0.0874	0.0607
1971	0.0000	0.0000	0.1433	0.0958	0.0443	0.0065	0.0000	0.0000	0.0966	0.1210	0.1261	0.1919
1972	0.0015	0.0002	0.4189	0.6669	0.2672	0.1157	0.0000	0.0000	0.0000	0.0000	0.0000	0.0050
1973	0.0000	0.0000	0.3319	0.1362	0.0000	0.0000	0.0000	0.0011	0.0075	0.0046	0.0118	0.0000
1974	0.0000	0.0000	0.1219	0.2660	0.1880	0.0000	0.0000	0.0000	0.0089	0.1682	0.1737	0.0000
1975	0.0561	0.1040	0.3142	0.3609	0.3336	0.0094	0.0000	0.0000	0.0000	0.0030	0.0000	0.0029
1976	0.0784	0.0126	0.0815	0.1141	0.0581	0.1177	0.0373	0.0000	0.0000	0.0287	0.1729	0.2400
1977	0.1888	0.0000	0.0012	0.4174	0.3558	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
1978	0.0000	0.0211	0.0000	0.0229	0.0236	0.0257	0.0118	0.0000	0.0003	0.0000	0.0072	0.0813
1979	0.0000	0.0000	0.1463	0.5154	0.0000	0.0000	0.0000	0.0000	0.0000	0.1142	0.0453	0.0000
1980	0.0000	0.0000	0.0000	0.0000	0.1128	0.0230	0.0000	0.0000	0.0000	0.0000	0.0000	0.0138
1981	0.0000	0.0000	0.0000	0.0031	0.0055	0.0053	0.0000	0.0000	0.0000	0.0037	0.0014	0.0207
1982	0.0000	0.0109	0.0360	0.0532	0.0782	0.1022	0.2027	0.0000	0.0048	0.0347	0.1722	0.2992

[a] estimated by division of the nominal monthly catch figures in Tsukayama and Palomares (1987) by the corresponding biomass estimates in Table 2.

Table 5. Catchability coefficient (q; month $(GRT)^{-1}$ $trip^{-1}$ x 10^{-7}) in the Peruvian anchoveta *(Engraulis ringens)* fishery between 4° and 14° South, by month and by year from 1960 to 1982.[a]
Tabla 5. Coeficiente de capturabilidad (q; mes $(GRT)^{-1}$ $viaje^{-1}$ x 10^{-7}) en la pesquería de anchoveta peruana (Engraulis ringens) *entre los 4° y 14° Sur, por mes y por año entre 1960 y 1982.*

Year	J	F	M	A	M	J	J	A	S	O	N	D
1960	(0.7461)	(0.6473)	(0.5616)	(0.5012)	(0.4633)	(0.4453)	(0.4434)	(0.4496)	0.3011	0.3765	0.6220	0.6657
1961	0.6942	0.5316	0.3476	0.3732	0.4260	0.3676	0.2943	0.2076	0.2484	0.3834	0.5769	0.6199
1962	0.4610	0.4199	0.3849	0.4712	0.5293	0.4949	0.3850	0.3027	0.3974	0.4306	0.7068	0.8377
1963	0.7305	0.6709	0.5745	0.5287	0.5897	0.3690	0.1743	0.1322	0.1893	0.2625	0.2835	0.3130
1964	0.4522	0.3290	0.4826	0.4299	0.2801	0.1963	0.2469	0.1806	0.2005	0.3906	0.6097	0.6373
1965	0.7971	0.7294	0.6393	0.5586	0.4715	0.3885	0.0253	(0.4763)	0.0621	0.1159	0.2211	0.3654
1966	0.4376	0.3076	0.3608	0.2686	0.3780	(0.3821)	(0.3877)	(0.3997)	0.3442	0.3724	0.4003	0.5473
1967	0.4466	0.3446	0.4642	0.3729	0.2965	0.0991	(0.2759)	(0.2821)	0.3243	0.3194	0.3427	0.4598
1968	0.5246	0.5231	0.5370	0.3854	0.3823	(0.4146)	(0.4295)	(0.4582)	0.6101	0.7065	0.6936	0.7002
1969	0.6981	(0.5646)	0.9635	0.6294	0.4063	(0.5233)	(0.4511)	(0.4040)	0.1859	0.1685	0.2235	0.4101
1970	0.5664	0.5418	0.5223	0.5416	0.6715	0.5300	0.2321	(0.4210)	0.4219	0.4230	0.3695	0.2929
1971	(0.3475)	(0.2893)	0.5078	0.6388	0.6805	0.6557	(0.3292)	(0.3581)	0.5305	0.6998	1.0993	1.4258
1972	1.6654	1.4708	2.1173	2.4568	1.4041	1.0917	(3.0805)	(2.9134)	(2.7477)	(2.3122)	(1.7308)	1.5183
1973	(1.5441)	(1.2264)	1.9309	1.1156	(1.9043)	(1.7143)	(1.5915)	(1.6228)	(1.6682)	(1.5837)	(1.4713)	(1.3645
1974	(1.2653)	(1.1187)	1.4208	2.3636	2.9346	(1.7694)	(1.6192	(1.3716)	1.1537	1.2069	0.9826	(1.5358)
1975	1.4227	1.4630	2.3276	2.5979	3.2590	2.2866	(3.3756)	(2.2482)	(1.6688)	0.2505	(1.5840)	0.6778
1976	1.0643	0.6752	1.2300	0.9009	0.7047	0.8571	0.7122	(1.2176)	(1.4105)	1.1931	1.8485	2.2112
1977	(4.4398)	(4.8923)	(5.1324)	(6.7283)	(11.5005)	(13.3551)	(11.1278)	(9.6545)	(8.3679)	(6.6073)	(4.7498)	(3.4009)
1978	(2.7018)	2.3674	(1.4104)	2.0056	3.2671	1.8793	1.5099	(1.2045)	(1.4043)	(1.5290)	(1.6086)	(1.7495)
1979	(1.8859)	(2.0283)	3.7091	7.1686	(4.9738)	(4.9376)	(5.1530)	(5.4595)	(6.2388)	9.3906	11.2360	(6.4131)
1980	(5.8025)	(5.0900)	(5.2594)	(4.6125)	5.7512	6.5653	(3.1751)	(2.9446)	(2.6617)	(2.2414)	(1.6635)	1.8979
1981	(1.1093)	1.1791	(0.5984)	0.7869	0.8272	0.8664	(0.4960)	(0.5482)	(0.6137)	0.6645	1.0269	1.1619
1982	(0.9560)	1.1791	2.9279	2.1544	2.3824	3.7051	5.2525	(5.3595)	4.2404	(9.1829)	(13.3386)	(17.2453)

[a]Values in parentheses are theoretical estimates of q made on the basis of the available estimates of anchoveta biomass (in Table 2) and equation (3); see text.

following the same procedures for the latter years using IMARPE records. Fishing effort is expressed in GRT-trip (gross registered tonnage per trip) and no adjustments for efficiency were made. Trips usually lasted for 12 to 24 hours and vessels were rarely allowed to make more than one trip per day. The effort data series start in September 1960, when the newly created Marine Resources Research Institute (now the Peruvian Marine Institute - IMARPE) started to collect catch and effort data. No observations are available for some months in 1973, 1977, 1978 and 1982, when catches were obtained through noncommercial operations (e.g., surveys or exploratory fishing), or when commercial operations were mostly directed to other species or were subject to severe regulations and/or restrictions and for which no proper effort records were provided. Total catches in those months were usually small. Fishing mortality per month (Table 4) was calculated by dividing the total catch per month by the estimated mean biomass of the exploited stock.

The catchability coefficient is taken here in the context defined by Paloheimo and Dickie (1964), and monthly values (Table 5) have been estimated by dividing the monthly fishing mortalities by the fishing effort exerted each month on the stock.

The model selected to describe the variation of the catchability coefficient with stock size is that proposed by Fox (1974) and MacCall (1976), which has the form:

$$q = a \cdot B^b \qquad \text{... 1)}$$

where q is the catchability coefficient, B is the mean population size (mean biomass of the exploited stock in this case) and a and b are constants.

In this model the catchability coefficient will increase or decrease depending on the size and absolute value of B, giving rise to a relationship between the catch per unit of effort (C/f) and the stock size (B) of the form

$$C/f = a \cdot B^{b+1} \qquad \text{... 2)}$$

where the usual assumption that catchability remains constant allowing C/f to become a perfect index of abundance is fulfilled when b = 0. Increase in q with decreases in stock size are given by values of b smaller than 0, and in the limiting case where b = -1, C/f will remain constant, or may fluctuate independently of stock size.

Results and Discussion

Seasonal fluctuations of catchability

A clear seasonality was found in the fluctuations of the catchability coefficient in the Peruvian anchoveta fishery. This is particularly visible from 1960 through 1971 (Fig. 1) where, on the average, catchability was lowest during the austral winter (July-August) and was highest during the austral summer (November through March). Over this period the minimum recorded values are those corresponding to June 1967 and to July, September and October during the 1965 "El Niño" (q values of 0.0991, 0.0253, 0.0621 and 0.1159 x 10^{-7}, respectively). Maximum values of q during this period occurred prior to another "El Niño" year, in November and December 1971, and in March 1969 (q values of 1.0993, 1.4258 and 0.9635 x 10^{-7}, respectively).

These seasonal fluctuations changed and blurred to some extent after the 1972 collapse of the anchoveta fishery. On the average, the catchability coefficient increased dramatically in all seasons, but it became much higher during mid-spring (October-November) and fall (April-June). This strongly influences the overall seasonality pattern when the whole 23 years of observations are taken into account (Fig. 2) where two peaks in the average catchability values occur during mid-spring (November) and fall (March-June) with lower values in mid-winter (July) and early summer (December-February). Also worth noting are the much higher catchability values reported in April 1979, June 1980 and October and November 1979 (q values of 7.1686, 6.5653, 9.3906 and 11.2360 x 10^{-7}, respectively).

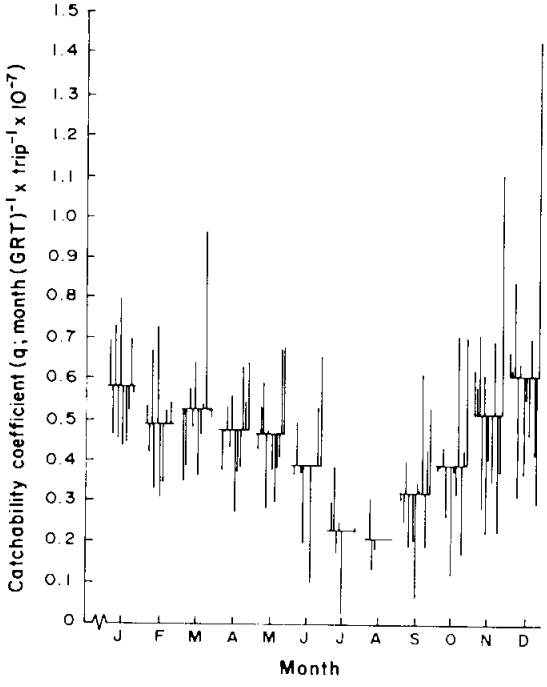

Fig. 1. Seasonal fluctuation of the catchability coefficient (q) in the Peruvian anchoveta *(Engraulis ringens)* fishery between 1960 and 1971. The horizontal lines represent, for each month, the 12-year average value of q, and the vertical lines represent the deviations of the actual values of the observations made each year with respect to the corresponding average.

Fig. 1. Fluctuación estacional del coeficiente de capturabilidad (q) en la pesquería de anchoveta peruana (Engraulis ringens) *entre 1960 y 1971. Las líneas horizontales representan para cada mes, el valor promedio de q para los 12 años, y las líneas verticales representan las desviaciones de los valores observados cada año con respecto al promedio.*

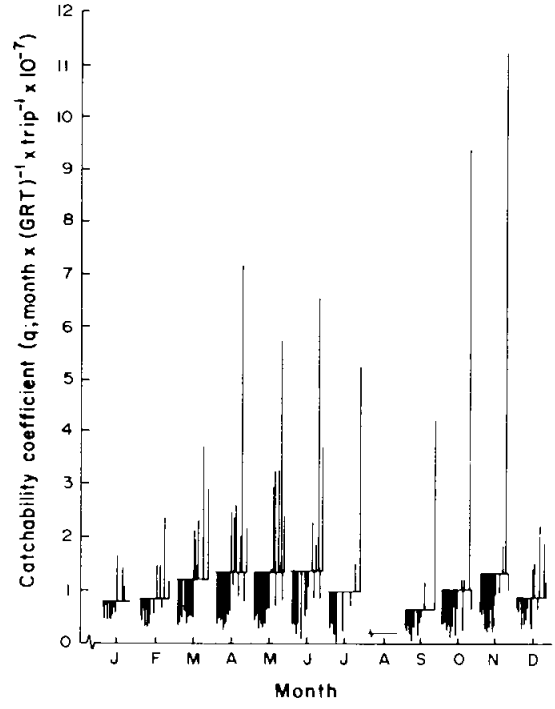

Fig. 2. Seasonal fluctuation of the catchability coefficient (q) in the Peruvian anchoveta *(Engraulis ringens)* fishery between 1960 and 1982. The horizontal lines represent, for each month, the 23 years average value of q, and the vertical lines represent the deviations of the actual values of the observations made each year with respect to the corresponding averages.

Fig. 2. Fluctuación estacional del coeficiente de capturabilidad (q) en la pesquería de anchoveta peruana (Engraulis ringens) *entre 1960 y 1982. Las líneas horizontales representan, para cada mes, el valor promedio de q para los 23 años, y las líneas verticales representan las desviaciones de los valores observados cada año con respecto al promedio.*

Over the entire period, seasonality could account for up to ±30% change in the monthly catchability coefficient, which is relatively small in comparison to the year-to-year fluctuation reported so far.

The occurrence of a seasonal pattern is not uncommon in fisheries, and it is obviously related to within-year seasonal changes of environmental conditions (temperature, turbulence, wind stress, etc.) that affect both fishing conditions and the distribution and behavior of fish. If consistent from one year to another, seasonal patterns are relatively easy to handle and do not pose major problems in fish stock assessment and other related analysis. What are troublesome are year-to-year changes in the seasonal pattern, as occurred in the anchoveta fishery in the more recent years. This could have been influenced by the reduced stock sizes and the associated higher catchability coefficients that, as it will be shown below, prevailed after the collapse in 1972. This, however, does not provide a sufficient explanation for the change in seasonal patterns.

A more in-depth analysis of the possible effects of some regulations adopted in the attempts to face the crisis in the anchoveta fishery would need to be undertaken before other natural

causes can be identified. During these years, fishing ports were frequently closed to protect juvenile and/or spawning anchoveta and, in some occasions, juvenile sardines caught along with anchoveta. This more often affected the traditionally highly productive ports in the north, besides limiting the number of observations in some key periods, particularly in summer and winter when the newly recruited and the spawning anchoveta were respectively, more abundant.

Density-dependent catchability

The plot of monthly estimates of catchability coefficient on mean-exploited biomass (Fig. 3) provides a clear evidence that in the Peruvian anchoveta fishery, there was a steep increase in the catchability coefficient with decreasing stock size. The power function proposed by Fox (1974) and MacCall (1976), fitted by a nonlinear regression procedure that uses the search algorithm developed by Marquardt (1963) gives the following estimates: intercept a = 0.352 and slope b = -0.97, with a correlation coefficient r = -0.888. The log-converted linear regression gives very similar estimates for a (= 0.286) and for the slope b (= -0.966) with a correlation coefficient r = -0.828, while the geometric mean regression (Ricker 1973) gives estimates that differ slightly (a = 11.3298 and b = -1.17).

The nonlinear regression method was assumed to produce the best estimates for prediction of q as a function of B. Besides an apparently better fit, it avoids the problems associated with the log conversion needed for the predictive linear regression and the geometric mean methods. The geometric mean could probably have been preferred to account for the expected natural variability in q and B, but it is noted that it is very likely that the two variables are subject to an undetermined observational variability as well, thus making the application of the geometric mean regression less adequate.

A major statistical problem arises from the regression of Y/X on X (q = C/Bf on B, in this case) which, as it is well known, may give a significantly high correlation even if the X and Y values are random variables. This, however, should not invalidate the main conclusions of this

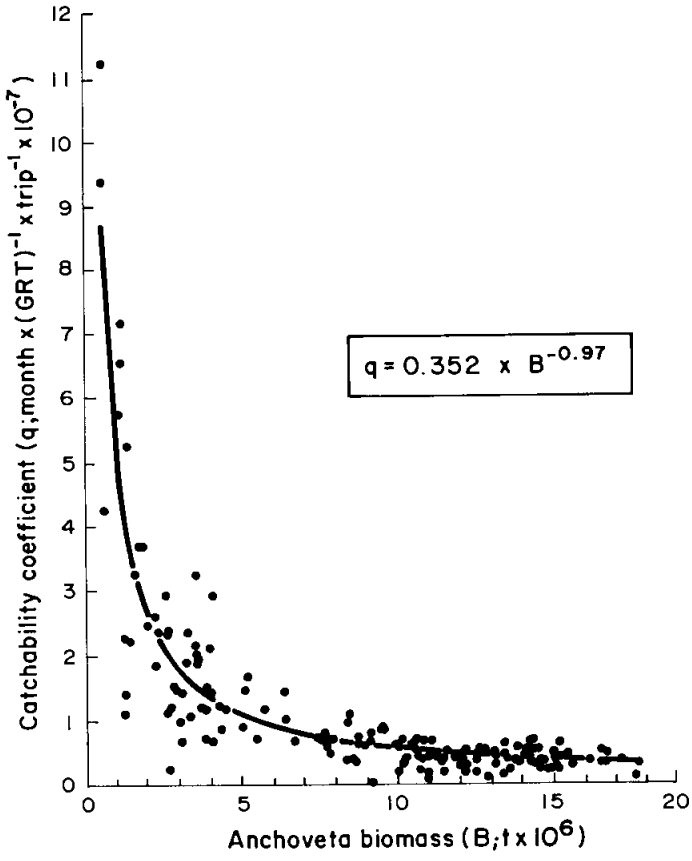

Fig. 3. Relationship between the catchability coefficient and the mean exploited stock biomass of the Peruvian anchoveta *(Engraulis ringens)*. The plotted values correspond to the actual observations of catchability and biomass, made each month, from 1960 to 1982, and the line has been fitted by a nonlinear regression procedure.

Fig. 3. Relación entre el coeficiente de capturabilidad y la biomasa media de la población explotada de anchoveta peruana (Engraulis ringens). *Los puntos corresponden a los valores mensuales observados entre 1960 y 1982, y la línea ha sido adjustada mediante una regresión no lineal.*

analysis which precisely points at the lack of correlation between C/f and B. The apparent statistical significance of the high correlation coefficient between q and B should, however, be taken with great caution, and it should be recognized that, in this case, the variability and bias of the estimates are unknown, although they may be expected to be relatively small.

With this warning in mind, one can then proceed to incorporate the parameters estimated above into equation (1), by which, in the Peruvian anchoveta fishery the expected variability of the catchability coefficient (q) with stock size (B) would be expressed by:

$$q = 0.352 \cdot B^{-0.97} \qquad \text{... 3)}$$

The curve generated by this equation is shown in Fig. 3 together with the observed values of q and B. The same equation has also been used to estimate theoretical values of q and corresponding values of fishing effort (f) for the months when original estimates or observed values were missing (see estimates in parentheses - Tables 3 and 5), thus allowing the completion of the whole set of monthly estimates of nominal catch (C), biomass (B), fishing effort (f), fishing mortality (F) and catchability coefficient (q) for possible further analyses.

The relatively low value of the slope (b, being very close to -1) and the model below resulting from equations (2) and (3) above:

$$C/f = 0.352 \cdot B^{0.03} \qquad \text{... 4)}$$

indicate that there is a very poor correspondence between the catch per unit of effort estimates used so far and the anchoveta stock size, and that except for stock sizes very close to 0, one should expect catch per unit of effort to remain constant, or to fluctuate independently of stock size. This is clearly illustrated in Fig. 4, where the flat-topped curve generated with equation (4) is shown together with the scatter diagram of observed monthly values of catch per unit of effort and anchoveta biomass.

From this, it can be concluded that there is a very poor relationship between the estimated fishing mortality and fishing effort expressed in terms of GRT-trip. It also follows that for the anchoveta fishery, the catch per GRT-trip is useless as an index of abundance, and should not be applied within this context for stock assessment purposes. This partially justifies the decision taken by IMARPE back in 1972 to abandon the use of fishing effort-based production models for the assessment of the Peruvian anchoveta.

The strong depensatory relationship between q and B is, to a great extent, a consequence of the shoaling behavior through which, even if in low abundance, anchovies and other small pelagics would still tend to aggregate in shoals of a given size. This could, in theory, allow

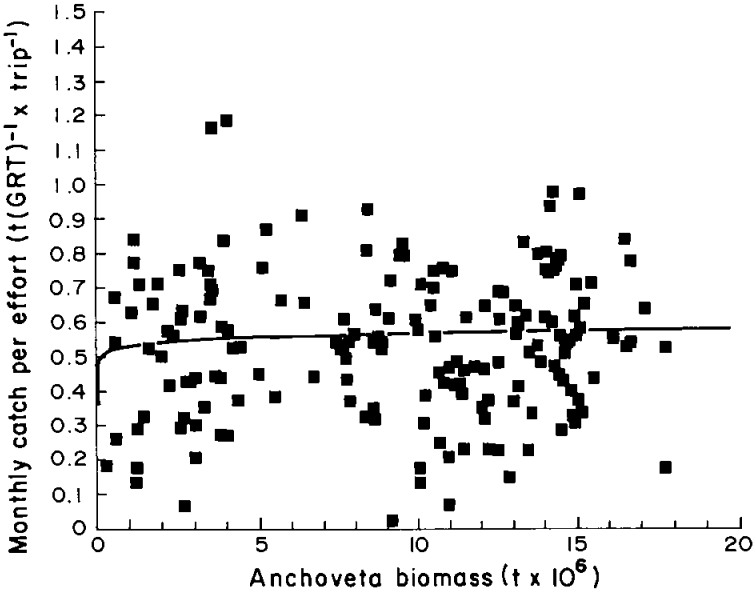

Fig. 4. Scatter diagram of the relationship between catch per unit of effort and biomass of Peruvian anchoveta *(Engraulis ringens)*, by month between 1960 and 1982, with theoretical curve generated by equation (4) (see text).
Fig. 4. Diagrama de dispersión de la relación entre la captura por unidad de esfuerzo y la biomasa de anchoveta peruana (Engraulis ringens), *por meses entre 1960 y 1982, y curva teórica generada con la ecuación (4) (ver texto).*

the catch rates to remain relatively high even while catching the last very few fish in a population, provided they are shoaling together and could be detected by the fleet. The fleet, on the other hand, has usually the capacity to increase its fishing power without this being reflected by an increase in nominal fishing effort. This has been particularly the case with the Peruvian anchoveta fishery. By using the GRT-trip as a unit, the nominal fishing effort cannot account for, or reflect changes or improvements introduced on an *ad-hoc* basis (i.e., when abundance was low) to maintain catch rates. In fact, there are indications that as the stock size decreased, the duration of the average trip increased, and so did the time, spent searching, the number of hauls per trip, not to mention the improvements in the cooperation amongst vessels and scouting. This necessarily made the original GRT-trip less valuable as a measure of real fishing effort, and partially explains the increase in q.

Low-cost abundance indexes are, however, always useful for monitoring and assessment purposes, and for future use it might be worth exploring the value of measurements of fishing effort that would more readily reflect changes in the real abundance of the anchoveta stock. Log-book information on number of hauls, fishing hours per trip, searching time (including scouting), etc., could be used to improve fishing effort estimates, which could be further corrected to account for changes in distribution and local abundance. This could be achieved by stratifying catch and effort data by geographical subareas in such a way that, once weighed by the size of the subarea, catch per unit of effort values for each subarea could be added together. The size of these subareas should be kept as small as allowed by the basic information, and the grids of 30' latitude by 10 miles parallel distance from the coast (called "areas isoparalitorales" by IMARPE) introduced together with the log-books in use in the mid-1970s might be a reasonably starting point.

One serious implication of the depensatory relationship represented by equation (3) is that the relationship between stock size, catch per unit of effort or equilibrium yield and fishing effort is no longer expected to be a straight line or a parabola, as is usually assumed in the simplest applications of fishing effort-based production models. If equations (1) and (2) are incorporated in the formulation of a simple production model, for values of $b < 0$ there is a range of values of fishing effort for which there are two equilibrium values of stock size (only one of which is stable), and the relationship between fishing effort and stock size, fishing mortality or equilibrium yield take all the form of backward bending curves. The departure from the traditional straight lines or the parabola will be greater, and backward bending more pronounced as the absolute value of b increases.

Figs. 5 and 6 represent the scatter diagrams of the relationship between estimated anchoveta total catch and mean anchoveta biomass with the corresponding values of fishing effort by year, between 1960 and 1982 (values compiled from Tables 1, 2 and 3). The same figures also show simulated curves of the theoretical relationship between equilibrium catch and fishing effort (Fig. 5) and equilibrium biomass (for two reference levels of virgin stock size) and fishing effort (Fig. 6) when the slope $b = -0.97$ is used in a depensatory version of a simple surplus production model. In the simulations mentioned above, a slope $b = 0$ will necessarily generate a perfect parabola in Fig. 5 and descending straight lines in Fig. 6 (more details about the other parameters used in the simulations follow).

The implications of this type of depensatory relationship for fishery monitoring and management are that, if gone unnoticed, fishing effort may be allowed to increase until the critical point at which the curve bends backwards is reached. From this point on, total catch will inevitably decrease and, contrary to what might be expected, fishing mortality would continue to increase and stock size to decrease, even if nominal fishing effort is reduced. One consequence is the switching of the system from an equilibrium path at a finite population level to an extinction path, from where the only way out, provided other conditions remain constant, is a massive reduction in fishing mortality.

This critical point on the backward bending of "depensatory" curve occurs (see also Csirke 1988) when the ratio between the mean biomass (B) and the virgin stock size (B_∞) is:

$$B/B_\infty = -b/(1-b) \qquad \text{... 5)}$$

If $b = -0.97$ in the Peruvian anchoveta fishery, this critical point would have been reached with a mean biomass reduction to approximately half the virgin stock size ($B/B_\infty = 0.49$). From

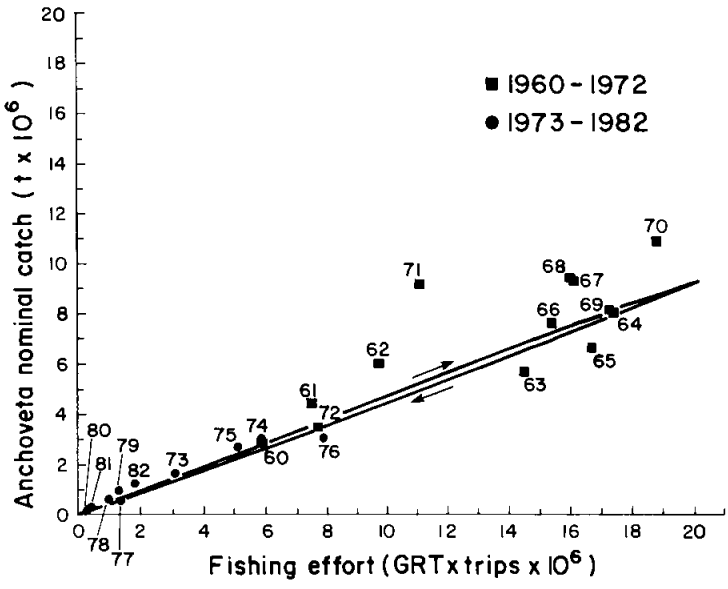

Fig. 5. Scatter diagram of the relationship between total catch of Peruvian anchoveta *(Engraulis ringens)* and corresponding fishing effort by year from 1960 to 1972 (squares) and 1973-1982 (circles), and theoretical curve of equilibrium catch and fishing effort generated by simulation with a depensatory surplus production model incorporating parameters from equation (3) (see text).

Fig. 5. Diagrama de dispersión de la relación entre la captura total de anchoveta peruana (Engraulis ringens) *y el esfuerzo de pesca correspondiente, por años entre 1960 y 1972 (cuadrados) y 1973-1982 (círculos), y curva de la relación teórica entre captura de equilibrio y esfuerzo de pesca generada mediante simulación con un modelo depensatorio de producción excedente incorporando los parámetros de la ecuación (3) (ver texto).*

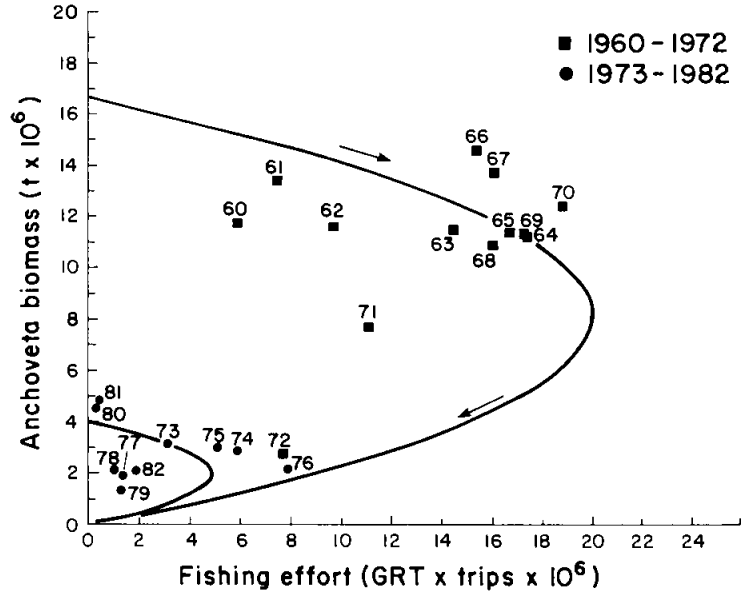

Fig. 6. Scatter diagram of the relationship between biomass (B_n, n+1) of Peruvian anchoveta *(Engraulis ringens)* and corresponding fishing effort (f_n) by year (n) from 1960 to 1972 (squares) and 1973-1982 (circles), and theoretical curves of equilibrium biomass on fishing effort generated by simulation with a depensatory surplus production model incorporating parameters from equation (3) and two reference levels of virgin stock size (see text).

Fig. 6. Diagrama de dispersión de la relación entre biomasa (B_n, n+1) de anchoveta peruana (Engraulis ringens) *y valores correspondientes de esfuerzo de pesca (f_n) por años (n) entre 1960 y 1972 (cuadrados), y 1973-1982 (círculos), y curvas teóricas de la relación entre biomasa de equilibrio y esfuerzo de pesca generadas mediante simulación con un modelo depensatorio de producción excedente incorporando los parámetros de la ecuación (3) y dos niveles de referencia del tamaño de la población al estado virgen (ver texto).*

the available biomass estimates it seems that the anchoveta stock was probably pushed close to, but still maintained above this critical point during the late 1960s and early 1970s. However, it surely flipped down well below this level with the advent of the 1972-1973 "El Niño".

Although heavy fishing continued for some time after the collapse, overall fishing pressure on the anchoveta stock has diminished. The stock, however, failed to recover. This, together with the changes in abundance of other predominant species in the Peruvian upwelling ecosystem leads to consider the possibility of more consistent and long-lasting changes affecting the anchoveta ecosystem, as opposed to the also noticeable but relatively transient effects one usually would expect from reversible fishing or environmental events alone.

In the scatter diagram of the relationship between mean biomass and fishing mortality presented in Fig. 7, the data point corresponding to 1972 (mean 1972-1973 biomass) stands as a cut-off point for splitting the observations into two groups, each one of which could be fitted by a straight line - one for 1960-1972, and the other for 1973-1982. The fitting of two lines by linear regression give for 1960-1972 an estimate of the intercept a' = 16.70 x 10^6 and the slope b' = -7.95 x 10^6, with a correlation coefficient r' = -0.798, while for the years 1973-1982 the estimates are a'' = 3.93 x 10^6 and b'' = -1.72 x 10^6, with r'' = -0.630.

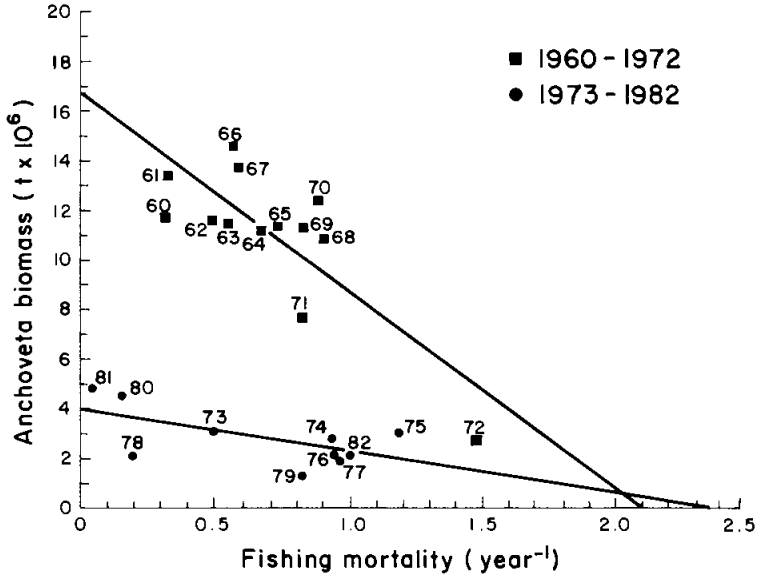

Fig. 7. Scatter diagram of the relationship between biomass ($B_{n,\ n+1}$) of Peruvian anchoveta *(Engraulis ringens)* and corresponding fishing mortality (F_n) by year (n) from 1960 to 1972 (squares) and 1973-1982 (circles), and lines fitted by linear regression to both groups of years.

Fig. 7. Diagrama de dispersión de la relación entre biomasa ($B_{n,\ n+1}$) de anchoveta peruana (Engraulis ringens) *y correspondiente mortalidad por pesca (F_n) por años (n) entre 1960 y 1972 (cuadrados) y 1973-1982 (círculos), con rectas adjustadas para ambos grupos de años por regresión lineal.*

The fact that the relationship between biomass and fishing mortality can easily be divided into two clearly identifiable series (one up to the collapse of the fishery in 1972 and the other after the collapse), is an indicator of a possible major change in the system of the Peruvian anchoveta, which modified the carrying capacity and thus the reference level of the virgin stock size (B_∞) for the anchoveta in this area. Since in terms of surplus production modelling the intercepts in the biomass axis in Fig. 7 (a' and a'') correspond to the virgin stock size, one may have a rough indication of the relative magnitude of this change. It is also worth noting that the intercept of the two lines in the fishing mortality axis (c' = 2.10 and c'' = 2.28) almost coincide. In the production model formulation these values correspond to "r_{max}" the intrinsic rate of instantaneous increase in the population at density approaching 0, and since in both cases this has remained more or less the same, this could mean that the intrinsic characteristics of the stock are the same, although the "surroundings" (i.e., the carrying capacity) had changed.

The estimates mentioned above (B'_∞ = 16.70 x 10^6, B''_∞ = 3.93 x 10^6 and mean r_{max} = 2.2) have been used in the simulations referred to above and shown in Figs. 5, 6 and 7. The information contained in these plots is not conclusive, but together with other evidence of changes starting in 1972 (see e.g., Senocak et al., this vol.) do contribute to support the idea that the Peruvian anchoveta stock has switched to a new population path with a much lower maximum equilibrium level.

References

Beverton, R.J.H., J.G. Cooke, J.B. Csirke, R.W. Doyle, G. Hempel, S.J. Holt, A.D. MacCall, D.J. Policansky, J. Roughgarden, J.G. Shepherd, M.P. Sissenwine and P.H. Wiebe. 1984. Dynamics of single species. Group Report. *In* R.M. May (ed.) Dahlem Konferenzen. Springer-Verlag, Berlin. (also Life Sci. Res. Rep. (32): 13-58).

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp. P.-V. Réun. CIEM (177): 307-313.

Csirke, J. 1988. Small shoaling pelagic fish stocks, p. 271-302. *In* J.A. Gulland (ed.) Fish population dynamics. 2nd ed. John Wiley & Sons, New York.

Fox, W.W. 1974. An overview of production modelling. Collect. Vol.-Sci. Pap. ICCAT (3): 142-156.

Jordán, R. 1971. Distribution of anchoveta (*Engraulis ringens* J.) in relation to the environment. Inv. Pesq. 35(1): 113-126.

IMARPE. 1970. Report of the panel of experts on population dynamics of Peruvian anchoveta. Bol. Inst. Mar Perú-Callao 2(6): 324-372.

IMARPE. 1972. Report on the Second Session of the Panel of Experts on population dynamics of Peruvian anchoveta. Bol. Inst. Mar Perú-Callao 2(7): 373-458.

IMARPE. 1973. Report of the Third Session of the Panel of Experts on the population dynamics of Peruvian anchoveta. Bol. Inst. Mar Perú-Callao 2(9): 525-599.

IMARPE. 1974. Report of the Fourth Session of the Panel of Expert on Stock Assessment on Peruvian anchoveta. Bol. Inst. Mar Perú-Callao 2(10): 605-719.

MacCall, A.D. 1976. Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse seine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 18: 136-148.

Marquardt, D.W. 1963. An algorithm for least-squares estimation of non linear parameters. J. Soc. Indust. Appl. Math. 11: 431-441.

Paloheimo, J.E. and L.M. Dickie. 1964. Abundance and fishing success. Rapp. P.-V. Réun. CIEM (155): 152-163.

Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987. VPA estimates of the monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. (30): 409-434.

Saville, A., Editor. 1980. The assessment and management of pelagic fish stocks. A Symposium held in Aberdeen, 3-7 July 1978. ICES Rapp. P.-V. Réun. CIEM 177. 517 p.

Schaaf, W.E. 1975. Fish population models: potential and actual links to ecological models, p. 211-239. *In* C.S. Russel (ed.) Ecological modelling in a resource management framework: the proceedings of a symposium. John Hopkins University Press, Maryland.

Schaaf, W.E. 1980. An analysis of the dynamic population response of Atlantic mehaden, *Brevoortia tyrannus*, to an intensive fishery. Rapp. P.-V. Réun. CIEM 177: 243-251.

Sharp, G.D. and J. Csirke, Editors. 1983. Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291. Vols. 2 and 3. 1225 p.

Shelton, P.A. and M.J. Armstrong. 1983. Variations in parent stock and recruitment of pilchard and anchovy population in the Southern Benguela system, p. 1113-1132. *In* G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to examine changes in abundance and species composition of neritic fish resources. San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291 Vol. 3.

Tsukayama, I. and L.M. Palomares. 1987. Monthly catch and catch composition of Peruvian anchoveta *(Engraulis ringens)* (northern-central stock, 4-14°S), 1953 to 1982, p. 89-108. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Ulltang, O. 1976. Catch per unit of effort in the Norwegian purse seine fishery for Atlanto-Scandian (Norwegian spring spawning) herring. FAO Fish. Tech. Pap. 155: 91-101.

Ulltang, O. 1980. Factors affecting the reaction of pelagic fish stocks to exploitation and requiring a new approach to assessment and management. Rapp. P.-V. Réun. CIEM 177: 489-504.

Adaptation of the Anchoveta *(Engraulis ringens)* to the Peruvian Upwelling System[a]

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MATHISEN, O.A. 1989. Adaptation of the anchoveta *(Engraulis ringens)* to the Peruvian upwelling system, p. 220-234. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.). The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Following a brief review of the adaptations of anchoveta *(Engraulis ringens)* to its highly variable upwelling ecosystem, the hypothesis is presented that the anchoveta stock off Peru consists of a large number of local subpopulations of which each is genetically adapted to "home" to a different upwelling plume, and to spawn during a specific period of the year.

The impact of selective overexploitation of the most productive of these subgroups is discussed in analogy to Pacific salmon and Atlanto-Scandian herring, and the implications for management and research are outlined.

Resumen

Luego de una breve revisión de las adaptaciones de la anchoveta *(Engraulis ringens)* a su altamente variable ecosistema de afloramiento, se presenta la hipótesis que el stock de anchoveta frente al Perú consiste de un gran número de subpoblaciones locales, cada una de las cuales está genéticamente adaptada a su "hogar" en una pluma de afloramiento diferente y desovan durante un período específico del año.

Se discute el impacto de la sobreexplotación selectiva de los subgrupos más productivos, en analogía con el salmón del Pacífico y el arenque del Atlántico-Escandiano y se esbozan las implicancias para su manejo e investigación.

Introduction

The meteoric rise of the Peruvian anchoveta fishery has been well documented. From miniscule catches prior to 1956-1957, the annual yield rose almost linearly to the end of 1970-1971, whereupon the catches fell from about 10 to about 4 million tonnes (Valdivia 1978), while the corresponding stock sizes declined even more. A drop from the previous high population levels was already suspected in 1960 by Saetersdal et al. (1965) who developed a corrected index of catch/effort proportional to stock size and demonstrated a reduction of 50% between the 1959 and 1962 levels of abundance.

In 1973, the total stock was estimated to be around 4 million tonnes while the catch varied from 2 to 3 million tonnes. In spite of the very small spawning stock in these years, there was a spectacular rise to biomass of 12 million tonnes in 1976 followed by an unprecedented crash to 1.9 million tonnes by early 1977, the lowest level of abundance recorded to the end of the 1970s (see Pauly and Palomares, this vol. and contributions in Pauly and Tsukayama 1987a).

Many different explanations have been offered to explain these oscillations in biomass and the overall decline of the anchoveta stocks. However, they can be referred to one of two

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[a]Editors' note: This is a slightly edited and updated version of a contribution presented at the USA/USSR Conference on Upwelling, Moscow, 8-18 October 1979, which had remained unpublished and which we include here because it contains concepts that are still highly pertinent.

categories: (i) environmental changes, such as those related to the El Niño events of 1957, 1965, 1969, 1972 and 1976, have been linked causally to declines in abundance; and (ii) withdrawals by the fishery as the principal cause of reduced levels of anchoveta abundance and observed increase in abundance of other components of nekton, especially sardines.

This paper attempts to propose a third, alternative explanation and a synthesis of previous ones. The basic premise is that the genetic structure of the anchoveta population has been altered by the sustained removals of about 10 million tonnes annually during the first half of the 1960s. Perturbations of the environment, therefore, now affect the stock in a different manner than prior to the onset of the fishery. It has been known for sometime that stressed clupeoid populations signal this by violent and rapid fluctuations in numbers concomitant with alterations of other vital parameters (Murphy 1973).

The mechanism whereby this is effected is the selective removal of the segments of fish forming peaks of abundance, such as during time of spawning, and which possess the highest reproductive potential. The remaining spawning stocks are therefore deficient in number and inefficient spawners. However, such a hypothesis cannot be sustained without an auxiliary one, stating the independence or semi-independence of a large number of subgroups constituting the overall anchoveta population. The argument is developed in analogy to that for anadromous salmonid species in the North Pacific, i.e., based on a racial stock concept and home stream theory.

The Peruvian Stock of Anchoveta

The range of distribution of *Engraulis ringens* extends from 4°30'S to 42°30'S, using the most distant places of occurrences as boundaries. This represents a linear extent of almost 4,000 km. The offshore distribution varies not only with the season but also with the configuration of the continental shelf and its width. The edge of the shelf may be placed at 200 m isobathyline. But even within this very narrow coastal shelf, most of the anchoveta are found within 60 km off the coast, and the bulk of the commercial catch have been made in the past within 10 km off the coast.

The temperature regime varies less than what could be expected over such a wide geographic range, primarily due to the upwelling along the Eastern Boundary Current which flushes the shoreline with waters of 16°C or thereabouts. Temperature limits can be set at 14°-19°C, but they are by no means well defined and can be exceeded, especially in the upper range.

Besides this two-dimensional dimension of the anchoveta's ecosystem, largely set by temperature, there is a vertical boundary set by the oxygen content. Below 40 meters depth on the shelf, the undercurrent is low in oxygen, generally less than 2 ml/l and diminishes rapidly with depth. Echograms fail to confirm large concentrations of anchoveta below 40 m or in waters with 2 ml/O_2/l. Most schools have been detected in depths from 20 to 40 m (Villanueva 1970).

The heaviest concentrations of anchoveta are found outside northern and central Peru. In the north, the abundance drops off quickly while in the south, it trails off gradually (Pauly and Tsukayama 1987b). But even within the optimal distribution range, sharp density gradients occur. The definitions of these can either be done visually from echograms, as was done from 1964 to 1972 or thereafter from integrated echo outputs. An example is given in Fig. 1 (left map), which is based on charts from Johannesson and Robles (1977). The mapping was done in February during the austral summer spawning season and the density chart clearly indicates the presence of isolated density centra. They are interpreted here as manifesting the existence of distinct subgroups, which are, to a large extent, isolated spatially during the spawning season.

This is contrary to the prevailing stock concept which postulates few but very large subpopulations based on meristic characters, especially vertebral counts. Brandhorst et al. (1965) thus separated the Chilean anchoveta into a northern and a southern group. Jordan (1963) failed to detect any differences in the population along the entire Peruvian coast. Tsukayama (1966) found that the average number of gill rakers for fish caught at Chimbote in the north differed from that established for samples from Mollendo in the south. Likewise, Rojas de Mendiola (1971) found that length of the intestine relative to body length was greater in northern than in

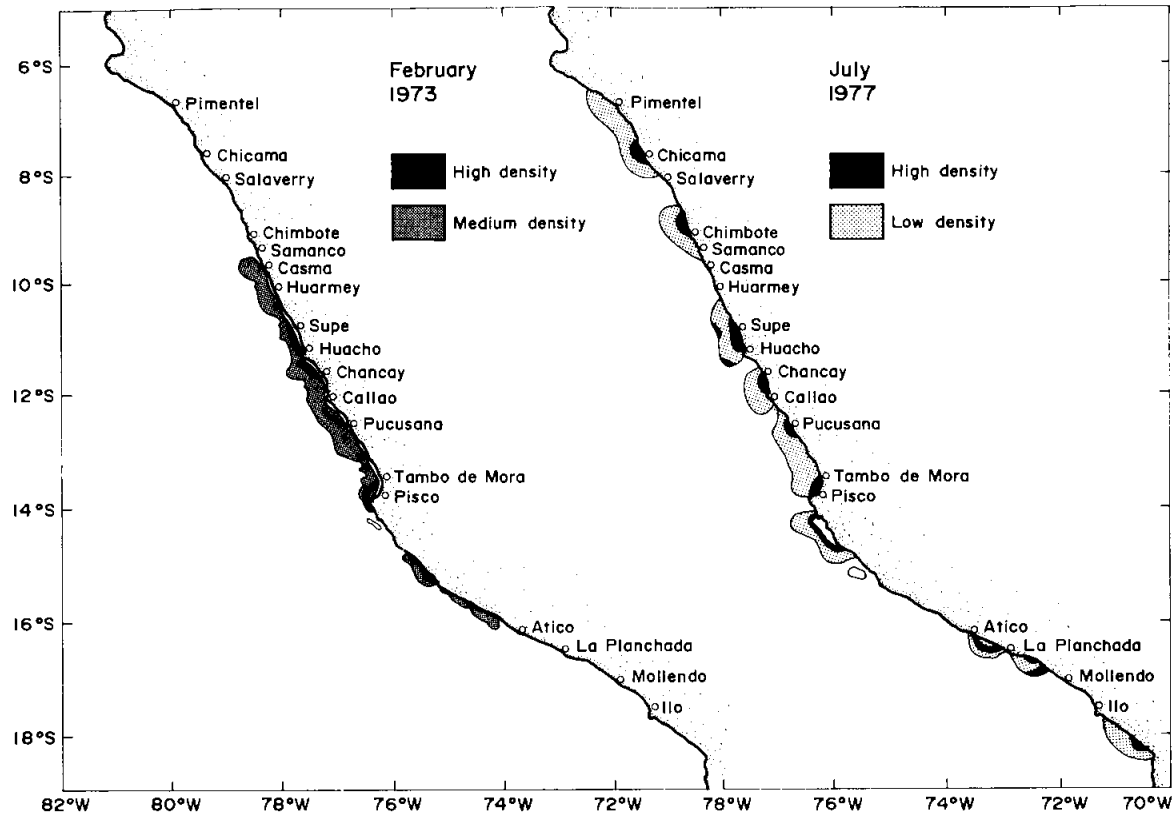

Fig. 1. Distribution of anchoveta during period of high (*left*) and of low (*right*) abundance. Note that on right side, the sub-units are well separated, and that their core roughly correspond to location of processing plants (adapted from Johannesson and Robles 1977 and Johannesson and Vilchez 1979).

Fig. 1. Distribución de la anchoveta durante períodos de alta (izquierda) y baja (derecha) abundancia. Nótese que en el lado derecho las subunidades están muy separadas y que sus núcleos corresponden groseramente con la ubicación de las plantas de procesamiento (adaptado de Johannesson y Robles 1977; y Johannesson y Vilchez 1979).

southern Peru and Chile. This in itself may point to a heavier component of zooplankton in the diet of the southern groups of anchoveta (see Pauly et al., this vol.).

However, for these large population units to represent a common gene pool, there must be free interchange of individuals and no reproductive barriers, neither spatial nor temporal. Some tagging experiments suggest rather long and rapid migrations, but there is a question as to what extent anchoveta tagged with an internal magnetic tag exhibit their normal behavior pattern. The most pronounced relocation of fish occur during El Niño events when the warm water from the north leaves the fish only two choices, either to retreat to the narrow coastal strip where upwelling maintains temperature within their tolerance limits or to migrate south. Valdivia (1978) reports that large numbers of anchoveta in 1972 were found only south of 10°S in March, south of 12°S in April and finally south of 15°S in the beginning of May. But a rapid southward retreat of this type does not guarantee that the relocated fish will successfully spawn in their new environment.

The opposite is a more likely event: independence of population units can be identified and established just as well from spawning time as from meristic characters. Anchoveta can spawn during the entire year, but practically speaking, spawning occurs for eight or nine months, from July to March. Within this time span, one can identify two periods, one during the austral spring from September to October, and a less intense spawning period in January-February (Senocak et al., this vol.).

It has been claimed by Paulik (1970) that the same anchoveta can spawn both in spring and, six months later, in the summer. However, there is no direct evidence to substantiate this[a].

[a]Editors' note: this was a valid point when the original version of this paper was written. By now, evidence to substantiate this is available (see references in Pauly and Soriano 1987). However, the author's main point is not affected by this.

Rather, the fact that the spring spawners are consistently two or more times more abundant than the summer spawners testifies to the independence of these two spawning units. In the catches made during or shortly after spring spawning, the mature fish dominate while the immature fish represent the strongest group in catches after the summer spawning. On the average, there must be factors or conditions during the spring spawning which render this the most successful of the two. In the course of the evolutionary process, this must then eventually manifest itself genetically.

This process has been going on for the last 11,000-12,000 years. Studies of sediment cores from a shelf region of 14°S turned up anchoveta scales in all layers as well as scales of hake. In contrast, sardine scales were present only intermittently and for relatively short time periods. No periodicity or regular patterns were detected between the sardine periods. The anchoveta scales account for 79% of all scales, hake for 16% and sardines less than 2%. Other groups were of very little significance (DeVries 1979; DeVries and Pearcy 1982).

During this long history, the anchoveta has maintained itself in the coastal waters. If scale abundance at different times are taken to reflect changes in population size, there would be of the order 1:5, based on a time scale of several centuries. No finer solution was possible, and no statements can be made regarding annual or short-term variability, such as observed during the last decade where changes have been of the order 1:10.

Originally, the Eastern Boundary Current was thought of as a rather stable environment. However, intensive studies by the Instituto del Mar del Peru (IMARPE), under the US Coastal Ecosystem Upwelling Analysis Program (CUEA), and by expeditions from the USSR, the Federal Republic of Germany, Canada and other countries, have shattered this concept. The strength of upwelling is not only governed by the wind force, but also by the deep undercurrent (Smith 1978). El Niño events are occurring more commonly than previously believed (Quinn et al. 1978). However, irrespective of the cause and nature of the perturbations, the anchoveta has maintained itself during millennia. The species must, therefore, have developed survival mechanisms or a resilience sufficient to overcome the variability of its ecosystem. This does not carry as an unescapable consequence population numbers should be stable. Rather the species possesses mechanisms to rebuild its population after a temporary environmental setback. This becomes more critical for the anchoveta than for the hake: the former has an average life span of perhaps two years, while it is double or more for hake. One can see this in the scale deposit where the number of hake scales has varied much less than that for the anchoveta over the last ten thousand years.

Several types of evolutionary strategies can be suggested. One would be the development of extremely wide tolerance limits for the physical and chemical factors of the environment as well as high survival rates of different life stages. Another mechanism, suggested by Walsh (1978), is that marine communities may respond to climatic oscillations by a relocation of their center of abundance.

However, there is a growing body of evidence, still largely circumstantial, that a population of fish consists of much smaller subunits than what is termed a "race" in fishery biology, and that other isolating mechanisms exist aside from spatial separation, such as time of spawning. The function of many independent or semi-independent units, many of which are small and perhaps should be termed plus or minus deviants from the strong central groups, is that of buffering against perturbations of the environment. An analogy can be made with a salmon population where the spawning colonies are visible and can be identified in the time-space domain even though they cannot easily, or not at all, be separated by their meristic characters alone. But even within a geographically confined "race", homogeneity of all its members does not exist.

Structure of Exploited Salmon Stocks

The members of the Pacific salmon of the genus *Oncorhynchus* began to ascend the various streams and river systems along the perimeter of the north Pacific Ocean as soon as the glaciers started to recede, some 12,000-13,000 years ago. (This corresponds to about the same time that the anchoveta has occupied the Peruvian upwelling system.) In due course, the genus split into six species, each occupying some specialized habitats, although considerable overlap does occur.

Separation of "races" on the common feeding grounds in the ocean from meristic or serological characters has met with limited success. But segregation occurs on the spawning grounds. Another distinguishing feature is the time of spawning. Thompson (1951) was perhaps the first to decisively point out that the usually bell-shaped time curve or ascendance into a trunk stream and associated peak of spawning essentially reflect survival rates. The center part with highest relative abundance represents the spawners best adapted to the average environmental conditions. If this were not so and reproduction was equally successful at all times during a year, the abundance curve would be a horizontal line. In time, the phenotypically differing units have assumed independence by karyotypic selection. Time of spawning as an inherited character has been demonstrated on several occasions by transplantation experiments.

This of course does not preclude that other factors, such as temperature, affect and alter spawning time in a poikilothermal organism such as salmon. Although changes in mean spawning time have proven to be rather invariant, annual variability is buffered by the presence of plus or minus deviants. By and large, the phenological sequence of events is tightly or loosely coupled, depending upon the variability of the environment; but seen in relation to other aquatic organisms, the variance for salmon "races" is small, which is to be expected in its high latitude environments with pronounced seasonal successions.

Conversely, the diversity of the plus or minus deviants from the mean, i.e., their distance in standard deviation units, expresses the variability of the environment and of the niche to which an organism has adapted itself.

If now a "race" is subjected to commercial exploitation, the brunt of fishing mortality will usually be directed - for purely economic reasons - toward the fish belonging to the peak of the abundance curve. This in turn causes a selective removal of the constituents of the group with the highest reproductive potential. If this process is continued long enough, the net result is a very lowered production. The history of various fisheries provides magnificent examples.

In the Columbia River, the peak abundance curve was July, as seen in 1876 when a gill net fishery commenced (Fig. 2). The heart of this run was removed by the fishery which preferred to operate in July, the month with the best summer weather and the highest abundance of fish. The central part of the run was eventually fished out. The early and late segments of the runs have

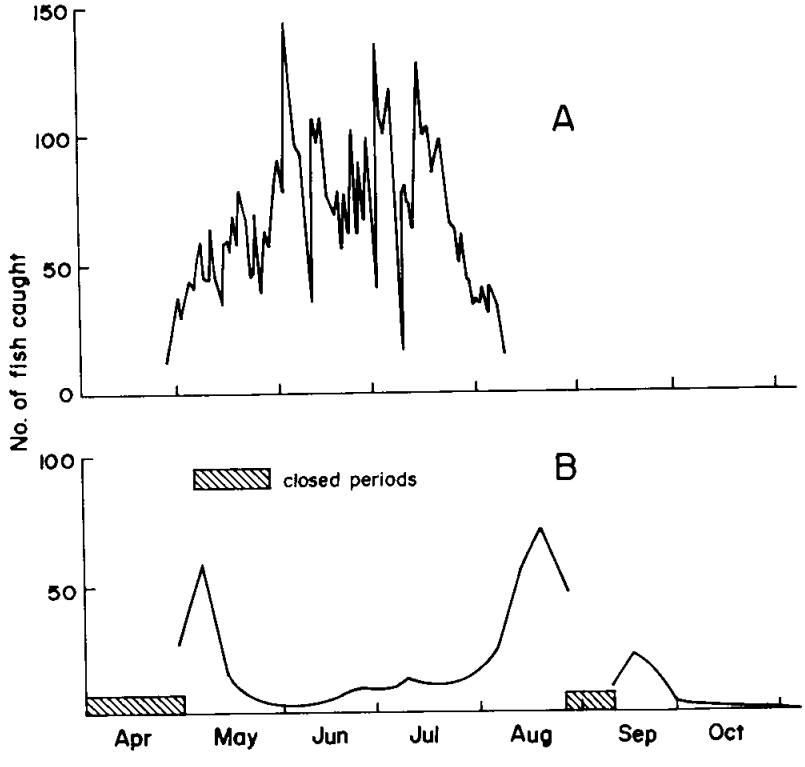

Fig. 2. Seasonal changes of catches of Columbia river chinook salmon *(Oncorhynchus tshawytscha)* (modified from Thompson 1951). A. Daily gill net catches in 1876. B. Catches in 1938, below Bonneville Dam.

Fig. 2. Cambios estacionales en las capturas del salmón chinook (Oncorhynchus tshawytscha) *del rio Columbia (modificado de Thompson 1951). A. Capturas diarias con redes agalleras en 1876. B. Capturas en 1938, Bonneville Dam.*

not increased nor filled in the middle part in spite of almost complete protection. Another example is the Karluk River in Alaska where the successive decline of the total stock can be traced very well from the catch records combined with weir counts of escapement. Again, the productive middle part of the bell-shaped abundance curve was destroyed by the fishery (Thompson 1951). The important point is that in both of these two cases, the early or late segments have not increased beyond their historical levels of abundance, in spite of extensive protection from harvesting.

If such a selective fishing pressure continues, not only will the center part of the run diminish, but eventually the plus and minus deviants will diminish because of their low reproductive potential. This is analogous to a fishery of a mixed stock where the marginal groups eventually succumb (Paulik et al. 1967). The end result is that eventually the continuous distribution pattern is broken and the fish appear in geographically isolated small groups with a low net production.

The important question is: Can this stock concept be applied to marine fishes? Superficially, there seems to be no fundamental obstacles to decompose a marine stock, such as herring, into a collection of independent subgroups. Devold (1963) reported that the spawning time of the Atlanto-Scandian stock of herring changed from November to December in 1890 to March to April in 1960 (Fig. 3). He estimated this progressive delay as a few days per year. Over a sufficiently long period of time, this would have the effect of retarding peak spawning time.

Fig. 3. The continued retardation of first appearance of herring *(Clupea harengus)* on the spawning grounds on the west coast of Norway. A. First day catch of winter herring. B. Decomposition of the original run into a subset of independent groups (modified from Devold 1963).

Fig. 3. Retardo continuado en la primera aparición del arenque (Clupea harengus) *en las áreas de desove en la costa oriental de Noruega. A. Captura del primer dia del arenque de invierno. B. Descomposición de la línea original en un conjunto de grupos independientes (modificado de Devold 1963).*

Another interpretation is that the original spawning group consisted of a number of units peaking successively in spawning time from November to March. Since an unrestricted fishery will hit the first segments hardest, they would be the first to go. Later units enjoyed some protection when processing facilities were clogged or overproduction reduced the financial gain from continuous fishing. In time, the early spawning units would succumb and cease to contribute a substantial part of the catch. The fishery would thus turn to the next one and so on with a net result of an apparent shift in peak spawning time as observed in the case of the Atlanto-Scandian stocks of herring.

In order for the homing and spawning time concept to be applicable to the anchoveta, several assumptions must be met. First, there must be a series of independent upwelling plume

with stability to form an identifiable environment. The "home stream theory", as developed for salmon and which refers to fixed geographic localities without specifying the environmental characteristics, must thus be redefined. Rather than referring to geographical terms, the implication for marine species must be that they "home" to water masses or an environment of a certain characteristic with regard to water velocities along all three spherical coordinates, temperature regime, salinity and oxygen distribution to mention some of the obvious attributes.

Next, the fish must be able to maintain themselves in their "home". Also, there must be a distinction in time of spawning (which should be rather short). Finally, the net result of an excessive commercial fishery must create a discontinuous distribution pattern. These aspects will be analyzed next and illustrated with some data generated during the JOINT II expeditions in 1976-1977.

Behavior of Anchoveta in an Upwelling Area

CHARACTERISTICS OF AN UPWELLING AREA

Upwelling is a universal feature along the entire Peruvian coast, but it occurs at rather well-defined, restricted areas. Commonly, several large upwelling areas are recognized, such as the San Juan area, the Callao region and off Chimbote, to mention some. But inside each area, there are a number of plume structures. Two placed in the San Juan region are located about 50 km apart. Upwelled water is recognized commonly by its low temperature, 15.5°-16.5°C, relative to the surrounding water masses (Fig. 4). The subsequent events after upwelled water reaches the

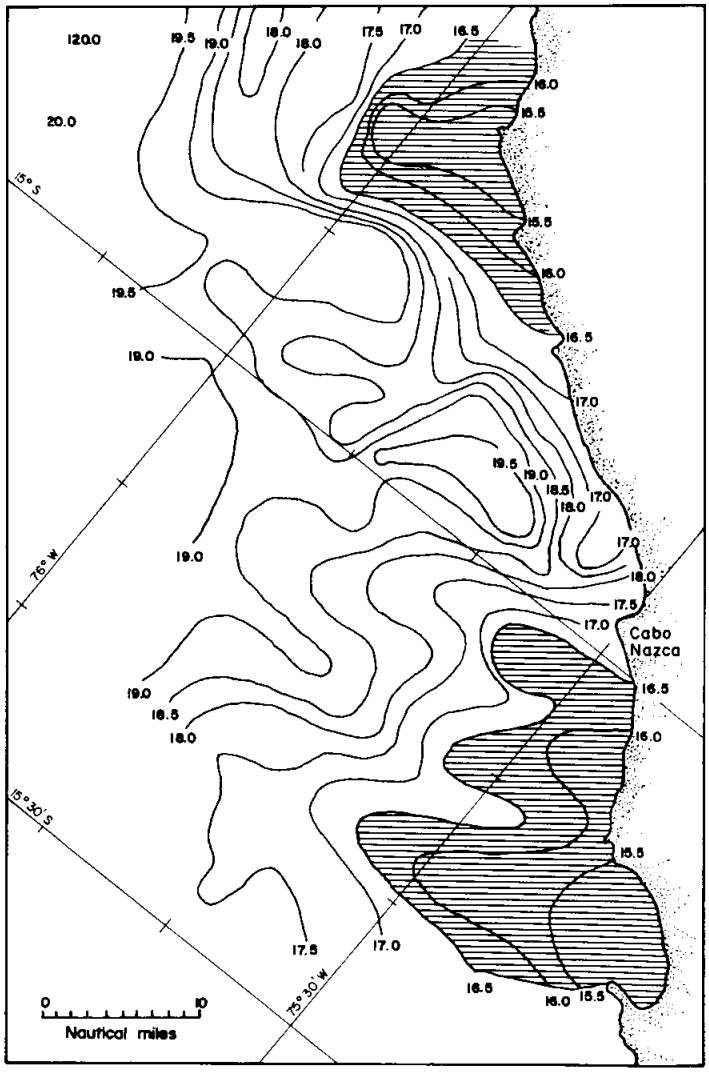

Fig. 4. Surface temperature distribution in the upwelling system around Cabo Nazca, Peru, in March/April 1976 as measured by temperature sensor mounted on an aircraft; shaded areas represent water ≤ 16.5°C (simplified from Stuart et al. 1976).

Fig. 4. Distribución de la temperatura superficial de un sistema de afloramiento, tomada por un sensor de temperaturas acoplado a una avioneta. Areas sombreados representan aguas ≤ 16.5°C (simplificado de Stuart et al. 1976).

surface are difficult to describe in general terms because of the inherent variability. But generally, the surface water is subjected to an equatorial flow along the coast of 11-12 cm/s velocity and an offshore component of 5-6 cm/s. The component vector is therefore veering away from the coast with a velocity of 12 km/day.

As the surface water flows away from the coast, the temperature rises to 18°-19°C, partly due to heating by the sun. Its nitrate and silica contents are consumed by the phytoplankters; wind mixing might deepen the layer and add more nitrate to the system. Thus we can expect the greatest phytoplankton production to be 10-20 km "downstream" from the plume center.

Eventually, the phytoplankters sink down and re-enter the upwelling area since at a depth ranging from 20 to 100 m, there is a counter current in almost opposite direction to the surface flow with velocities ranging from 5 to 10 km/day (Fig. 5).

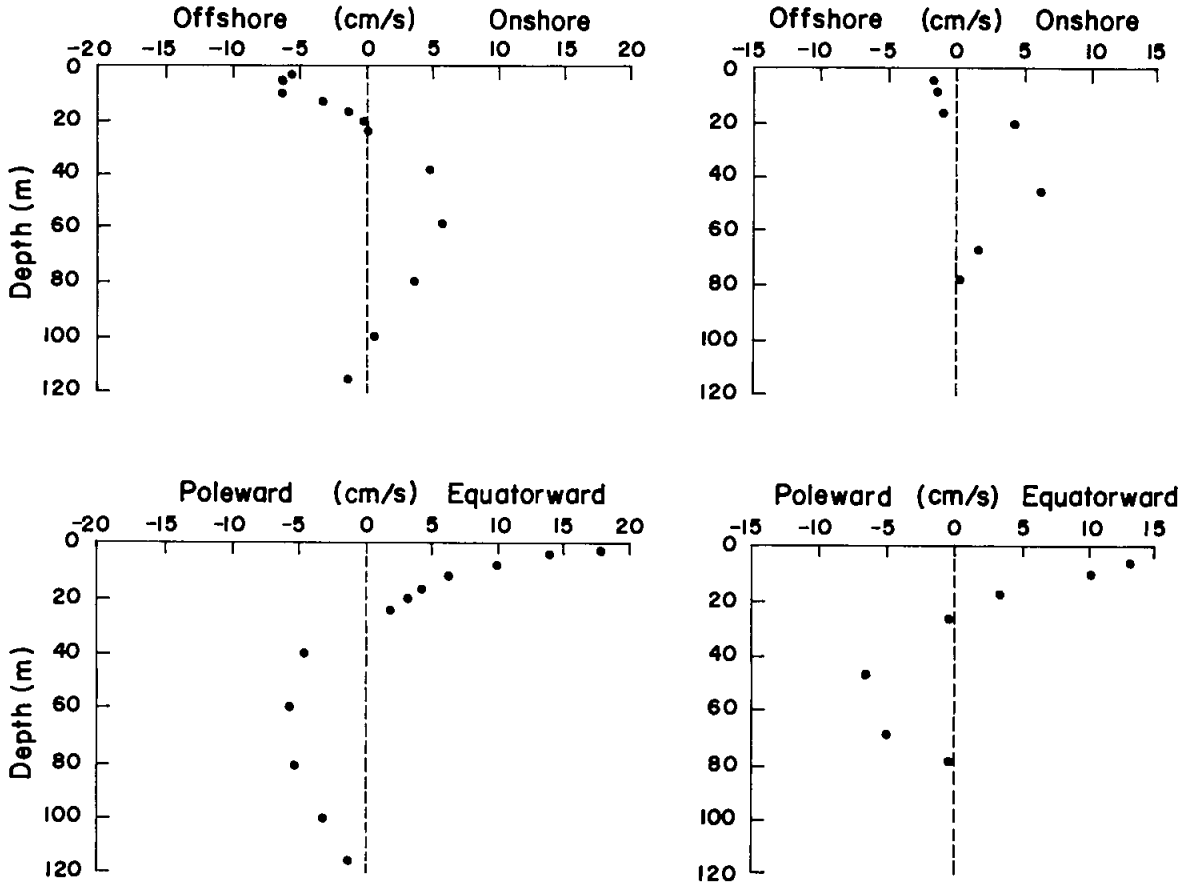

Fig. 5. Onshore/offshore and north/south components of the surface currents at Stations PS/MILA (*left*) and PPS/AFAVE (*right*) at JOINT-II area, 22 March to 10 May 1977 (from Brink et al. 1978).
Fig. 5. Componentes hacia la costa fuera de la costa y norte/sur de las corrientes en la estación PS/MILA (izquierda) y PPS/AFAVE (derecha) en el área de JOINT-II, 22 de Marzo a 10 de Mayo de 1977 (de Brink et al. 1978).

If one were to draw successional cycles, zooplankters would follow the phytoplankter shortly, both in time and space. Ammonia released by the excretion of the zooplankter is quickly re-entered in the production cycle through uptake by phytoplankters.

Clearly then, plume structure is governed by the location and bottom topography, but the wind is the prime mover of the plume upwelling and determines both its strength and duration.

It should be noted that the location of plumes may shift; but with the time scale on which anchoveta operates, the individual events are of lesser importance. Only the integrated picture or mean parameters become the important ones. Hence, it is not only permissible but necessary to define a generalized plume structure and a series of upwelling locations. However, a certain degree of constancy of an environment is required to which the fish can adapt itself and "home"

to. A first requisite is that the fish can maintain themselves in a structure of this type with a minimum of expended energy. Diel behavior seems to be one mechanism whereby a closed trajectory can be established in a changing current system.

ACOUSTIC ASSESSMENT OF NEKTON

Echo mapping of the Peruvian anchoveta and other members of the nekton community began in 1964 with visual inspection of the echograms, according to a density classification based on sharing or blackening of the echograms (Villanueva 1970). A next major step was absolute quantification through analog integration of the signals over a given distance, such as one nautical mile, and over a specified depth interval. A further advance was the introduction of digital integration which permitted a resolution down to 1-m depth intervals and a time interval down to one single transmission. The latter feature proved to be one of the most useful in determining the density of a school by depth intervals.

The basic data acquisition during JOINT II consisted of a Braincon V-fin towed at the side of the ship extended from a yard arm and with a transducer towed about 1 1/2-2 m below the surface. In the case of hull-mounted transducers, the dead surface space is usually about 5 m or more. The echosounder was a SIMRAD EK 120 and signals were either stored on tape or processed in real time onboard with a PDP 11/10 computer with a basic output after 1- or 5-minute integration by 14 continuous depth zones down to 60 m depth. The data expressed in gm^{-3} were stored on discs and could later be recombined by appropriate computer programs to give densities by volume or by surface unit area.

DIEL FEEDING OF THE ANCHOVETA

It has been known for along time that anchoveta possess a pronounced diel feeding (Pauly et al., this vol.) and migration behavior. The commercial purse seine fishery has taken advantage of this behavior pattern by mainly operating after daybreak, when the fish formed the most dense schools and the anchoveta was most easily captured.

Diel behavior in the JOINT-II area was studied by selecting a square on the shelf with sides one nautical mile long in an area with a concentration of fish. Transecting was continued for 18-24 hours to include the time before sunset, the night and daybreak to noon. Total biomass was expressed as g/m^2 surface and output every minute. If the anchoveta were schooling, this would show up as a few adjacent points with high biomass estimates followed by long periods of near-zero values. During a feeding phase, the schools would break apart and form layers where the individual fish would be filtering while cruising along, and adjacent estimates would all be of approximately the same order. This is well illustrated in Fig. 6 showing the contrast between night and day.

Basically, the schools were dissolved at onset of dusk and the anchoveta commenced feeding singly. This continued during the night until daybreak when dense schools formed. They largely persisted during the day except that the schools started to break apart in the afternoon. One direct interpretation is to see the dense school formation at daybreak as a resting phase after extensive feeding during the night. Then during the afternoon, sporadic feeding commences and the dense schools break culminating in a full-fledged feeding during the nighttime.

More important in this connection is the change in depth distribution, which was explored by using night and day values obtained during transects at the shelf area to insure that mainly anchoveta were insonified. The computer output was, in this case, the average density over one nautical mile expressed in gm^{-3} for the selected depth intervals. The vertical bars in Fig. 7 represent the biomass observed in each depth stratum and converted to a percentage basis in order to make all observations directly comparable. The basic pattern is for the greatest density to be close to the surface at night or at least above 20 m depth. At daybreak when the resting schools are forming, the mean density distribution is normally below 20 m. The ecological importance is immediate. As mentioned earlier, the 20 m depth zone forms the boundary line between the offshore equatorward drift in the top layer and onshore poleward subsurface current.

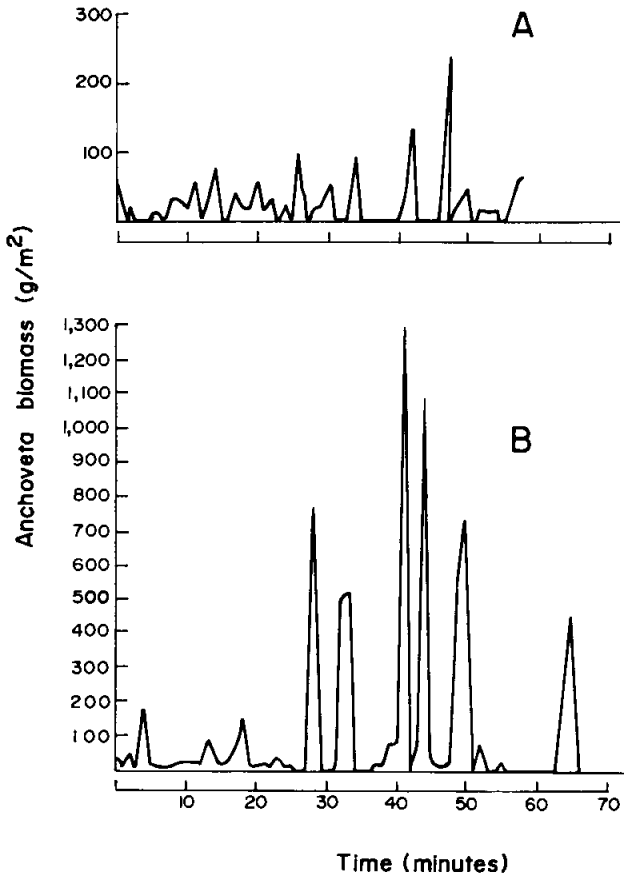

Fig. 6. Distribution of anchoveta biomass in a square transect course off Cabo Nazca. Biomass values outputted at one-minute intervals: A. Prior to daybreak (05h52' - 06h48'), the biomass is evenly distributed along the entire transect. B. After daybreak (07h35' - 08h43'), the biomass is distributed in high density areas.
Fig. 6. Distribución de la biomasa de anchoveta en el recorrido de un transecto cuadrado. Los valores de biomasa se dan en intervalos de un minuto: A. Antes del alba (05h52'-06h48'), la biomasa está igualmente distribuída a lo largo de todo el transecto. B. Despues del alba (07h35'-08h43'), la biomasa está distribuida en áreas de alta densidad.

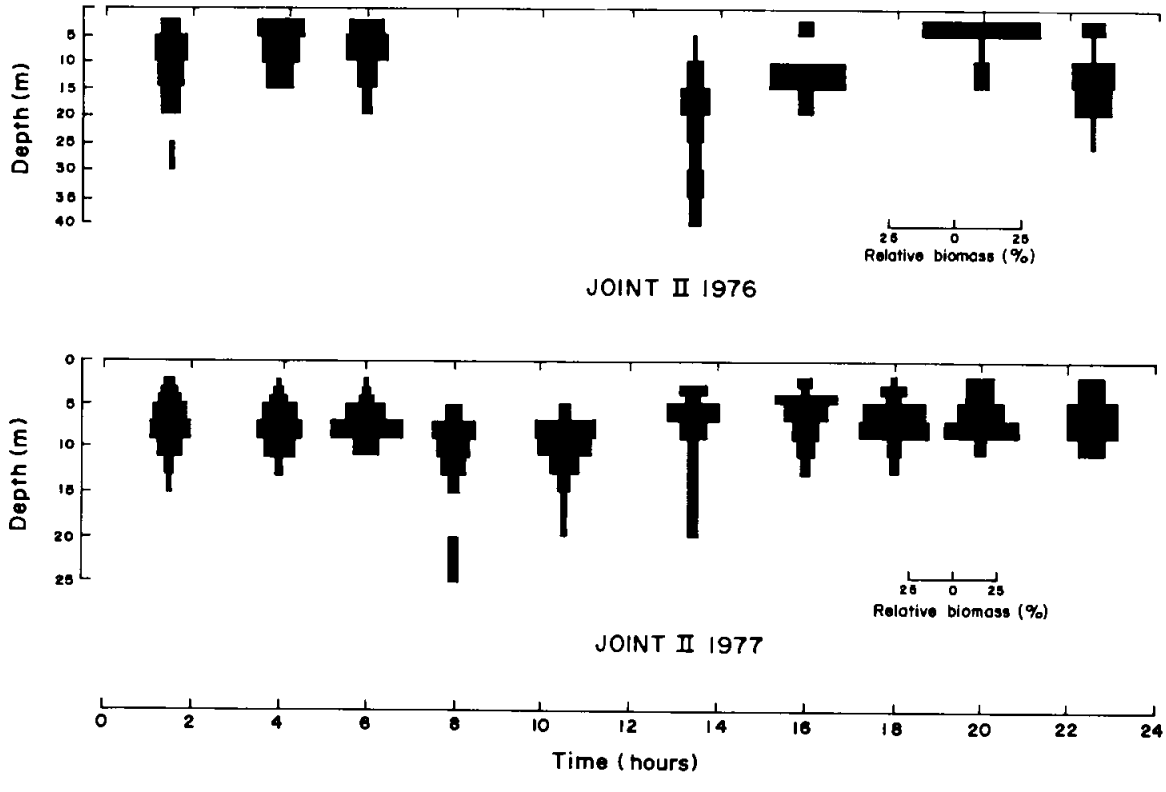

Fig. 7. Depth distribution of Peruvian anchoveta off Cabo Nazca during two 24-hour periods, in March-May 1976 and 1977 (note different vertical and horizontal scales between periods).
Fig. 7. Distribución vertical de la anchoveta peruana frente a Cabo Nazca durante dos períodos de 24 horas, en 1976 y 1977 (nótese las diferentes escalas vertical y horizontal entre períodos).

Since these two component vector velocities are nearly equal in absolute value but in almost opposite directions, the anchoveta can maintain its trajectory with a minimum energy expenditure by alternating its position in the water column.

Some drogue experiments conducted simultaneously show that the drift of a drogue at 10 m was distinctly different from that of a drogue at 35 m. The vertical shearing velocities[a] were:

$$\frac{(\delta u)}{(\delta z)} = .411 \text{ cm/s/m and } \frac{(\delta v)}{(\delta z)} = .329 \text{ cm/s/m}$$

The 1977 season may serve as a contrast. The anchoveta population fell to an all-time low due to the failure of the fish below 11 cm to survive and to grow to mature size in proper time, and secondly, for the spawners to reproduce successfully. Partly, this must be related to the exceptional hydrographical conditions which existed in 1977. The oxygen distribution in this year prevented the fish from descending deeper than 20 m without exceeding a provisional oxygen limit of 2 ml/l. The depth distribution in this year bears this out, with no anchoveta registered below 20 m (Fig. 7). To aggravate the situation, the high surface temperature forced the fish close to shore where upwelling provided temperatures below 18-20°C. The net result was an exceptional expenditure of energy required to maintain a position in the upper 20 m close to shore or basically within the 50 m contour line. The alternative could be to drift away from shore with the Ekman drift and literally become lost at sea. Both alternatives probably were realized and contributed to the low point of the biomass of anchoveta in 1977.

But in general, the normal behavior pattern of the anchoveta will serve to maintain its position in a geographically restricted upwelling system, which clearly is conducive to the development of a "homing" tendency.

Even more conclusive evidence can be derived from changes in distributional pattern of the anchoveta population which has been subjected to the stress of sustained and intensive commercial exploitation.

RECENT CHANGES IN DISTRIBUTION OF THE ANCHOVETA

The general description of the range of anchoveta is one of a continuous distribution from 5°S to 42°S, but within the heaviest distribution from 6°S to 17°S there exist definite and very sharp density gradients. This could be surmised from the location of fish processing facilities which developed largely during an unrestricted fishery.

The earliest map of density gradients of the anchoveta population drawn from quantified integration values are given by Johannesson and Robles (1977), and their data are summarized in Fig. 1, left side. Although the distribution is almost continuous, there are some very distinct and well-defined high density areas. Schematically, this can be illustrated in Fig. 8a where a series of independent or semi-independent populations overlap and produce an apparent continuous distribution. If the effect of fishing is removal of the best adapted and most productive and therefore, most numerous spawners as alluded to in the case of the salmon, the net result of the rapidly diminishing populations will be a discontinuous distribution with isolated cells or pockets of fish, as illustrated in Fig. 8b. This appears to be very much the case as illustrated by the distribution map produced in March/April of 1977 (Fig. 1, right side). But in addition to the very disjointed distribution, the very striking fact is that the locations where fish were found largely corresponds to the places where a processing facility developed in the early days of the fishery and presumably where the supply of fish was best and most consistent.

In addition to the geographical separation, there is also a temporal separation. Historically, there have always been two spawning populations, one consisting of spring spawners, which spawn in September-October and one group of summer spawners in February-March. The strength of the former was usually twice to thrice that of the latter (see Senocak et al., this vol.). They also differed in age composition with the total biomass in September to be dominated by mature fish. The reverse was true for the summer spawners where the immature fish, spawned six months earlier and now with a length of less than 11 cm, dominated the catch.

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[a] u = Eastward, v = Northward components.

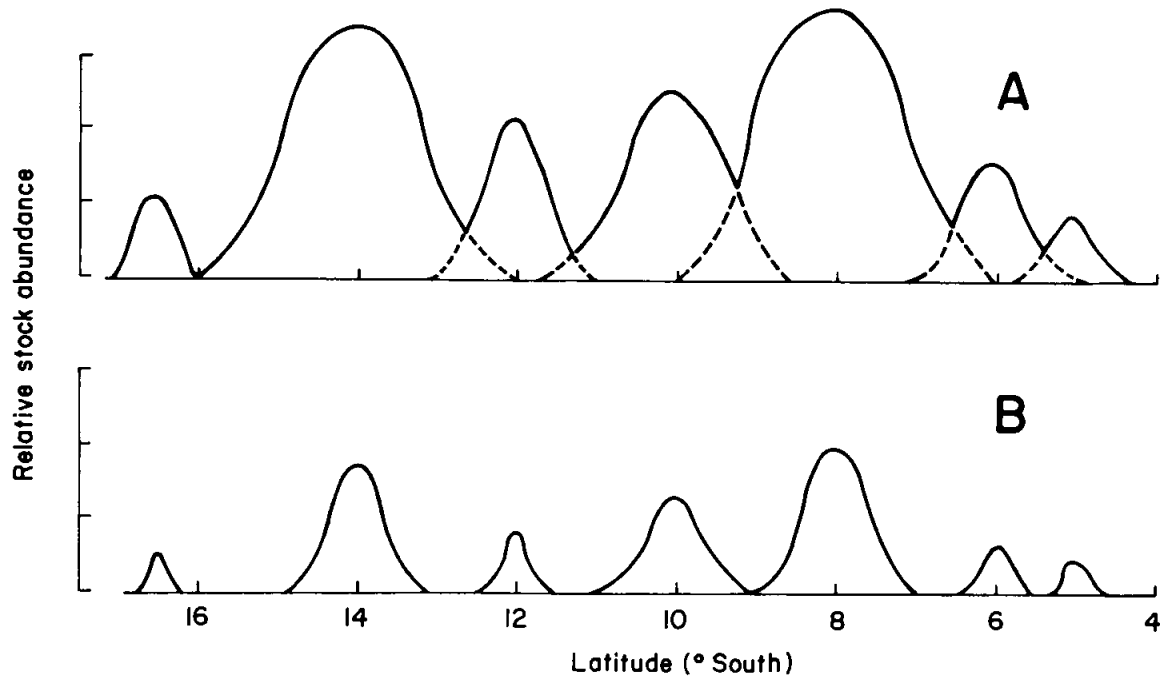

Fig. 8. Schematic representation of the ranges of a series of (A) unexploited (sub)stocks of Peruvian anchoveta, and (B) exploited and stressed (sub)stocks of the same species (see text).
Fig. 8. Representación esquemática de las amplitudes de una serie de (A) (sub) stocks inexplotados de anchoveta peruana y (B) (sub) stocks explotados y fatigados de la misma especie (ver texto).

The mere fact that these differences persist year after year provides the basis which in time will lead to independent groups. One consequence is that the anchoveta basically has one spawning season per year, either in early spring or late summer. In this respect, there has only been an expansion in the time basis. Earlier, the curve of abundance for a group of spawners was taken to reflect differences in survival rate with time. The same argument can be extended to the two principal groups of spawners. The fact that anchoveta can spawn during the entire year, and regularly over an eight-to-nine-month period, does not detract from this argument. There are two time periods when survival is better than the average, and one is decidedly the better one of the two.

If one inquires into the function of the plus and minus deviants, one answer is that they buffer against adversities and perturbation of the environment. The year 1972/73 may be taken as an example when temperatures rose above average for a long time, almost an entire year. As a result, the phenological events of spring spawners were not synchronized and only the summer spawners reproduced successfully (Fig. 9).

Anchoveta and Salmon - a Comparison

An argument has been advanced that the structure of salmon runs and the conduct and effect of harvest on individual salmon "races" have some similarity to and validity for the Peruvian anchoveta populations. But whereas the former exhibits definite spatial and temporal segregation among its various units, in the latter case these boundaries are more vague; areas overlap and events are superimposed.

Ecological efficiency is an attribute which in the evolutionary process demands its price in a closely-knit coupling to an environment. It can only be reached in populations whose environments possess some stability or where the animals have acquired some measure of independence from the environment. Resilience thus becomes a quantity related to the

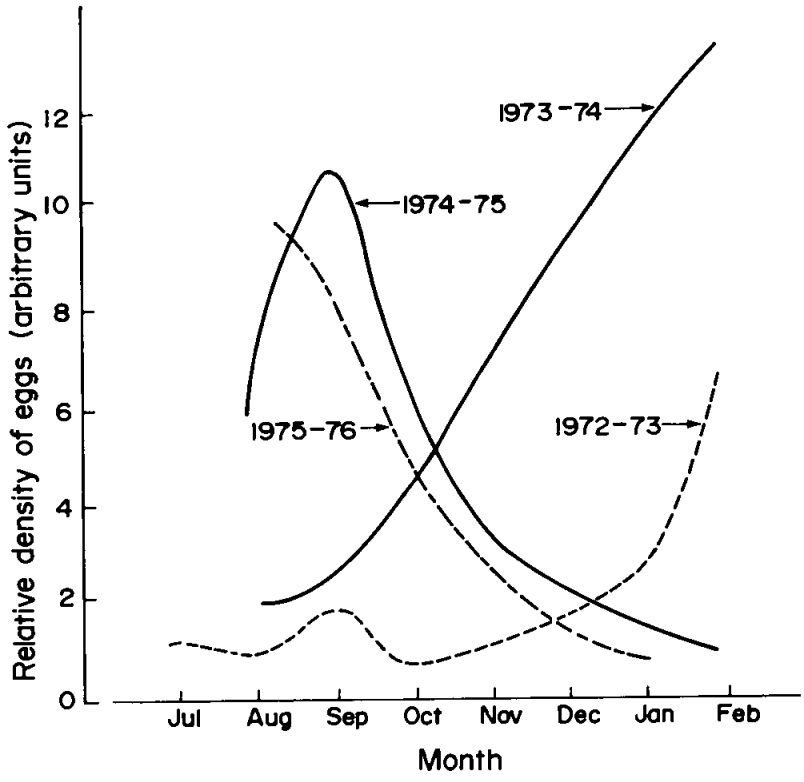

Fig. 9. Alternation between successful spring and summer spawning of Peruvian anchoveta as a result of the temperature anomalies in 1972/1973 (adapted from Valdivia 1978 and Johannesson and Vilchez 1979).

Fig. 9. Alternancia entre desoves exitosos de la anchoveta peruana en la primavera y verano, como resultado de las anomalías de temperatura ocurridos en 1972/1973 (adaptado de Valdivia 1978 y Johannesson y Vilchez 1979).

environmental variability which the animals must overcome in order to successfully reproduce and sustain themselves.

The Peruvian upwelling system is far from stable. The occurrence of El Niño is a common event, although variable in strength and duration (Bohle-Carbonell, this vol.). Research in progress seems to bring out that more profound alterations of the temperature regime and water quality are governed by the deeper undercurrents with both polar and equatorial flow components. Nevertheless, throughout its history during the last 12,000 years, the anchoveta population in Peru has maintained itself.

Some regulatory mechanisms are obvious: separate spring and summer spawners, each group again broken down in many units. The main question is how much interchange there is between these units. Clearly, in the case of the salmon, the evolutionary process has progressed further and the population units have reached a high degree of independence. But even within the various members of the genus *Oncorhynchus* we see different amounts of straying. The extent to which reproduction is successful is usually inversely related to the distance of straying. If a barrier, such as a waterfall is bridged by a fishway, the newly opened territory is quickly occupied and utilized. If a transplantation involves new streams, distance from donor streams becomes a governing factor.

The contention of this paper is that the same principles apply to anchoveta but in a more diffuse form. Thus, the wholesale migration south in 1972 described by Valdivia (1978) did not result in a successful spawning in the new environment (if spawning took place at all). But clearly, some interchange must take place between populations occupying adjacent upwelling plumes and even between temporarily segregated units in the same area. Basically, one must adopt the view that marine populations of fish have not achieved the same degree of adaptation as anadromous species; however, the same structural concepts can be used and the effect of the

fishery remains largely the same. Accordingly then, the decline of the Peruvian stock of anchoveta was accelerated by not only the removal of a large biomass of spawners, but perhaps more, by the removal of the best reproductive units. The doubly stressed population could consequently not withstand the environmental stress imposed in 1972-1973 and 1976-1977, leading, ultimately, to the depressed state of the population today.

An inescapable corollary is that the object of management is not to define a "maximum sustainable yield" or an "optimum sustainable yield", but to prescribe the necessary spawning population. This is by no means a fixed quantity but varies according to the status of the environment and the risk the manager is willing to take. In addition to numbers, the manager must prescribe the characteristics of the fish to be preserved with an emphasis on securing these from the central or most abundant part of the spawning population in each upwelling area.

The future course of fishery science possibly will not be to define management principles but to describe the evolutionary process which enables different components of the nekton to occupy various ecological niches. While the physical environment can be described rather easily through various observable parameters, the independence of nekton units, such as within the Peruvian anchoveta stock, defies the usual approaches. The open question is how the members of a unit recognize an environment essentially which is an imprinting process. In the case of anadromous species, pheromones seem to play a rather important role in local navigation (Nordeng 1971). But the amount of chemical substances is so minute that common analytical tools do not suffice. In most cases, this phenomenon must be studied indirectly by long-term monitoring of both the physical environment and the nekton groups occupying this environment.

Acknowledgements

The Coastal Upwelling Ecosystem Analysis program (CUEA) envisioned and eventually executed a complete study of all energy levels in an upwelling system except for a minor emphasis on nekton. However, through cooperative arrangements with Instituto del Mar del Perú (IMARPE), access was provided to part of the rich material on nekton collected over the years. Credit for use of material from these two sources must be given through the cited papers.

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References

Brandhorst, W., M. Carreño and O. Rojas. 1965. El numero de vertebras de la anchoveta (*Engraulis ringens* Jenyns) y otras especies de la superfamilia Clupeidae en aquas Chilenas. Bol. Cient. Inst. Fom. Pesq. Santiago. (1): 1-9.

Brink, K.H., R.L. Smith and D. Halpern. 1978. A compendium of time series measurements from moored instrumentation during the MAM '77 phase of JOINT II. CUEA Tech. Rep. 45. School of Oceanography, Oregon State University, Corvallis, Oregon 72 p.

Devold, F. 1963. The life history of the Atlanto-Scandian herring. Rapp. P.-v. Reún CIEM 154: 98-108.

DeVries, T.J. 1979. Nekton remains, diatoms, and holocene upwelling off Peru. Dept. of Oceanography, University of Oregon. MS dissertation.

DeVries, T.J. and W.G. Pearcy. 1982. Fish debris in sediments of the upwelling zone off Central Peru: a late quartenary record. Deep-Sea Res. 28(IA): 87-109.

Johannesson, K.A. and A.N. Robles. 1977. Echo surveys of Peruvian anchoveta . Rapp. P.-v. Reún. CIEM 170: 237-244.

Johannesson, K. and R. Vilchez. 1979. Application and some results of echo-integration methods in monitoring Peruvian anchovy resources. USA/USSR Meeting on Acoustics, Massachusetts Institute of Technology, June 1979.

Jordan, R. 1963. Un análisis del número de vertebras de la anchoveta peruana (*Engraulis ringens* J.). Bol. Inst. Mar. Perú-Callao 1(2): 25-43.

Murphy, G.I. 1973. Clupeoid fishes under exploitation with special reference to the Peruvian anchovy. Tech. Rep. 30, University of Hawaii, Hawaii Institute of Marine Biology. 73 p.

Nordeng, H. 1971. Is the local orientation of anadromous fishes determined by pheromones? Nature 233(5319): 411-413.

Paulik, G.J., A.S. Hourston and P.A. Larkin. 1967. Exploitation of multiple stocks by a common fishery. J. Fish. Res. Board Can. 24: 2527-2537.

Paulik, G. 1970. The anchoveta fishery of Peru. Quant. Sci. Pap. 13. Center for Quant. Science in Forestry, Fisheries and Wildlife. University of Washington, Seattle, Washington 79 p.

Pauly, D. and M. Soriano. 1987. Monthly spawning stock and egg production of Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1984, p. 167-178. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D. and I. Tsukayama, editors. 1987a. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D. and I. Tsukayama. 1987b. On the implementation of management-oriented fishery research: the case of the Peruvian anchoveta, p. 1-13. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Quinn, W.H., D.O. Zopf, K.S. Short and R.T.W. Kuo Yang. 1978. Historical trends and statistics of the southern oscillation, El Niño, and Indonesian droughts. Fish. Bull. 76(3): 663-678.

Rojas de Mendiola, B. 1971. Some observations on the feeding of the Peruvian anchovy *(Engraulis ringens)* in two regions of the Peruvian coast, p. 417-440. *In* J. Costlow (ed.) Fertility of the sea. Vol. 2. Gordon and Breach Science Publ., New York.

Saetersdal, G., I. Tsukayama y B. Alegre. 1965. Fluctuaciones en la abundancia aparente del stock de anchoveta en 1959-1962. Inst. del Mar del Perú Bol. I(2): 33-104.

Smith, R.L. 1978. Poleward propagating perturbations in currents and sea levels along the Peru Coast. J. Geophys. Res. 83(C12): 6083-6092.

Stuart, D.W., M.A. Spetseries and M.M. Nanney. 1976. Meteorological data - JOINT II: March, April, May 1976. CUEA data Rep. 34. Dept. of Meteorology, Florida State University, Tallahassee, Florida. 71 p.

Thompson, W.F. 1951. An outline for salmon research in Alaska. Fish. Res. Inst., Univ. of Washington. Circ. No. 18. 49 p.

Thompson, W.F. 1959. a approach to population dynamics of the Pacific red salmon. Trans. Am. Fish. Soc. 88: 206-209.

Tsukayama. I. 1966. El número de branquiespinas como caracter diferencial de sub-poblaciones de anchoveta (*Engraulis ringens* J.) en las costas del Perú. Primer Seminario Latino-Americano Sobre el Océano Pacífico Oriental. Univ. San Marcos, Lima, Perú.

Valdivia, J.E. 1978. The anchoveta and El Niño. Rapp. P.-v. Reún. CIEM 173: 196-202.

Villanueva, R. 1970. The Peruvian Eureka programme. Food and Agriculture Organization of the United Nations. Technical Conference on Fish Finding, Purse Seining and Aimed Trawling. FII:FF/70/5. 12 p.

Walsh, J.J. 1978. The biological consequences of interactions of the climatic, El Niño, and event scales of variability in the eastern tropical Pacific. Rapp. P.-v. Réun. CIEM 173: 182-192.

Mechanisms for Density-Dependent Growth in Peruvian Anchoveta: Alternatives to Impact on the Regional-Scale Food Supply

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Abstract

Two alternate classes of mechanisms that could account for evidence of density-dependent growth are introduced: (i) effects of potential linkages of school size with population size, and (ii) effects of size-dependent predation. These may lead to different interpretations with respect to resilience to exploitation, carrying capacity of the habitat, etc., from those implied by the more commonly cited class of mechanisms which involve impact of the population on its food supply.

Resumen

Dos mecanismos alternos que evidenciarían la denso-dependencia del crecimiento son introducidos: (i) efectos de relaciones potenciales del tamaño del cardumen con el tamaño de la población y (ii) efectos de la dependencia del tamaño con la predación. Estos pueden conducir a diferentes interpretaciones con respecto a la repercusión para la explotación, capacidad de carga del habitat, etc., de aquellas implicadas por las clases de mecanismos más comunmente citadas que abarcan el impacto de la población sobre su suministro de alimento.

Introduction

An apparent dependence of growth on population density is a common finding in studies of the dynamics of natural fish populations (e.g., Beverton and Holt 1957; Ware 1980). The mechanism commonly proposed involves increased competition for available food at high population density.

In the case of small coastal pelagic fish such as anchovies and sardines inhabiting coastal upwelling systems, the extent to which this type of mechanism might really be acting is not clear. For example, Lasker (1970) estimated that at peak population size, the Pacific sardine would have consumed more than the entire secondary production in California's current ecosystems. Nevertheless, no growth increase was noted among adults as the population declined (Murphy 1973). In the similar eastern ocean boundary upwelling ecosystem off Northwest Africa, Mathisen et al. (1978) compared food consumption to food production. Results suggested that food does not directly control the size of adult or recruited fish populations. Mathisen et al. cited Gulland (1971), Murphy (1973) and Steele (1974) as having questioned food limitation as a

control for adult fish "since in those cases where fish have been reduced to a low level through fishing, the structure and size of the next lower trophic level has not changed drastically". In the case of the Peru Current upwelling system, Lasker (1989) estimates that the anchoveta population, at a pre-collapse biomass level of 20 million t, would consume about one-fourth of the primary production of the ecosystem (note that the value "40", rather than "4", in Lasker's published paper is apparently a typographical error). Since anchoveta obviously will consume some quantity of secondary production, the question as to whether it may at times be limited by its food supply is unanswered.

Indeed, Palomares et al. (1987) found a significant correlation between growth performance and population biomass of Peruvian anchoveta over the period 1954-1982. They discussed three different effects which might have increased growth rates as the population declined: (1) decreased competition for available food due to fewer competing individuals, (2) a relative increase in abundance of more nutritious zooplankton, due to lessened competition for food resources and lessened predation by anchoveta, *vis à vis* less nutritious phytoplankton, and (3) a corresponding increased proportion of more efficient particulate feeding on zooplankton relative to less efficient filter feeding on phytoplankton. All three effects fall under the class of mechanisms implying a substantial impact of feeding activity on the amount or composition of the regional-scale food supply. Since natural mortality is generally size-dependent, and therefore growth-dependent, such a directly-linked impact of the population on its own food supply would seem to constitute a powerful compensatory mechanism with respect to effects of fisheries exploitation.

The purpose of this chapter is to point out that plausible alternative mechanisms exist which do not necessarily imply a substantial impact on the large-scale food supply. Two classes of mechanisms will be addressed: (1) effects of school size, and (2) effects of size-dependent predation. These may lead to different interpretations of evidence of density-dependent growth with respect to resilience of the population to exploitation, potential carrying capacity of habitat, etc.

Effects of School Size

Consequences of Fish School Geometry

As fish schools vary in diameter, they may also vary correspondingly in vertical thickness, i.e., large schools may be thicker in vertical dimension than small schools. To the extent that school thickness may vary in rough proportion to school diameter, the areal aspects of the school geometry, such as the surface area encompassing the volume occupied by the school or the cross-sectional area swept by school movement, will vary as the second power of δ (where δ = school diameter or other appropriate characteristic length scale). However, the volume of the school, and therefore, the number of individual fish contained, will vary as the third power of δ. Thus,

$$\frac{\text{school surface area}}{\text{school volume}} \propto \frac{\text{cross-sectional area swept}}{\text{no. of individuals in school}} \propto \frac{1}{\delta} \qquad \text{...1)}$$

The consequence of expression (1) is that as δ (i.e., school size) increases, the average supply per individual within the school of food and other substances (e.g., replenished dissolved oxygen where concentration may have been depleted by respiration) that must enter the school interior through the cross-sectional area swept by a moving school (or diffused through the outer surface area of a stationary school) decreases in proportion to δ^{-1}. Thus, a fish in a larger school (of size ~ δ_1) must, in comparison to a fish in a smaller school (of size ~ δ_2), either accept an average food ration which is smaller by the factor δ_2/δ_1 (and to the extent that a school may be capable of depleting the oxygen within the water volume occupied, the additional detriment of a lowered uptake rate of oxygen) or carry the metabolic costs of swimming faster by a factor of

δ_1/δ_2. Kils (1979) discussed this effect as a factor limiting the school size of the Antarctic krill *Euphausia superba*.

Of course, it is possible that large schools are strictly limited in the vertical dimension by external constraints (water column structure, total water depth in shallow areas, vertical distribution of food organisms, etc.). In the case of a flattened school shape of constant vertical dimension, the volume and the surface area of a school vary nearly in direct proportion. Even so, the ratio of cross sectional area swept to the volume of a moving school would continue to vary as δ^{-1} so long as both horizontal dimensions tend to increase or decrease together (i.e., excluding the case where the length of the school axis parallel to its motion remains constant while school width, normal to the direction of motion, increases.) Actually, Mais (1974) finds seasonal, diurnal, and other (e.g., relation to topography) tendencies for school sizes and for school thicknesses to vary somewhat in phase, such that thicknesses of larger schools of northern anchovy off California tend to be greater than those of smaller schools. However, one finds little information in the literature on school thickness in relation to school diameter; this may indicate a lack of appreciation of the potential importance of school surface to volume ratios with respect to nutrition and metabolism of schooling fish.

Should Average School Size Increase with Population Size?

Pitcher (1986) cites potential advantages of schooling behavior in fish including hydrodynamic advantages, countering predation, discovery of food patches, and opportunities for group learning. In any case, it seems clear that for species with pronounced schooling behavior, individuals or small groups of fish must tend to increase their probability of survival and successful propagation of their genetic material by joining with other conspecific groups of similar body size that might be encountered. Thus, in the absence of processes tending to fragment the school, school size would tend to increase with time. The expected rate of increase depends on the rate of encounter with other individuals or schools; that is, all other factors being equal, it should be roughly proportional to population density, i.e.,

$$\text{number of individuals joining a given school per unit time} \propto P^c \qquad ...2)$$

where P is the size of the population, and the exponent c ($0<c\leq1$) represents MacCall's (1980) suggestion for incorporation of variable habitat size in representing a density-dependent mechanism (i.e., $c = 0$ implies that habitat size varies in proportion to population size and thus, that population density does not vary with population size; $c = 1$ implies that there is no habitat size variation and thus, that population density varies directly with population size; $0<c<1$ implies the less-than-proportional increase of habitat size with population size which, for coastal pelagic fish populations, appears to fit observations).

Obviously, processes tending to fragment schools become substantial at some point or the entire population would tend to aggregate into a few very large schools, whereas large numbers of disjoint schools is the observed situation. This implies that, while the tendency for aggregation must dominate when the school size is small, processes of fragmentation must become increasingly important as school size increases, i.e.,

$$\text{number of individuals leaving a given school per unit time} = F(N) \qquad ...3)$$

where F(N) is some increasing function of N (N = number of individuals in a school), at least over an observed range of school sizes. Combining expressions (2) and (3) yields

$$\frac{dN}{dt} = kP^c - F(N) \qquad ...4)$$

where k is the constant of proportionality implied by expression (2). Using a formulation equivalent to equation (4), Anderson (1981) added the assumptions that the number leaving was linearly proportional to N (i.e., F(N) = K N, where K is a constant) and that the number joining (kP^c) was constant with time. He added stochastic terms to the entrance and exit rates and to the relationship of N to δ. He thereby constructed a model that reproduced the frequency distribution of pelagic fish school diameters off Southern California reported by Smith (1970).

The question of the form of F(N) is an important one. There must be some ultimate limiting point at which the school size becomes too large for its members to meet their metabolic requirements. Upon growing to that point, it would seem that the school must become unstable and break apart. However, Smith (1981) reports a substantial range of school sizes of coastal pelagic fish rather than the tight modal distribution that would suggest that school size is controlled only by the ultimate metabolic limit. Apparently, other processes of fragmentation act over a range of sizes well below that point.

The hypothesis that individuals altruistically leave the school when they perceive that it is becoming too large for peak efficiency appears to be untenable. A principle of behavioral ecology states that animals do not sacrifice their own fitness for the good of their group (e.g., Grafen 1984). Various models (Sibly 1983; Pulliam and Caraco 1984; Clark and Mangel 1984) indicate that the optimum group size is unstable and that group sizes in natural systems are considerably larger than optimal size. This is because individuals do better in a group (even an oversized group), than on their own. Pitcher (1986) draws the analogy to an overcapitalized fishery in which individuals will not withdraw in order to increase the profit of those remaining in the fishery as long as they themselves have not reached the point of zero profit. The effect of natural selection is to ensure that individual fish within a school maximize the probability of successfully propagating their own genetic material relative to that of other individuals in the school. Natural selection would thus act to obliterate this type of altruistic behavior.

Having rejected the hypothesis that altruistic behavior by individuals provides the mechanism for removing fish from a school, it is difficult to envision behavioral responses that would induce other individuals to exit the school while allowing the initiators to stay. The remaining possibilities include stochastic effects such as amplified random motions within a school that might lead to polarized movements in different directions by different segments of a school such that fish in between must relinquish their attraction to one of the segments to stay with the other. The two segments could thereby lose contact, thus splitting the school into two smaller schools. A related effect might occur when two separate food patches are encountered at two sides of the moving school front. Feeding behavior would attract school members to one or the other of the food patches, leading to a similar loss of contact between school segments (Paul E. Smith, pers. comm.). Also, it is possible that predator attack could fragment a school, although Pitcher (1986) emphasizes that the observed tendency under attack is for increased school cohesiveness.

In these cases, the average number of fish leaving a school per unit time should, on average, be proportional to the total number in the school at the time a fragmentation occurs; i.e., F(N) = K N (where K is a constant of proportionality), as assumed by Anderson (1981). With this substitution, the equilibrium solution to equation (4) is $kP^c = K N$, or

$$\text{equilibrium school size} \equiv \tilde{N} = \left(\frac{k}{K}\right) P^c \qquad \text{...5)}$$

Equation (5) predicts that average school size will increase with population size provided $c \neq 0$ (i.e., provided population density increases with population size.) In fact, even if k and K are not constants, the two premises: (i) that the rate of entry into a school increases with population size, and (ii) that the rate of leaving the school increases with school size, must lead to an equilibrium that shifts to larger school sizes as population size increases. Of course, the actual distribution of school sizes might reflect large, possibly highly nonsymmetrical, stochastic variability about such an equilibrium.

Mais (1974) found that the discrete daytime schools of northern anchovies off California tended to break up into scattering layers at night. This is in accord with the common pattern for clupeoids (Blaxter and Hunter 1982). This particular type of shift in school size and character does not necessarily imply altruism by individuals, but merely an alteration in attraction and

cohesion due to changes in visual acuity with the drastic day-night change in light. Different values of k and F(N) in equation (4) resulting from the changed attractive and cohesive properties would lead to two different effective equilibrium school sizes depending on day or night conditions. Mais also found that the distribution of school sizes is somewhat dependent on season. Seasonal changes in behavior, food patch size spectra, etc. could result to variations in attraction to the school (i.e., in k) or in cohesiveness (i.e., in F(N)) leading to seasonal variation in $\tilde{N}$. He also noted extremely large dense schools forming along steep bottom gradients of submarine canyons or escarpments. In this case, the topographic features could in themselves attract fish (i.e., act to effectively increase k on a very local scale) and provide points of orientation which could counteract the tendency for school fragmentation as a result of random motions of polarized school segments (thereby decreasing F(N)). The result would be a corresponding local increase in $\tilde{N}$. In all of these cases, equation (4) could separately apply to each diurnal, seasonal, or local situation, with the net integrated result that average school size in the habitat would increase with population size.

Applicability to the Anchoveta

Jordan (1971) notes that anchoveta form large, dense schools during the daylight hours which break up at night into smaller feeding schools. This may be a simplification of a more complex situation similar to that described by Mais (1974) for the northern anchovy. However, it will be useful to discuss the problem on this basis. In that case, the considerations presented above could act on both scales: (i) in the formation of the large daytime schools from a background "population" of feeding schools, and (ii) in the determination of the size distribution of nighttime feeding schools from the background population of individuals. In both cases, the effective value of P in equation (4) could depend on the total population size and the considerations presented above could thereby hold.

In the case of food ration, the nighttime case seems to be the pertinent situation to consider. In the smaller "feeding schools", a proportional variation of vertical dimension with horizontal dimension is most likely. In a tank experiment wherein relatively large food particles induced the "particulate" (i.e., "biting") feeding response, Leong and O'Connell (1969) found that a 64-fish school of northern anchovies received substantially less ration per unit time at a given particle density than did schools of 16 fish and less. J.R. Hunter (pers. comm.) has observed that anchovies in smaller schools tend to be less polarized in their behavior and more apt to make excursions from the main school trajectory in order to take particles lying outside of the school's main path; in larger schools, the individuals seem more controlled by cohesive behavior and therefore, apt to get less ration per individual.

In the case of oxygen supply, the large densely-packed daytime resting schools may constitute a situation where effects on oxygen uptake affect the ability to metabolize, and thereby utilize for growth, food taken during the feeding period (Pauly 1981). This writer is aware of no measurements of oxygen depletion taken at sea within a school of clupeoids. However, McFarland and Moss (1967) measured oxygen depletion within schools of striped mullet (*Mugil cephalus*). They found a reduction of dissolved oxygen within all schools measured. The magnitude of the reduction correlated with school size, ranging up to 29% (in a school of size δ = 150 m). Actual values of the reduction were in the range of 0.12-0.40 mg L^{-1} for "small" (δ = 4-9 m) schools, 0.50-0.80 mg L^{-1} for "medium" (δ = 18-30 m) schools, and 0.70-2.10 mg L^{-1} for "large" (δ = 75-300 m) schools. Typical separation between fish within daytime anchoveta schools is of the order of one fish length (Jordan 1971) and so comparable reductions in dissolved oxygen concentration seem possible for large anchoveta schools. Brett (1979), in experiments with different fish species, found that a drop of dissolved oxygen of one mg L^{-1} causes a 30% reduction in growth rate.

Effect of Size-Dependent Predation

Small coastal pelagic fish such as anchovies attract a varied community of natural predators including sea birds, marine mammals and predatory fish. These predators tend to live longer than

their smaller prey, and thus their population responses would tend to lag variations in their food supply. In many systems the predators have access to alternative prey. Switching of predation pressure to these alternate food resources is one likely response to population decline of a major prey species. But, because of the enormous size of the Peruvian anchoveta population prior to the 1971/72 collapse , and its corresponding dominance within the current Peru ecosystem, the opportunities for switching to alternative prey during the decline of the anchoveta might have been more limited than in more diversely populated ecosystems. Thus, predators without an option of migration to other feeding grounds, e.g., sea birds, marine mammals, etc., with strong local affinities, may have to attempt to derive continued sustenance by extracting an increased share of a declining food base.

On the other hand, predator populations that habitually migrate to exploit spatially separate food bases may not have to experience population declines due to decline in one of its major food bases. For example, Muck and Sanchez (1987) consider mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus murphyi*) the most important predators of anchoveta throughout the entire era of high anchoveta biomass and the more recent era of lowered biomass. These fish exploit both the nearshore habitat of the anchoveta and the habitat further offshore. They are opportunistic feeders, shifting to zooplankton and euphasids where anchoveta are less available. In fact, Muck and Sanchez (1987) assume a constant biomass of mackerel and horse mackerel over the entire period of high anchoveta biomass and recent decline, and thereby infer a relative increase in specific predation rate in the recent period.

These considerations suggest a substantial increase in natural predation pressure on the anchoveta, per unit anchoveta biomass, since the decline. If, as suggested in the previous section, school size has also declined, this could further increase predation mortality (if one accepts the argument of Clark (1974)).

Predation mortality is thought to be size-dependent in both larval (Hunter 1971; Folkvord and Hunter 1986; Miller et al. 1988) and juvenile (Parker 1971; Healy 1982; Hargreaves and LeBrasseur 1986) fish. Thus, animals which grow quickly through the various vulnerable stages increase their chances of successful recruitment. Any larva or juvenile which by chance gets access to a better ration or other favorable growth condition thereby acquires an incrementally increased probability of avoiding predation. This effect cascades as the fish grow through the multitudinous series of size increments between hatching and recruitment, with the net result that slower-growing individuals make up a reduced portion of the survivorship as age increases. The mode of the distribution of size at age is shifted toward larger sizes (Fig. 1). Thus, the apparent growth rate computed from samples of survivors would be larger than the true growth rate, merely because of the biased mortality.

For example, Parker (1971) experimented on replicate populations of juvenile salmon in eight separate aquaria each having an identical, continually replenished food density. Thus, the true growth rates should have been identical. In half of the aquaria, three larger salmon were introduced as predators; the other half were kept predation-free as controls. After allowing time for the populations affected by predation to be substantially reduced, all the populations were measured. An increased growth rate of 0.3-0.5% per day was measured in the populations affected by predation, due entirely to the bias caused by size-dependent predation.

If, as suggested earlier, the relative predation pressure was indeed increased during the population decline of the anchoveta, this bias toward larger size at age and corresponding larger apparent growth rate would have been amplified. In such case, there is no need for alteration of actual growth rates to have occurred in order to produce the evidence of density-dependent growth in anchoveta reported by Palomares et al. (1987).

Discussion

Three classes of hypothetical mechanisms for density-dependent growth have been put forth for consideration:

1. Impact of the population variations on the ambient food supply,
2. Effects of linkages of school size with population size,
3. Effects of amplified size-dependent predation during population decline.

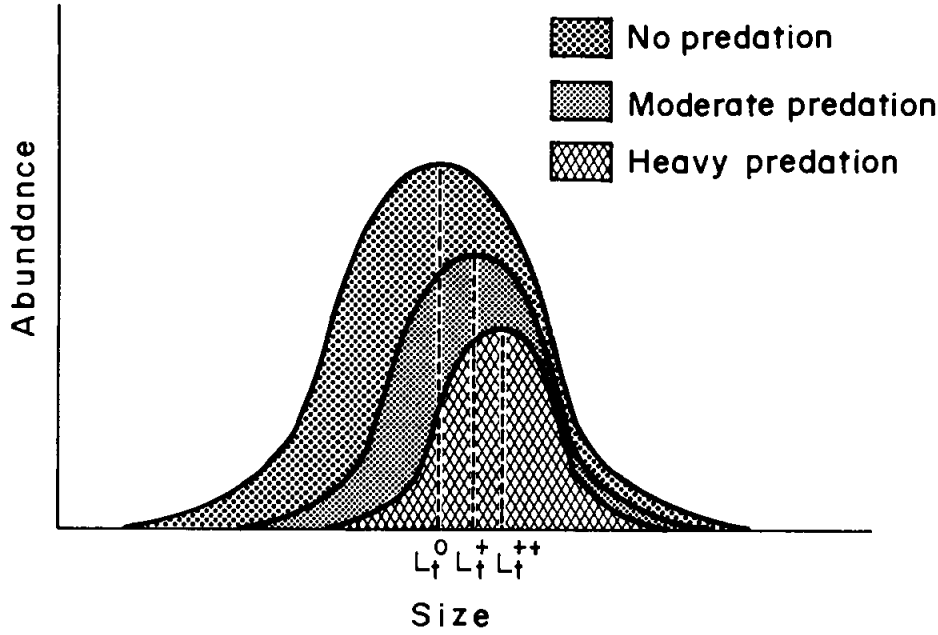

Fig. 1. Illustration of the apparent shift to larger size at age due to size-dependent predation. Where, if there had been no mortality due to predation the observed mean size at age "t" may have been L_t^o, at a moderate level of predation it would be L_t^+. If predation mortality is increased, the abundance at age is lowered further, the distribution is shifted toward larger sizes and the observed size at age would be L_t^{++}. The result is: $L_t^o < L_t^+ < L_t^{++}$.

Fig. 1. Ilustración del cambio aparente a tamaños mayores en una edad debido a la predación dependiente tamaño. Donde, si no ha habido mortalidad debido a predación el tamaño promedio observado a una edad "t" puede haber sido L_t^o, a un nivel moderado de predación este sería L_t^+. Si la predación es incrementada, la abundancia a una edad es reducida además, la distribución es cambiada hacia mayores tamaños y el tamaño observado a esa edad sería L_t^{++}. El resultado es: $L_t^o < L_t^+ < L_t^{++}$.

The first class is the one often considered. It has the comforting implication that, since the population would appear to be effectively eating up its food supply at high biomass, there must be substantial surplus production and associated compensatory resilience to exploitation. The second class of mechanisms also has compensatory implications, but does not imply, as does the first, that the population at high biomass may be nearing the limit of the carrying-capacity of its habitat. The third class of hypothetical mechanisms is not comforting at all, implying nothing but increased predation mortality during a population decline, i.e., a depensatory density-dependent process rather than a compensatory one.

In addressing the potential effect of school size, the relationship of vertical thickness to horizontal scale is a crucial aspect. To the extent that vertical and horizontal aspects may be functionally linked, important consequences of school size to nutrition, growth and metabolism are indicated. In fact, a general tendency toward vertically-flattened school shapes (Blaxter and Hunter 1982) may constitute an adaptation to avoid some of these consequences. Information on this functional linkage is surprisingly absent in the literature, although it would seem not difficult to acquire.

If there is a "moral" to this contribution, it illustrates the need for an "integrated ecosystem" view of marine resource population dynamics. We have seen the possibilities of three different interpretations of the same evidence, each with crucial, but highly differing, implications to stock management and preservation. To a fisheries oceanographer, the situation feels familiar. It is not very different from the dilemma faced in attempts to empirically sort out marine biological-environmental linkage mechanisms when one finds, in the typical case, that the available time series relating to various causal mechanisms are all highly intercorrelated and autocorrelated (e.g., Bakun 1987; Mendelssohn and Mendo 1987). The result is that available information is simply too limited to empirically differentiate among the possibilities.

How can we expect to make progress in sorting out the factors controlling marine resource population variability? Clearly, we need innovative approaches. And we need to recognize,

integrate and utilize information on all the various scales, both spatial and temporal, that can be accessed. For example, this contribution indicates that in addressing issues of population ecology, it is important to consider processes occurring on the scale of the school (for that matter on perhaps two school scales, both of the nighttime "feeding" school and of the daytime "resting" school), as well as on the population habitat scale. To be blunt, fisheries science needs to expand beyond the "giant guppy tank" concept of an ecosystem, and relinquish the conventional "one-spatial/temporal aggregate-data-point-per-year" approach to variability, so as to be capable of utilizing all the information in the rich patterns of variation within years, and both within and among regions (Bakun, in press). The cooperative assembly and integrative analysis of various types of data reported in this volume and in the earlier companion volume (Pauly and Tsukayama 1987) can perhaps serve as a model in this direction, both in the attempt to address variability of higher than annual frequency, despite difficulties caused by interferences related to seasonal tuning of various processes, and in its making readily available the basic data for use by anyone with an innovative idea. If the concept were to be emulated in other regional systems, the comparative method of science (Mayr 1982) might constitute a potent tool for increasing the power of empirical analysis (Bakun 1985).

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References

Anderson, J.R. 1981. A stochastic model for the size of fish schools. U.S. Fish. Bull. 79: 315-323.

Bakun, A. 1985. Comparative studies and the recruitment problem: Searching for generalizations. CalCOFI Rep. 26: 30-40.

Bakun, A. 1987. Monthly variability in the ocean habitat of Peru as deduced from maritime observations, 1953-1984, p. 46-74. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bakun, A. Recruitment and its relationship to environment: accessible pathways to greater insight. *In* R. Jordan (ed.) Simposio Internacional Sobre Recursos Vivos y Pesquerías en el Pacifico Sudeste. Comisión Permanente de Pacifico Sur, Bogotá, Colombia. (In press)

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II. Vol. 19. 533 p.

Blaxter, J.H.S. and J.R. Hunter. 1982. The biology of the clupeid fishes. Adv. Mar. Biol. 20: 1-223.

Brett, J.R. 1979. Environmental factors and growth, p. 599-677. *In* W.S. Hoar, D.J. Randall, and J.R. Brett (eds.) Fish physiology. Vol. VIII. Bioenergetics and growth. Academic Press, New York.

Clark, C.W. 1974. Possible effects of schooling on the dynamics of exploited fish populations. J. Cons. CIEM 36: 7-14.

Clark, C.W. and M. Mangel. 1984. Foraging and flocking strategies: information in an uncertain environment. Am. Nat. 123: 626-641.

Folkvord, A. and J.R. Hunter. 1986. Size-specific vulnerability of northern anchovy (*Engraulis mordax*) larvae to predation by fishes. U.S. Fish. Bull. 84: 859-869.

Grafen, A. 1984. Natural selection, kin selection and group selection, p. 62-84. *In* J.R. Krebs and N.B. Davies (eds.) Behavioral ecology. Second edition, Blackwell, Oxford.

Gulland, J.A. 1971. Ecological aspects of fishery research. Adv. Ecol. Res. 7: 115-176.

Hargreaves, N.B. and R.J. LeBrasseur. 1986. Size-selectivity of coho (*Oncorhynchus kisutch*) preying on juvenile chum salmon (*O. keta*). Can. J. Fish. Aquat. Sci. 43: 581-586.

Healy, M. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. Can. J. Fish. Aquat. Sci. 39: 952-957.

Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae, p. 33-79. *In* R. Lasker (ed.) Marine fish larvae. Washington Sea Grant Program, University of Washington Press, Seattle.

Jordan, R. 1971. Distribution of anchoveta (*Engraulis ringens* J.) in relation to the environment. Inv. Pesq. 355(1): 113-126.

Kils, U. 1979. Performance of Antarctic krill *Euphausia superba*, at different levels of oxygen saturation. Meeresforsch. 27(1): 35-47.

Lasker, R. 1970. Utilization of zooplankton energy by a Pacific sardine population in the California current, p. 265-284. *In* J.H. Steele (ed.) Marine food chains. University of California Press, Berkeley.

Lasker, R. 1989. Food chains and fisheries: an assessment after 20 years, p. 173-182. *In* B.J. Rothschild (ed.) Toward a theory on biological-physical interactions on the world ocean. Kluwer Academic Publications.

Leong, R.J.H. and C.P. O'Connell. 1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Board Can. 26: 557-582.

MacCall, A.D. 1980. The consequences of cannibalism in the stock-recruitment relationship of planktivorous fishes such as *Engraulis*, p. 201-220. *In* G.D. Sharp (ed.) Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, Peru, April-May 1980. IOC Workshop Rep. 28. UNESCO, Paris. 323 p.

Mais, K.F. 1974. Pelagic fish surveys in the California current. Calif. Dep. Fish. Game, Fish. Bull. 162. 79 p.

Mathisen, O.A., R.E. Thorne, R.J. Trumble and M. Blackburn. 1978. Food consumption of pelagic fish in an upwelling area, p. 111-123. *In* R. Boje and M. Tomczak (eds.) Upwelling ecosystems. Springer-Verlag, Berlin.

Mayr, E. 1982. The growth of biological thought. Harvard University Press, Cambridge, Massachusetts.

McFarland, W.N. and S.A. Moss. 1967. Internal behavior in fish schools. Science 156: 260-262.

Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Resources Management (ICLARM), Manila, Philippines.

Miller, T.J., L.B. Crowder, J.A. Rice and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45: 1657-1670.

Muck, P. and G. Sánchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Murphy, G.I. 1973. Clupeoid fishes under exploitation with special reference to the Peruvian anchovy. Tech. Rep. No. 30, University of Hawaii, Hawaii Institute of Marine Biology. 73 p.

Palomares, M.L., P. Muck, J. Mendo, E. Chumán de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. 1981. The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforsch. 28(4): 251-282.

Pauly, D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Parker, R.R. 1981. Size-selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28: 1503-1510.

Pitcher, T.J. 1986. Functions of shoaling behavior in teleosts, p. 294-337. *In* T.J. Pitcher (ed.) The Behavior of Teleost Fishes. John Hopkins University Press, Baltimore.

Pulliam, H.R. and T. Caraco. 1984. Living in groups: Is there an optimal group size? p. 122-142. *In* J.R. Krebs and N.B. Davies (eds.) Behavioral ecology. Second edition. Blackwell, Oxford.

Sibly, R.M. 1983. Optimal group size is unstable. Anim. Behav. 31: 947-948.

Smith, P.E. 1970. The horizontal dimensions and abundance of fish schools in the upper mixed layer as measured by sonar, p. 563-591. *In* G.B. Farquhar (ed.) Proceedings of the International Symposium on Biological Sound Scattering in the Ocean. Maury Cent. Ocean Sci., Dep. Navy, Washington, DC.

Smith, P.E. 1981. Fisheries on coastal pelagic schooling fish, p. 1-32. *In* R. Lasker (ed.) Marine fish larvae. Washington Sea Grant Program, University of Washington Press, Seattle.

Steele, J.H. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge.

Ware, D.M. 1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37: 1012-1024.

A Preliminary Bibliography of Anchoveta (*Engraulis ringens*)

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Abstract

A preliminary bibliography of anchoveta (*Engraulis ringens*, Jenyns 1842) (Pisces: Engraulidae) is presented, consisting of almost 500 references on its biology, ecology, and the fishery and processing industry depending on it. Much of the literature is published in English, and most of the Spanish papers include English abstracts. The major part of research which led to the publications included here was conducted in Peru. References from Chile and Ecuador have been included as far as available. An updated, computerized version of the bibliography is available as Microsoft Word or ASCII file from ICLARM at a nominal fee.

Resumen

Se presenta una bibliografía preliminar de la anchoveta (*Engraulis ringens*, Jenyns 1842) (Pisces: Engraulidae), consistente en alrededor de 500 referencias acerca de su biología, ecología y la pesquería y su procesamiento industrial dependiente de ella. La mayor parte de la bibliografía está publicada en inglés, y muchos de los trabajos en español incluyen resúmenes en Inglés. La mayoría de las investigaciones que generaron los trabajos incluidos en ésta publicación fueron realizadas en Perú. Referencias de Chile y Ecuador han sido incluidas en la medida que se dispuso de ellas. Una versión actualizada y computarizada de la bibliografía en archivos Microsoft Word ó ASCII puede ser obtenida en ICLARM con un pago nominal.

Introduction

The anchoveta *(Engraulis ringens* Jenyns 1842) (Pisces: Clupeoidea: Engraulidae) is distributed along the west coast of South America between 4°S (northern Peru) and 42.5°S (southern central Chile) in the waters of the Humboldt Current. Being abundant in large schools, the anchoveta was heavily exploited by the world's largest single species fisheries in the late 1960s until its collapse in 1972. The fishery continues albeit on a reduced level. The catch is mainly used for the production of fish meal and oils.

The biology of the anchoveta has been investigated since the 1950s. Research on this species has been extended and intensified in the 1970s in order to understand its dependency on the South American upwelling ecosystem and its interaction with its other members, and to develop management plans for the Chilean and especially for the Peruvian anchoveta fisheries. A considerable number of papers has been written during this time, either published in the primary literature, forming a part of the "grey" (report) literature or being circulated as manuscripts.

This preliminary bibliography is an attempt to summarize the available information on the biology of anchoveta to date. Unpublished manuscripts and internal reports of IMARPE, however, have not been included. Synonyms of *Engraulis ringens* were included based on Whitehead et al. (1988). The literature search was performed in two steps, of which the first one used the following sources of information:

(i) Aquatic Sciences and Fisheries Abstracts (ASFA) (from January 1977 to October 1988);
(ii) Bio Sciences Information Services (BIOSIS) Previews (from January 1969 to January 1989);
(iii) a list of publications available from IMARPE, Centro de Información y Documentación en Ciencias Acuáticas y Pesqueras, Esq. Gamarra y Gra. Valle s/n, Apartado 22, Callao, Perú;
(iv) a bibliographic compilation on "El Niño" (Mariátegui et al. 1985);
(v) a list of PROCOPA publications (Appendix II, this vol.)
(vi) holdings of the ICLARM library, and
(vii) collections of ICLARM staff, especially that of this book's senior editor.

In the second step, the available publications were accessed individually and their reference sections checked for further citations. This "snowballing" will continue during further expansion of the bibliography.

The references are numbered continuously in the bibliographic part. Numbers in brackets indicate incomplete information, e.g., with respect to page numbers. An asterisk (*) following the number indicates that the reference is part of the ICLARM library collection and/or private collections of ICLARM staff. We emphasize that the present version of this bibliography is incomplete. For example, there is limited access to the literature from Chile and the Soviet Union. As presented here, the bibliography forms the core of a computerized version, which is available as Microsoft Word or ASCII file from ICLARM at a nominal fee (see Appendix II, this vol.). This computerized version will be updated as new reprints become available and eventually will be annotated. We would be pleased to receive further information, particularly with respect to the "grey literature", i.e., unpublished reports and popular articles.

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References

Jenyns, L. 1842. Fish. *In* C. Darwin (ed.) (Blomefield, L.). The zoology of the voyage of H.M.S. BEAGLE, under the command of Captain Fitzroy, R.N., during the years 1832-1836. Smith, Elder and Company, London. 172 p.

Mariátegui, J., A. Chirinos de Vildoso y J. Veléz. 1985. Bibliografiá sobre el fenómeno El Niño desde 1891 a 1985. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 136 p.

Whitehead, P.J.P., G.J. Nelson and T. Wongratana. 1988. FAO species catalogue. Vol. 7. Clupeoid fishes of the world (suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, anchovies and wolf-herrings. Part 2 Engraulidae. FAO Fish. Synop. 125 (7) Pt. 2:305-579.

Bibliography

001 Abbot, J.F. 1899. The marine fishes of Peru. Proc. Acad. Sci. Philad.: 324-364.

002 Aguayo, H.M. 1976. Edad y crecimiento de la anchoveta *(Engraulis ringens*, Jenyns*)* del norte de Chile (Arica-Iquique). Inv. Pesq. (23): 1-27.

003 Aguayo, M., V. Erbs, E. Estay, R. Gili y H. Steffens. 1983. Elaboración de claves edad-talla de sardina española, jurel, anchoveta y caballa para el año 1982. Corporación de Fomento de la Producción (AP 83-33). Inst. Fom. Pesq. Chile. 84 p.

004 * Agüero, M. 1987. A bioeconomic model of the Peruvian pelagic fishery, p. 307-304. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

005 * Alamo, A. 1981. Estudio sobre la alimentación de la anchoveta peruana *Engraulis ringens* J. durante los años 1976 y 1977, p. 258-263. *En* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.

006 * Alamo, A. 1989. Stomach contents of anchoveta *(Engraulis ringens)*, 1974 to 1985, p. 105-108. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

007 * Alamo, A.A. and M. Bouchon. 1987. Changes in the food and feeding of the sardine *(Sardinops sagax sagax)* during the years 1980 to 1984 off the Peruvian coast. J. Geophys. Res. 92(C13): 14411-14415.

008 * Alarcón, V. y J. Alheit. 1984. Frecuencia de desove y proporción sexual de la anchoveta *(Engraulis ringens)*, y de la sardina *(Sardinops sagax)*, p. 23. *En* Libro de Resúmenes: Primer Congreso Nacional de Biología Pesquera, 28 de Junio al 1 de Julio 1984, Colegio de Biólogos Regional del Norte, Trujillo, Perú. 115 p.

009 * Alegre, B. y J. Alheit. 1984. Estudio comparativo de fecundidad parcial de anchoveta *(Engraulis ringens)* y sardina *(Sardinops sagax)*, p. 22. *En* Libro de Resúmenes: Primer Congreso Nacional de Biología Pesquera, 28 de Junio al 1 de Julio 1984, Colegio de Biólogos Regional del Norte, Trujillo, Perú. 115 p.

010 * Alheit, J. 1985. Egg production method for spawning biomass estimates of anchovies and sardines. Int. Counc. Explor. Sea, Council Meet. 1985/H:41. Pelagic Fish Committee, 10 p.

011 * Alheit, J. 1986. Egg cannibalism versus egg predation: their significance in anchovies. S. Afr. J. Mar. Sci. 5: 467-470.

012 * Alheit, J. 1986. Spawning frequencies of Peruvian anchovies taken with a purse seine, p. 59-62. *In* R. Lasker (ed.) An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS 36. U.S. Department of Commerce; National Oceanic and Atmospheric Administration; National Marine Fisheries, Seattle, Washington, DC. 99 p.

013 Alheit, J. and B. Alegre. 1986. Fecundity of Peruvian anchovy, *Engraulis ringens*. Int. Counc. Explor. Sea, Council Meet. 1986/H 60. 12 p.

014 * Alheit, J., V.H. Alarcón and B.J. Macewicz. 1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens* J. Calif. Coop. Oceanic Fish. Invest. Rep. 25: 43-52.

015 * Alheit, J., B. Alegre, V.H. Alarcón and B. Macewicz. 1983. Batch fecundity and spawning frequency of various anchovy (Genus: *Engraulis*) populations from upwelling areas and their use for spawning biomass estimates. FAO Fish. Rep. 291(3): 977-985.

016 * Ancieta, F. 1981. The importance of coastal upwelling research to Peru, p. 4-5. *In* F.A. Richards (ed.) Coastal upwelling. Coastal and Estuarine Sciences 1. American Geophysical Union, Washington, DC. 529 p.

017 Anon. 1968. Nutrition from the sea: limits and possibilities. *Engraulis ringens-Euphausia* food chain. Umsch. Wiss. Tec. 68 (11): 336-338.

018 * Anon. 1979. Catch rise. Fish. News Int. 18(6): 96.

019 Anon. 1986. Análisis de las condiciones meteorológicas, oceanográficas y biológico pesqueras durante 1984-1985 y comienzos de 1986. Com. Perm. Pacif. Sur Bol. ERFEN (17): 36-37.

020 Armstrong, D.W. 1975. Errores en los datos del programa de recuperación de las marcas de anchoveta. Diseño para los futuros experimentos y análisis de los datos obtenidos de ellos. FAO Informe Pesca 15: 33 p.

021 * Arntz, W.E. 1986. The two faces of El Niño 1982-83. Meeresforsch. 31: 1-46.

022 * Arntz, W.E. 1988. Marine ecosystem research in Peru - a basis for rational management of the fishery resources, p. 71-82. *In* Federal Ministry for Economics Cooperation (BMZ) and Federal Ministry of Food, Agriculture and Forestry (BML) (eds.) Highlights of German research projects in the tropics and subtropics. International Cooperation and Transfer, Berlin, Federal Republic of Germany.

023 * Arntz, W.E. y J. Valdivia. 1985. Visión integral del problema "El Niño": introducción, p. 5-10. *En* W. Arntz, A. Landa and J. Tarazona (eds.) "El Niño", su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 222 p.

024 * Arrizaga, A. y C. Veloso. 1988. Efectos de factores ambientales en la variación composición y distribución de las capturas de la sardina comun *(Strangomera bentincki)* y anchoveta *(Engraulis ringens)*, en la zona de Talcahuano, Chile, p. 28. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

(025) Arrue, H. y J. Arakaki. 1972. Contribución al estudio de la utilización de la anchoveta para consumo humano directo: anchoveta *(Engraulis ringens)* sazonada deshidratada. Anales Científicos 10. Universidad Nacional Agraria La Molina, Lima, Perú.

026 Avila, E. 1953. "El Niño" en 1953 y su relación con las aves guaneras. Problemas básicos referente a la anchoveta. Bol. Cia. Admin. Guano 29(5): 13-19.

027 Bacigalupo, A. and M. Vara. 1967. The anchovy *Engraulis ringens* in chicken feed. Assoc. Latinoamer. Prod. Anim. Mem.: 35-46.

028 Bakun, A. 1985. Comparative studies and the recruitment problem: searching for generalizations. Calif. Coop. Oceanic Fish. Invest. Rep. 24: 30-40.

029 * Bakun, A. 1989. Mechanisms for density-dependent growth in Peruvian anchoveta: alternatives to impact on the regional-scale food supply, p. 235-243. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

030 * Bakun, A. and R.H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru current systems. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 99-112.

031 * Barber, R.T. and F.P. Chávez. 1983. Biological consequences of El Niño. Science 222(4629): 1203-1210.

032 * Barber, R.T., F.P. Chávez and J.E. Kogelschatz. 1985. Biological effects of El Niño. Efectos biológicos de El Niño. Com. Perm. Pacif. Sur Bol. ERFEN (14): 3-29. [reprinted as p. 399-438. *En* Ciencia, tecnologia y agresion ambiental: el fenómeno El Niño. Consejo Nacional de Ciencia y Tecnologia, CONCYTEC. Lima, Perú. 682 p.].

(033) Barreda, M. 1950. Informe sobre las investigaciones efectuadas con relación al desove de la anchoveta en la bahía de Pisco. Bol. Cia. Admin. Guano 26(5): 55-63.

034 * Barreda, M. 1953. Un método científico para estudiar la edad y crecimiento de los peces. Bol. Cia. Admin. Guano 1(1): 51-62.

035 * Beddington, J.R. and J.G. Cooke. 1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242. 47 p.

036 Bellido, D.A. 1984. Case history study of fish product development in Peru. Rec. Proc. Int. Assoc. Fish Meal Manuf. 23: 87-91.

037 Bernal, P., F. Robles y O. Rojas. 1982. Variabilidad física y biológica en la región meridional del sistema de corrientes, Chile-Perú. Monogr. Biol. 2: 75-102.

038 * Beverton, R.J.H. 1982. Resource variability and exploitation strategy. Monogr. Biol. 2: 121-133.

039 * Blondet, J. 1986. Peruvian fisheries. INFOFISH Mark. Dig. (3): 12-15.

040 * Boerema, L.K. 1970. Southeast Pacific, p. 164-175. *In* J.A. Gulland (ed.) The fish resources of the oceans. FAO Fish. Tech. Pap. 97. 425 p.

041 * Boerema, L.K. and J.A. Gulland. 1973. Stock assessment of the Peruvian anchovy and management of the fishery. J. Fish. Res. Board Can. 30(12): 2226-2235.

042 * Boerema, L.K., G. Saetersdal, I. Tsukayama, J.E. Valdivia and B. Alegre. 1965. Report on the effects of fishing on the Peruvian stock of anchovy. FAO Fish. Tech. Pap. 55. 44 p. (reprinted 1967 as "Informe sobre los efectos de la pesca en el recurso peruano de anchoveta." Bol. Inst. Mar Perú-Callao 1(4): 133-186).

(043) Bore, D. and C.F. Martínez. 1981. Chilean fisheries resources catalogue. Bol. Inst. Fom. Pesq. (Chile). 86 p.

044 * Bore, D., R. Hugo, R. Trucco, M.L. Fernández y J. Inda. 1988. Evaluación preliminar de la presencia de metales pesados en recursos pesqueros de importancia comercial de la III region de Chile, p. 86. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeast Pacific).

045 Borgo, J.L., I. Vásquez y A. Paz. 1967. La pesquería marítima peruana durante 1967. Informe Inst. Mar Perú-Callao (26). 46 p.

046 Brandhorst, W. 1963. Der Stand der Chilenischen Fischerei und die weiteren Aussichten für ihre Entwicklung. Bundesauslandshilfe für Entwicklungsländer. Valparaiso, Chile. 151 p.

047 Brandhorst, W. 1965. Die chilenische Fischerei und ihre weiteren Entwicklungsaussichten. Ber. über Landw. 43(1): 148-187.

048 Brandhorst, W. 1966. Las condiciones oceanográficas y la pesca de anchoa *(Engraulis ringens* J.*)* en la zona norte de Chile, p. 17-28. *En* Memoria 1er Seminario Latino Americano Sobre el Océano Pacífico Oriental. Univ. Nacional Mayor de San Marcos, Lima, Perú.

049 Brandhorst, W. y O. Rojas. 1967. Investigaciones sobre los recursos de la anchoveta *(Engraulis ringens* J.*)* y sus relaciones con las condiciones oceanográficas en Agosto-Septiembre de 1963 y Marzo-Junio de 1964. Bol. Inst. Fom. Pesq. (Chile) 31. 38 p.

050 Brandhorst, W. y J.R. Cañón. 1968. Resultados de estudios oceanográfico-pesqueros aéreos en el norte de Chile. Publ. Inst. Fom. Pesq., Santiago, Chile 29. 44 p.

051 Brandhorst, W. y O. Rojas. 1968. Investigaciones sobre los recursos anchoveta *(Engraulis ringens* J.*)* y sus relaciones con las condiciones oceanográficas en agosto-octubre de 1964. Bol. Inst. Fom. Pesq. 36. 17 p.

052 Brandhorst, W., M. Carreño y O. Rojas. 1965. El número de vertebras de la anchoveta *(Engraulis ringens*, Jenyns*)* y otras especies de la superfamilia Clupeoidea en aguas chilenas. Bol. Inst. Fom. Pesq. (Chile) (1): 1-9.

053 Brandhorst, W., M. Méndez y O. Rojas. 1966. Observaciones oceanográfico-biológicas sobre los recursos de la anchoveta *Engraulis ringens* J. en la zona norte de Chile. Parte I. Bol. Inst. Fom. Pesq. (Chile) 22. 43 p.

054 Brandhorst, W., O. Rojas and J.G. Simpson. 1967. Seasonal variations of the fat content solid yield and condition factor of the anchoveta *Engraulis ringens* in Chile. Arch. Fischereiwiss. 18(1): 44-66.

055 * Brandhorst, W., J.G. Simpson, M. Carreño and O. Rojas. 1968. Anchoveta resources in northern Chile in relation to environmental conditions from January to February 1965. Archiv. Fischereiwiss. 19(2/3): 167-235.

056 Brandhorst, W., J.G. Simpson, O. Rojas, J. Pineda and M. Méndez. 1967. Oceanographic and biological observations on the anchoveta resources in northern Chile. Part II. Bol. Inst. Fom. Pesq. (Chile) 23. 89 p.

057 * Canales, G. 1981. Estimación cuantitativa de peces pelágicos frente a Huarmey - Salaverry en Noviembre 1977 con el método de eco-integración, p. 280-288. *En* L.M. Dickie and J.E. Valdivia (eds.) Investigacion Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.

058 Cañón, J.R. 1978. Distribución de la anchoveta *(Engraulis ringens* Jenyns*)* en el norte de Chile en relación a determinadas condiciones oceanográficas. Inv. Pesq. (Chile) 30: 122 p.

059 Cañón, J.R. 1985. La variabilidad ambiental en la zona norte de Chile y su influencia en la pesquería pelágica durante El Niño 1982-1983. Inv. Pesq. (Chile) 32: 119-128.

(060) Cañón, J.R. 1986. Variabilidad ambiental en relación con la pesquería nerítica pelágica de la zona norte de Chile, p. 195-205. *En* P. Arana (ed.) La pesca en Chile. Escuela de Ciencias del Mar, Universidad Católica de Valparaiso, Chile.

061 * Cañón, J.R. 1988. Impacto ambiental de El Niño 1987 sobre la pesquería pelágica en Chile, p. 56. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

062 * Castillo, J. 1988. Sardina española. Biomasa y distribución espacial en la costa norte de Chile y su relación con la temperatura del mar, p. 47. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

063 * Castillo, S. and J. Mendo. 1987. Estimation of unregistered Peruvian anchoveta *(Engraulis ringens)* in official catch statistics, 1951 to 1982, p. 109-116. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

064 Cavicchioli-Barrera, G. and M.E. Miller-Aguilera. 1968. Monthly variation of the content of water proteins and extractable lipids: their reactiviy and trocepherol content in the Chilean anchovy *Engraulis ringens*. An. Fac. Quim. Farm. Univ. Chile 20: 24-29.

065 * Caviedes, C.N. 1981. The impact of El Niño on the development of the Chilean fisheries, p. 351-368. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York. 491 p.

066 Chirichigno, N. 1969. Lista sistemática de los peces marinos comunes para Ecuador-Perú-Chile. Inst. Mar Perú-Callao, Publicaciones Independientes. 108 p.

067 * Chirichigno, N. 1974. Clave para identificar los peces marinos del Perú. Informe Inst. Mar Perú-Callao (44). 388 p. (Revised and reprinted in 1980).

068 Chirinos de Vildoso, A. y B. Alegre. 1969. La madurez sexual de la anchoveta *(Engraulis ringens* J.*)* en los períodos reproductivos 1961/1968. Bol. Inst. Mar Perú-Callao 2(3): 112-125.

069 Chirinos de Vildoso, A. y E. Chumán de Flores. 1968. Validez de la lectura de otolitos para determinar la edad de la anchoveta *(Engraulis ringens)*. Informe Inst. Mar Perú-Callao (22). 34 p.

070 * Chirinos de Vildoso, A. y B.A. de Haro. 1969. La madurez sexual de la anchoveta *(Engraulis ringens* J.*)* en los períodos reproductivos 1961-1968. Bol. Inst. Mar Perú-Callao 2(3):112-125.

071 Chumán de Flores, E. 1968. Validez de la lectura de otolitos para determinar la edad de la anchoveta *(Engraulis ringens)*. Informe Inst. Mar Perú-Callao (22). 34 p.

072 Cifuentes, T.A. de la y W.O. Tarky. 1986. Utilización de especies pelágicas en usos no tradicionales, p. 269-279. *En* P. Arana (ed.) La pesca en Chile. Escuela de Ciencias del Mar, Universidad Católica de Valparaiso, Chile.

073 * Clark, F. N. 1954. Biología de la anchoveta. Bol. Cia. Admin. Guano 1(2): 98-132.

074 Clark, W.C. 1975. A study of the virtual population of the Peruvian anchoveta in the years 1962-1972. Washington University, Washington, DC. 300 p.

075 Clark, W.G. 1977. The lessons of the Peruvian anchoveta fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 19.

076 Clarke, R. 1962. Research on marine resources in Chile, Ecuador and Peru. Fish. News Int. 1(5): 44-50.

077 Contreras, G.E., H.L. Guzman y B.N. Karl. 1976. Variación estacional de la reactividad de los lípidos de anchoveta *(Engraulis ringens)*. Informe Pesq. (62): 1-13.

078 Cotroneo, H.M. y M.F. Muñoz. 1986. Perspectivas del sector pesquero semindustrial en la explotación de los recursos pelágicos de la zona norte de Chile, p. 207-221. *En* P. Arana (ed.) La pesca en Chile. Escuela de Ciencias del Mar, Universidad Católica de Valparaiso, Chile.

079 * Cowles, T.J., R.T. Barber and O. Guilleń. 1977. Biological consequences of the 1975 El Niño. Science 195: 285-287.

080 Csirke, J. 1979. El reclutamiento en la anchoveta peruana y su dependencia de la población adulta en los años 1961-1976. Bol. Inst. Mar Perú-Callao. 4(1): 1-30.

081 * Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population . Rapp. P.-v. Réun. Cons. int. Explor. Mer 177:307-313. (Abstract reprinted 1981 *En* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.).

082 * Csirke, J. 1988. Small shoaling pelagic fish stocks, p. 271-302. *In* J.A. Gulland (ed.) Fish population dynamics. 2nd ed. John Wiley and Sons, Chichester. 422 p.

083 * Cury, P. 1988. Pressions sélectives et nouveautés evolutives: une hypothèse pour comprendre certains aspects des fluctuations à long terme des poissons pelagiques côtiers. Can. J. Fish. Aquat. Sci. 45: 1099-1107.

084 * Cushing, D.H. 1978. Upper trophic levels in upwelling areas, p. 101-110. *In* R. Boje and M. Tomczak (eds.) Upwelling ecosystems. Springer-Verlag, Berlin. 303 p.

085 * Cushing, D.H. 1981. Fisheries biology: a study in population dynamics. 2nd ed. University of Wisconsin Press, Madison, Wisconsin, USA. 295 p.

086 * Cushing, D.H. 1981. The effect of El Niño upon the Peruvian anchoveta stock, p. 449-457. *In* F.A. Richards (ed.) Coastal upwelling. Coastal Estuarine Sciences 1. American Geophysical Union, Washington, DC.

087 * Cushing, D.H. 1982. Climate and fisheries. Academic Press, London. 373 p.

088 * Cushing, D.H. 1983. The outlook for fisheries research in the next ten years, p. 263-277. *In* B.J. Rothschild (ed.) Global fisheries: Perspectives for the 1980s. Springer-Verlag, New York. 289 p.

089 * Cushing, D.H. and J.H.K. Harris. 1973. Stock and recruitment and the problem of density dependence. Rapp. P.-v. Réun. Cons. Perm. int. Explor. Mer 164: 142-155.

090 * Dávila, F. 1984. Estudio osteológico de la anchoveta peruana *Engraulis ringens* Jenyns, 1842 (Pisces: Engraulidae), p. 77. *En* Libro de Resúmenes: Primer Congreso Nacional de Biología Pesquera, 28 de Junio al 1 de Julio 1984, Colegio de Biólogos Regional del Norte, Trujillo, Perú. 115 p.

091 * Dávila, F. 1984. Los órganos epibranquiales en los peces óseos de la familia *Engraulidae*, p. 78. *En* Libro de Resúmenes: Primer Congreso Nacional de Biología Pesquera, 28 de Junio al 1 de Julio 1984, Colegio de Biológos Regional del Norte, Trujillo, Perú. 115 p.

(092) De Buen, F. 1953. Las familias de peces de importancia económica. FAO, Santiago de Chile, 3-311.

093 * De Buen, F. 1955. El estudio de la edad y el crecimiento de peces, viviendo en medios oceánicos diferentes, y especialmente en la anchoveta o chicora *(Engraulis ringens)*. Bol. Cia. Admin. Guano 2(2): 41-47.

094 De Buen, F. 1957. Informe al gobierno de Chile sobre biología pesquera. FAO Informe 573. 41 p.

095 De Buen, F. 1958. Peces de la superfamilia Clupeoidea en aguas de Chile. Rev. Biol. Mar. 8(1-3): 83-110.

096 De Buen, F. 1959. Lampreas, tiburones, rayas y peces de la Estación de Biología Marina de Montemar, Chile. Rev. Biol. Mar Valparaiso 9(1-3): 1-200.

097 De Vries, T.J. and W. Pearcy. 1982. Fish debris in sediments of the upwelling zone of central Peru: a late quarternary record. Deep-Sea Res. 29(1A): 87-109.

098 Del Solar, E. 1942. Ensayo sobre la ecología de la anchoveta. Bol. Cia. Admin. Guano 28(1): 1-23

099 Delfin, F.T. 1901. Catálogo de los peces de Chile. Rev. Chil. Hist. Nat. 4(1): 4-6, 21-25.

100 Doe, L.A.E. 1978. Project ICANE: a progress and data report on a Canada-Peru study of the Peruvian anchovy and its ecosystem. Rep. Ser. No. BI-R-78-6. Bedford Institute of Oceanography, Dartmouth, Canada. 211 p.

101 * Doucet, W.F. and H. Einarsson. 1967. A brief description of Peruvian fisheries. Calif. Coop. Oceanic Fish. Invest. Rep. 11: 82-87.

102 Doucet, W. F., G. Saetersdal y I. Vásquez. 1962. La pesca de la anchoveta. Estadística de pesca y esfuerzo en Octubre, Noviembre y Diciembre de 1961. Bol. Inst. Inv. Rec. Mar, Callao 1. 12 p.

103 Doucet, W.F., G. Saetersdal y I. Vásquez. 1962. La pesca de la anchoveta. Estadística de pesca y esfuerzo en Enero, Febrero y Marzo de 1962. Bol. Inst. Inv. Rec. Mar, Callao 2. 9 p.

104 Doucet, W., G. Saetersdal y I. Vásquez. 1962. La pesca de la anchoveta. Estadística de pesca y esfuerzo en Abril, Mayo y Junio de 1962. Bol. Inst. Inv. Rec. Mar, Callao 5. 9 p.

105 Doucet, W.F., G. Saetersdal y I. Vásquez. 1963. La pesca de la anchoveta. Estadística de pesca y esfuerzo en los meses de Julio a Diciembre de 1962 y resumen de los resultados de la pesca total durante el año 1962. Bol. Inst. Inv. Rec. Mar, Callao 15. 24 p.

106 * Drago, G. y E. Yáñez. 1985. Dinámica de los principales stocks pelágicos *(Engraulis ringens* y *Sardinops sagax)* explotados en la zona norte de Chile(18°20'S-24°00'S) entre 1959 y 1983, p. 97-106. *En* T. Melo Fuentes (ed.) Estudios en Pesquerías Chilenas. Universidad Católica de Valparaiso, Chile.

107 Duffy, D.C. 1983. The foraging ecology of Peruvian seabirds. Auk 100(4): 800-810.

108 * Dutt, S. 1981. A comparison of some ecological features of the populations of clupeid fishes of cold and tropical waters. Proc. Symp. Ecol. Anim. Popul. Zool. Surv. India 1: 149-154.

109 Einarsson, H. y B. Rojas de Mendiola. 1963. Descripción de huevos y larvas de anchoveta peruana *(Engraulis ringens)*. Bol. Inst. Inv. Rec. Mar, Callao 1(1): 23.

110 * Einarsson, H. and B. Rojas de Mendiola. 1967. An attempt to estimate annual spawning intensity of the anchovy *(Engraulis ringens* J.*)* by means of regional egg and larval surveys during 1961-1964. Calif. Coop. Oceanic Fish. Invest. Rep. 11: 96-104.

111 Einarsson, H., F. Flores y J. Miñano. 1966. El ciclo de madurez de la anchoveta peruana *(Engraulis ringens)*, p. 128-135. *En* Memoria ler Seminario Latino-Americano Sobre el Océano Pacifico Oriental. Univ. Nacional Mayor de San Marcos, Lima, Perú.

112 Einarsson, H., B. Rojas de Mendiola y H. Santander. 1966. Los desoves de peces en aguas peruanas durante 1961-1964, p. 110-128. *En* Memoria 1er Seminario Latino-Americano Sobre el Océano Pacífico Oriental. Univ. Nacional Mayor San Marcos, Lima, Perú.

113 ERFEN. 1983. Informe del Comité Científico de ERFEN sobre "El Niño" 1982-1983. Com. Perm. Pacif. Sur, Bol. ERFEN 4: 4-22.

114 Espino, M. y C. Wosnitza-Mendo. 1988. Posible relación entre poblaciones de merluza *(Merluccius gayi peruanus)* y anchoveta *(Engraulis ringens)*, p. 18. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

115 Evermann, B. and L. Radcliffe. 1917. The fishes off the west coast of Perú and the Titicaca Basin. U.S. Nat. Mus. Bull. 95: 174 p.

116 * FAO. 1975. Report of the Workshop on the Phenomenon known as "El Niño", Guayaquil, Ecuador, 4-12 December 1974. FAO Fish. Rep. 163. 24 p.

117 Fiedler, R., N. Jarvis y M. Lobell. 1943. La pesca y las industrias pesqueras del Perú. Cia. Admin. Guano, Lima, Perú. 367 p.

118 * Fischer, W. 1958. Huevos, crias y primeras prelarvas de la "anchoveta" *(Engraulis ringens* Jenyns*)*. Rev. Biol. Mar Univ. Chile 8(1-3): 111-124.

119 Flores, M. 1984. Socio-economical effect of El Niño 1982-83 in the Peruvian coast fisheries. Com. Perm. Pacif. Sur Bol. ERFEN (10): 11-14.

120 * Flores, M. 1985. El potencial de los recursos pesqueros en el mar peruano. Actualidad Pesquera. Año IV(21-22): 46-49.

121 Flores, M., R. Hidalgo y J. Acosta. 1983. Informe estadístico y económico de la pesca exploratoria de recursos pelágicos realizadas por las PEEAS (Pequeñas Empresas de Extracción de Anchoveta) en el período del 13 de Febrero al 20 de Junio de 1982. Informe Inst. Mar Perú-Callao (84). 41 p.

122 Fonseca, T.R., E.R. Yáñez y O.A. Barra. 1986. Relación entre la temperatura superficial del mar y capturas comerciales en área de Talcahuano (1965-1976), p. 243-248. *En* P. Arana (ed.) La pesca en Chile. Escuela de Ciencias del Mar, Universidad Católica de Valparaiso, Chile.

123 Fowler, H.W. 1945. Fishes of Chile. Systematic catalog. Apart. Rev. Chilena His. Nat. Pts. (1-2) 36. 171 p.

124 Freundt, J. y D. Roa. 1966. Desarollo y aplicación de un proceso de salado fermentado en la utilización de la anchoveta *(Engraulis ringens)* para consumo humano. Universidad Nacional Agraria, La Molina, Lima, Perú. Tesis.

125 * Freyre, A. 1967. Fishery development in Peru. Stud. Trop. Oceanogr. Miami 5: 391-411.

126 * Fuentes, O.G. 1966. Informe sobre la estructura de la administración de las pesquerías en el Perú y Ponencias. FAO Conf. on Fish. Admin. and Services, 21-25 November 1966. Working Pap. 2: 90-95.

127 * Furness, R.W. 1982. Competition between fisheries and seabird communities. Adv. Mar. Biol. 20: 225-307.

128 * Garcilaso de la Vega. 1609 (1st part) and 1617 (2nd part). Comentarios reales de los Incas. Reimpreso por Univ. Nacional Mayor de San Marcos, 1960 (First English Edition: 1688; paperback reprint edition titled "The Incas" by Avon Books, 1961).

129 Garland, D. and M. Araya. 1988. Validity of the age reading by the method of daily growth increments on the Chilean pilchard *(Sardinops sagax musica)* on the north of Chile, p. 60. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

131 * George, C.J. 1985. Notes on the Peruvian fisheries. Fisheries 10(3): 13-17.

132 Girard, C. 1856. Abstract of a report to Lieut. Jas. M. Gilliss, U.S.N., upon the fishes collected during the U.S.N. astronomical expedition to Chile. Proc. Acad. Natl. Sci. Philad. 7: 197-199.

133 * Glantz, M. H. 1979. Science, politics and economics of the Peruvian anchoveta fishery. Mar. Pol. 3(3): 201-210.

134 * Glantz, M.H. 1981. Consideration of the societal value of an El Niño forecast and the 1972 to 1973 El Niño, p. 449-476. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York. 491 p.

135 * Gorbunova, N.N., S.A. Evseenko and S.V. Garetovskiy. 1985. Distribution of ichthyoplankton in the frontal zones of the Peruvian waters. J. Ichthyol. 25(6): 67-79.

136 Guerrero, A. 1985. Dinámica de los principales recursos explotados en la zona de Talcahuano 36°10'S-37°10'S entre 1965 y 1984. Escuela de Ciencias del Mar, Universidad Católica de Valparaiso, Chile. 86 p. Tesis.

(137) Guerrero, A.C. y E.R. Yáñez. 1986. Análisis de las principales pesquerías pelágicas desarrolladas en la zona de Talcahuano (37°S-73°W) entre 1965 y 1984, p. 223-241. *En* P. Arana (ed.) La pesca en Chile. Escuela de Ciencias del Mar, Universidad Católica de Valparaiso, Chile.

138 * Guillén, O.G. and R.Z. Calienes. 1981. Biological productivity and El Niño, p. 255-282. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York. 491 p.

139 Guillén, O. y H. Santander. 1970. Informe del Crucero SNP-1, 7006, condiciones biooceanográficas. Informe Esp. Inst. Mar Perú-Callao (68). 16 p.

140 Guillén, O., R. Calienes y R. Izaguirre de Rondán. 1969. Contribución al estudio del ambiente de la anchoveta *(Engraulis ringens* J.*)*. Bol. Inst. Mar Perú-Callao 2(2): 49-76.

141 * Gulland, J.A. 1968. Informe sobre la dinámica de la población de anchoveta peruana. Bol. Inst Mar Perú-Callao. 1(6):305-346. (reprinted as: Report on the population dynamics of the Peruvian anchoveta, FAO Fish. Tech. Pap. 72. 29 p.).

142 * Gulland, J.A. 1971. Science and fishery management. J. Cons. int. Explor. Mer 33(3): 471-477.

143 * Gulland, J.A. 1974. Fishery science, and the problems of management, p. 413-430. *In* F.R. Harden Jones (ed.) Sea fisheries research. Paul Elek (Scientific Books) Ltd., London. 510 p.

144 * Gulland, J.A. 1974. The management of marine fisheries. Scientechnica, Bristol, UK. 198 p.

145 * Gulland, J.A. 1976. Production and catches of fish in the sea, p. 283-316. *In* D.H. Cushing and J.J. Walsh (eds.) The ecology of the seas. Blackwell Scientific Publications, Oxford. 467 p.

146 * Gulland, J.A. 1983. Managing fisheries in an imperfect world, p. 179-194. *In* B.J. Rothschild (ed.) Global fisheries: perspectives for the 1980s. Springer-Verlag, New York. 289 p.

147 * Harder, W. 1957. Die Darmlänge bei Clupeoiden von Fundorten verschiedener geographischer Breite. Année Biol. 33: 171-178.

148 Harder, W. 1958. El intestino como caracter diagnóstico para la identificación de ciertos clupeoides (Engraulidae, Clupeidae, Dussumieriidae) y como carácter morfométrico para la comparación de las poblaciones de anchoveta *(Cetengraulis mysticetus)*. Inter-Amer. Trop. Tuna Comm. Bull. 2(8).

149 * Harder, W. 1960. Vergleichende Untersuchungen zur Morphologie des Darmes bei Clupeoidea. Zeitschrift für wiss. Zoologie 163(1-2): 65-167.

150 Hayasi, S. 1965. A biological proposal to advance the fishery of anchovy *Engraulis ringens* along the Peruvian coast. Bull. Mar. Sci. 7: 75-80.

151 Hays, C. 1986. Effects of the 1982-1983 El Niño on Humboldt penguin *Spheniscus humboldtii* colonies in Peru. Biol. Conserv. 36(2): 169-180.

152 * Herrera, G., E. Aguilera, G. Castillo y P. A. Bernal. 1985. Crecimiento de larvas de anchoveta *Engraulis ringens* en Chile Central, determinado por conteo de incrementos diarios en otolitos. Biol. Pesq. 14: 11-15.

153 Hildebrand, S.F. 1943. A review of the American anchovies *(family Engraulidae)*. Bull. Bingham Oceanogr. Coll. 8(2): 1-165.

154 Hildebrand, S.F. 1946. A descriptive catalogue of the shore fishes of Peru. U.S. Natl. Mus. Bull. (189): 1-530.

155 Hildebrand, S.F. and O. Barlon. 1949. A collection of fishes from Talara, Peru. Smithson. Inst. U.S. Natl. Mus. Bull. 189. 530 p.

156 * Holmsen, A. 1973. Management of the Peruvian anchoveta resource, p. 106-111. *In* A.A. Sokoloski (ed.) Ocean fishery management: discussions and research. NOAA Tech. Pap. NMFS Circ-371. U.S. Department of Commerce; National Oceanic and Atmospheric Administration; National Marine Fisheries Service, Seattle, Washington, DC. 173 p.

157 Holt, S. 1979. Marine fisheries, p.38-83. *In* E.M. Borgese and N. Ginsburg (eds.) Ocean yearbook, Vol. 1. University of Chicago Press, Chicago, USA. 907 p.

158 * Hudtwalcker, A. 1955. La industria pesquera peruana en 1952. Pesca y Caza (6): 39-50.

159 Hutchinson, G.E. 1950. Survey of existing knowledge on biochemistry. 3. The biochemistry of vertebrate excretion. Bull. Amer. Mus. Natl. Hist. (96): 1-554.

160 Icochea, E. U., R.C. Lam y J.T. Sánchez. 1971. Preservación de la anchoveta a bordo de las embarcaciones pesqueras, con fines industriales de reducción (nivel de laboratorio). Informe Inst. Mar Perú-Callao (37). 24 p.

161 Instituto del Mar del Perú. 1966. La pesquería de la anchoveta. Informe Inst. Mar Perú-Callao (14). 20 p.

162 Instituto del Mar del Perú. 1967. Informe complementario de la pesquería de la anchoveta. Informe Inst. Mar Perú-Callao (15). 13 p.

163 Instituto del Mar del Perú. 1968. Encuestas sobre las embarcaciones anchoveteras realizada en Junio de 1967. Informe Inst. Mar Perú-Callao (23). 41 p.

164 Instituto del Mar del Perú. 1968. La pesquería de la anchoveta y recomendaciones para la temporada 1967-68. Informe Inst. Mar Perú-Callao (20). 14 p.

165 * Instituto del Mar del Perú. 1970. Informe del cuadro de expertos sobre dinámica de la población de la anchoveta peruana. Report of the Panel of Experts on Population Dynamics of Peruvian Anchoveta. Bol. Inst. Mar Perú-Callao 2(6): 323-371.

166 * Instituto del Mar del Perú. 1970. Panel de expertos informes sobre los efectos económicos de diferentes medidas regulatorias de la pesquería de la anchoveta peruana. Informe Esp. Inst. Mar Perú-Callao (34). 83 p. (reprinted in 1981 as "Panel of experts' report (1970) on the economic effects of alternative regulatory measures in the Peruvian anchoveta fishery", p. 369-400. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York. 491 p.).

167 * Instituto del Mar del Perú. 1972. Informe sobre la segunda reunión del panel de expertos en dinámica de población de la anchoveta peruana. Report of the Second Session of the Panel of Experts on the Population Dynamics of Peruvian anchovy. Bol. Inst. Mar Perú-Callao 2(7): 406-457.

168 Instituto del Mar del Perú. 1972. Regulación de la pesquería de anchoveta para el año calendario 1972. Informe Esp. Inst. Mar Perú-Callao IM-97.

169 Instituto del Mar del Perú. 1972. Exploración de peladilla y distribución de cardúmenes de anchoveta 24-25 de Febrero 1972. Informe Esp. Inst. Mar Perú-Callao (98). 19 p.

170 Instituto del Mar del Perú. 1972. Operación Eureka XX, 28-29 Abril 1972. Informe Esp. Inst. Mar Perú-Callao (105). 19 p.

171 Instituto del Mar del Perú. 1972. Operación Eureka XXII, 18-19 Julio 1972. Informe Esp. Inst. Mar Perú-Callao (111). 25 p.

172 Instituto del Mar del Perú. 1972. Operación Eureka XXIII, 3-6 Agosto 1972. Informe Esp. Inst. Mar Perú-Callao (112). 52 p.

173 Instituto del Mar del Perú. 1972. Notas sobre el estado actual del stock de anchoveta a base del informe del panel de expertos realizado en Julio de 1972 y de los últimos estudios y prospecciones biooceanológicas efectuados por el Instituto del Mar. Informe Esp. Inst. Mar Perú-Callao (114). 14 p.

174 Instituto del Mar del Perú. 1972. Operación Eureka XXIV, 5-8 Setiembre 1972. Informe Esp. Inst. Mar Perú-Callao (115). 89 p.

175 Instituto del Mar del Perú. 1972. Operación Eureka XXV, 20-23 Octubre. Informe Esp. Inst. Mar Perú-Callao (117). 74 p.

176 Instituto del Mar del Perú. 1972. La pesca en el sur y la situación del stock de anchoveta. Informe Esp. Inst. Mar Perú-Callao (119). 11 p.

177 Instituto del Mar del Perú. 1972. Resultados de la pesca exploratoria realizada del 4 al 7 de Diciembre 1972 (Paita-Punta Lomas). Informe Esp. Inst. Mar Perú-Callao (121). 18 p.

178 Instituto del Mar del Perú. 1972. La anchoveta en relación con el fenómeno de "El Niño 1972". Informe Esp. Inst. Mar Perú-Callao (194). 20 p.

179 * Instituto del Mar del Perú. 1973. Tercera sesión del panel de expertos sobre dinámica de la población de anchoveta peruana. Report of the Third Session of the Panel of Experts on the Population Dynamics of Peruvian Anchovy. Bol. Inst. Mar Perú-Callao 2(9): 521-599.

180 Instituto del Mar del Perú. 1973. Operación Eureka XXVI, 20-23 de Enero 1973. Informe Esp. Inst. Mar Perú-Callao (122). 77 p.

181 Instituto del Mar del Perú. 1973. Situación del stock de anchoveta a principios de 1973. Informe Esp. Inst. Mar Perú-Callao (125). 32 p.

182 Instituto del Mar del Perú. 1973. Operación Eureka XXVIII (12-13 de Noviembre de 1973) y diagnóstico del stock de anchoveta en noviembre de 1973. Informe Esp. Inst. Mar Perú-Callao. IM-146.

183 * Instituto del Mar del Perú. 1974. Informe de la cuarta sesion del panel de expertos de la evaluación del stock de anchoveta peruana. Report of the Fourth Session of the Panel of Experts on Stock Assessment on Peruvian Anchoveta. Bol. Inst. Mar Perú-Callao 2(10): 604-723.

184 Instituto del Mar del Perú. 1974. Operación Eureka XXIX, 28-30 de Mayo 1974. Informe Esp. Inst. Mar Perú-Callao (158). 77 p.

185 Instituto del Mar del Perú. 1974. Informe sobre el estado del Recurso Anchoveta a fines de Septiembre y las perspectivas para la pesquería en la temporada Octubre-Diciembre 1974. Informe Esp. Inst. Mar Perú-Callao (165). 30 p.

186 * Instituto del Mar del Perú. 1974. Segundo panel de expertos; informes sobre los efectos económicos de diferentes medias regulatorias de la pesquería de la anchoveta peruana. Second Panel of Experts: Report on the Effects of Alternative Regulatory Measures in the Peruvian Anchoveta Fishery. Bol. Inst. Mar Perú-Callao 3(1): 4-40.

187 Instituto del Mar del Perú. 1975. La recuperación de la anchoveta y "El Niño". Rev. Com. Perm. Pacif. Sur (3): 97-102.

188 Instituto del Mar del Perú. 1976. La situación de la población de anchoveta y el clima marino a Octubre de 1976. Informe Esp. Inst. Mar Perú-Callao IM-146. 180 p.

189 Instituto del Mar del Perú. 1976. Operación Eureka 32 (14-15 Febrero 1975). Inst. Mar Perú-Callao Informe Esp. IM-177. 56 p.

190 Instituto del Mar del Perú. 1976. Operación Eureka (6-7 Agosto 1975). Inst. Mar. Perú-Callao Informe Esp. IM-178. 52 p.

191 Instituto del Mar del Perú. 1981. Informe sobre la situación de los recursos pelágicos a principios de 1981 y las proyecciones de pesca. Inst. Mar Perú-Callao, Publicaciones Independientes. 30 p.

192 * Instituto del Mar del Perú. 1986. Informe del crucero BIC SNP-1 8604-05 frontera norte Callao y diagnóstico de la situación de los recursos pelágicos a Mayo de 1986. Serie Informe Esp. Inst. Mar Perú-Callao IM-193. 61 p.

193 Instituto del Mar del Perú and UNDP/FAO. 1975. Research on the anchovy - models and reality. Instituto del Mar del Perú, Lima. 21 p.

194 Iparraguirre, L. 1960. La pesca peruana en 1960. Min. Agric. (Perú) (15): 5-6.

(195) Jenyns, L. 1842. Fish. *In* C. Darwin (ed.) (Blomefield, L.). The zoology of the voyage of the H.M.S. Beagle, under the command of Captain Fitzroy, R.N., during the years 1832-1836. Smith, Elder and Company, London. 172 p.

196 Johannesson, K.A. and O.A. Mathisen. 1980. Monitoring surveys of the Peruvian anchovy *(Engraulis ringens)*. Working Party-News 2(3) April 1980.

197 * Johannesson, K.A. and A.N. Robles. 1977. Echo surveys of Peruvian anchoveta. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 170: 237-244.

198 * Johannesson, K. and R. Vílchez. 1981 Application and some results of echo-integration methods in monitoring Peruvian anchovy resources, p. 765-815. *In* J.B. Suomala (ed.) Meeting on Hydroacoustical Methods for the Estimation of Marine Fish Populations, 25-29 June 1979. II (b): Contributed papers, discussion, and comments. The Charles Stark Draper Laboratory, Inc., Cambridge, Massachusetts. 964 p.

199 Johannesson, K.A. and R. Vílchez. 1981. Note on hydroacoustic observations of changes in distribution and abundance of some common pelagic fish species in the coastal waters of Peru, with special emphasis on anchoveta. IOC Workshop Rep. 28: 287-323.

200 Jones, R. 1982. Population fluctuations and recruitment in marine populations. Phil. Trans. R. Soc. Lond. (297B): 353-368.

201 Jordán, D.S. and A. Seale. 1935. The analysis of the genera of anchovies or *Engraulidae*. Copeia (141): 27-32.

202 * Jordán, R. 1959. Observaciones sobre la biología de la anchoveta *(Engraulis ringens* J.*)* de la zona pesquera de Huacho. Bol. Cia. Admin. Guano 35(11): 1-22.

203 Jordán R. 1963. Un análisis del número de vertebras de la anchoveta peruana *(Engraulis ringens* J.*)*. Bol. Inst. Inv. Rec. Mar. Perú-Callao 1(2): 25-43.

204 * Jordán, R. 1967. The predation of guano birds on the Peruvian anchovy *(Engraulis ringens* Jenyns*)*. Calif. Coop. Oceanic Fish. Invest. Rep. 11: 105-109

205 * Jordán, R. 1971. Distribución de la anchoveta *(Engraulis ringens* J.*)* en relación con el ambiente. Análisis de sistemas de afloramientos. Inv. Pesq. 35(1): 113-126.

206 * Jordán, R. 1976. Biología de la anchoveta. Parte I. Resumen del conocimiento actual. Actas de la Reunión de Trabajo sobre el Fenómeno conocido como "El Niño". FAO Fish Rep. 185:359-399. (reprinted in 1980 as "Biology of the anchoveta. I: Summary of the present knowledge, p. 249-276. *In* Proceedings of the Workshop on the Phenomenon known as "El Niño". UNESCO, Paris. 284 p.).

207 * Jordán, R. 1982. Hematotalasia y mortandad de peces en la costa peruana. Com. Perm. Pacif. Sur, Bol. ERFEN 3(1-2): 34-37.

208 Jordán, R. 1982. La anchoveta y su captura frente a las costas del Perú. Monogr. Biol. (Chile) 2: 51-63.

209 * Jordán, R. 1983. Variabilidad de los recursos pelágicos en el Pacífico Sudeste. FAO Fish. Rep. 291(2): 113-130.

210 Jordan, R. 1985. Ecological changes and economic consequences of El Niño phenomenon in the southeastern Pacific. Com. Perm. Pacif. Sur Bol. ERFEN (12): 27-33.

211 * Jordán, R. 1985. Los efectos de "El Niño" 1982-83 y los mecanismos internacionales para la investigación, p. 207-216. *En* W. Arntz, A. Landa and J. Tarazona (eds.) "El Niño", su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 222 p.

212 Jordán, R. y A. Chirinos de Vildoso. 1965. La anchoveta *(Engraulis ringens* J.*)*, conocimiento actual sobre su biología, ecología y pesquería. Informe Inst. Mar Perú-Callao (6). 52 p.

213 Jordán, R. y A. Málaga. 1972. Resultados de la primera marcación experimental de anchoveta *(Engraulis ringens* J.*)* en el mar. Informe Inst. Mar Perú-Callao (39). 23 p.

214 Jordán, R., A. Málaga y A. Pastor. 1971. Los estudios de factibilidad de marcaciones de anchoveta. Informe Esp. Inst. Mar Perú-Callao 82:28.

215 Jordán, R., J. Csirke y I. Tsukayama. 1978. Situación de los recursos anchoveta, sardina, jurel y caballa a Junio 1978. Bol. Inst. Mar Perú-Callao 56. 32 p.

216 Kelly, R. y J.L. Blanco. 1983. Fluctuaciones ambientales y su relación con la abundancia de recursos pelágicos en la zona norte-centro de Chile. Bol. Inst. Fom. Pesq. (Chile). 22 p.

217 * Kesteven, G.L. 1976. Recovery of the anchovy and El Niño. CUEA Newsl. (5): 17 p.

218 Klekowsi, R.Z. and K.W. Opalinski. 1980. Review of bioenergetic investigations. Pol. Arch. Hydrobiol. 27(4): 439-466.

219 * Lam, R. 1968. Estudio sobre la variación del contenido de grasa en la anchoveta peruana *(Engraulis ringens* J.*)*. Informe Inst. Mar Perú-Callao (24). 29 p.

220 Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers on successful first feeding. Fish. Bull. 73: 453-462.

221 * Lasker, R. and A. MacCall. 1983. New ideas on the fluctuations of the clupeid stocks off California, p. 110-120. *In* Proceedings of the Joint Oceanographic Assembly 1982 - general symposia. Canadian National Committee/ Scientific Committee on Oceanic Research, Ottawa, Canada.

222 Leible, M. y E. Alveal. 1982. Catálogo de peces que habitan las aguas costeras y dulceacuícolas en la provincia de Concepción. Pontifica Universidad Católica Chile, Talcahuano, Chile. 104 p.

223 * Loeb, V.J. and O. Rojas. 1988. Interannual variation of ichthyoplankton composition and abundance relations off northern Chile, 1964 to 83. Fish. Bull. 86(1): 1-24.

224 * Longhurst, A. 1971. The clupeoid resources of tropical seas. Oceanogr. Mar. Biol. Ann. Rev. 9: 349-385.

225 * Longhurst, A. and D. Pauly. 1987. Ecology of tropical oceans. Academic Press, San Diego, California. 407 p.

226 Lorenzen, S., C. Gallardo, C. Jara, E. Classing, G. Pequeño and C. Moreno. 1979. Mariscos y peces de importancia comercial en el sur de Chile. Univ. Austral de Chile. 131 p.

227 * MacCall, A.D. 1981. The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*. IOC Workshop Rep. 28: 201-220.

228 * MacCall, A.D. 1982. Seabird-fishery trophic interactions in eastern Pacific boundary currents: California and Peru, p. 136-148. *In* D.N. Nettleship, G.A. Sanger and P.F. Springer (eds.) Marine birds: their feeding ecology and commercial fisheries relationships. Southwest Fisheries Center, California.

229 * Macer, C.T. 1974. Industrial fisheries, p. 193-222. *In* F.R. Harden Jones (ed.) Sea fisheries research. Paul Elek (Scientific Books), London. 510 p.

230 Málaga, A. 1974. Las marcaciones de anchoveta en el mar de Febrero y Agosto, 1974. Informe Esp. Inst. Mar Perú-Callao IM-152.

231 * Málaga, A. y D. Armstrong. 1977. Estimaciones de tasas de mortalidad de la anchoveta peruana *(Engraulis ringens* J.*)* determinadas por marcaciones, p. 107. *En* Libro de Resúmenes. V Congreso Nacional de Biología, 24-30 Abril 1977, Cusco, Perú. Cultura Andina, Cuzco, Perú.

232 * Malpica, C. 1976. Anchoveta y tiburones. Runamarka, Lima, Perú. 71 p.

233 * Mariátegui, J., A. Chirinos de Vildoso y J. Vélez. 1985. Bibliografía sobre el fenómeno El Niño desde 1891 a 1985. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 136 p.

234 Martínez, C., C. Salazar y G. Böhm. 1981. Análisis de las pesquerías pelágicas 1980. Informe Técnico. Corporación de Fomento de la Producción/Inst. Fom. Pesq. (Chile). 199 p.

235 Martínez, C., G. Böhm y C. Salazar. 1982. Análisis de las pesquerías pelágicas 1981. Informe Técnico. Corporación de Fomento de la Producción/Inst. Fom. Pesq. (Chile). 96 p.

236 Martínez, C., C. Salazar y G. Böhm. 1984. La pesquería cerquera ejercida en la zona norte de Chile y su relación con los cambios biológico-pesqueros asociados al fenómeno de El Niño 1982-83. Rev. Com. Perm. Pacif. Sur. 15: 203-221.

237 Martínez, C., A. Aranis, P. Barris, G. Böhm y O. Rojas. 1988. La pesquería pelágica ejercida en la zona económica exclusiva y Chilena: estado de situación y perspectivas, p. 119. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

238 Martínez, C., C. Salazar, G. Böhm, J. Mendieta y C. Estrada. 1985. Efectos del fenómeno El Niño 1982-83 sobre los principales recursos pelágicos y su pesquería (Arica-Antofagasta). Inv. Pesq. 32: 129-139.

239 * Mathisen, O.A. 1986. Bases biológicas del sistema de monitoreo y manejo, p. 149-160. *En* O.A. Mathisen and I. Tsukayama (eds.) Bases biológicas y marco conceptual para el manejo de los recursos pelágicos en el Pacífico Suroriental, BID/SELA/OLDEPESCA, Documento de Pesca 1, Lima, Perú. 196 p.

240 McCarthy, J.J. and T.E. Whitledge. 1972. Nitrogen excretion by anchovy *(Engraulis mordax* and *E. ringens)* and jack mackerel *(Trachurus symmetricus)*. Fish. Bull. 70(2): 395-401.

241 * Mendelssohn, R. 1989. Reanalysis of recruitment estimates of the Peruvian anchoveta in relation to other population parameters and the surrounding environment, p. 364-385. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling and ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

242 * Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

243 * Miñano, J. 1958. Algunas apreciaciones relacionadas con la anchoveta peruana y su fecundidad. Bol. Cia. Admin. Guano 34: 11-24.

244 Miñano, J. 1968. Estudio de la fecundidad y ciclo sexual de la anchoveta *(Engraulis ringens* J.*)* en la zona de Chimbote. Bol. Inst. Mar Perú-Callao 1(9): 505-533.

245 Miñano, J. 1968. Preliminary report of the fall 1967 sea cruise 6705-06 Cabo Blanco-Ilo, Peru: *Engraulis ringens*, guano birds, zooplankton, phytoplankton. Informe Inst. Mar Perú-Callao (21). 13 p.

246 * Möller, H. 1984. Causes of the collapse of pelagic swarm fish stocks. Fisch. Umwelt. (13): 187-199.

247 * Morales-Nin, B. 1989. Age and growth of the southern stock of Peruvian anchoveta based on otolith microstructures and length-frequency analysis, p. 179-188. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

248 * Morgan, G.R. and D. Pauly. 1987. Analysis of length-frequency data: some available programs and user's instructions, p. 373-462. *In* D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines; and Kuwait Institute for Scientific Research, Safat, Kuwait.

249 Morrow, J. and G. Posner. 1957. Studies in ichthyology and oceanography in coastal Peru. Bull. Bingham Ocean. Coll. Peabody Mus. Natl. Hist. Yale Univ. 16: 5-71.

250 * Muck, P. 1989. Anchoveta consumption of Peruvian hake: a distribution and feeding model, p. 306-320. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

251 * Muck, P. 1989. Major trends in the upwelling system off Peru and their implications for management, p. 386-403. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

252 * Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystems: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

253 * Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

254 * Muck, P. and G. Sánchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystems: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

255 Muck, P. y R. Vilchez. 1986. Biomasa y su distribución en el espacio y tiempo - Perú, p. 110-119. *En* O.A. Mathisen and I. Tsukayama (eds.) Bases biológicas y marco conceptual para el manejo de los recursos pelágicos en el Pacífico Suroriental. Documento de Pesca No. 001. Organización Latinoamericana de Desarollo Pesquero, Lima, Perú.

256 * Muck, P., B. Rojas de Mendiola and E. Antonietti. 1989. Comparative studies on feeding in larval anchoveta *(Engraulis ringens)* and sardine *(Sardinops sagax)*, p. 86-96. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

257 * Muck, P., O. Sandoval de Castillo and S. Carrasco. 1987. Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Perú, p. 268-275. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystems: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

258 * Muck, P., M. Espino, H. Fuentes, C. Wosnitza-Mendo y M. Esquerre. 1988. Predación de la merluza Peruana *(Merluccius gayi peruanus)* sobre la anchoveta *(Engraulis ringens)*, p. 249-254. *En* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento Peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario.

259 Mujica, A. y O. Rojas. 1980. Estudio de reproducción, fecundidad y desove de la sardina común *(Clupea (Strangomera) bentincki)* y de la anchoveta *(Engraulis ringens)* de la zona de Talcahuano. Informe Técnico. Corporación de Fomento de la Producción/Inst. Fom. Pesq. (Chile) AP 80-3-38.

260 * Murphy, G.I. 1968. Pattern in life history and environment. Am. Nat. 102: 391-403.

261 Murphy, G.I. 1972. Fisheries in upwelling regions - with special reference to Peruvian waters. Geoforum 11: 63-71.

262 * Murphy, G.I. 1977. Clupeoids, p. 283-308. *In* J.A. Gulland (ed.) Fish population dynamics. John Wiley and Sons, New York. 372 p.

263 * Murphy, R.C. 1954. The guano and the anchoveta fishery. American Museum of Natural History, New York. (reprinted as p. 81-136. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York).

264 Musaeva, E.I. and I.A. Solokova. 1980. Caloric equivalents of planktonic animals in the Peruvian upwelling region. Pol. Arch. Hydrobiol. 27(4): 471-476.

265 * Nelson, G. 1984. Identity of the anchovy *Hildebrandichthys setiger* with notes on the relationships and biogeography of the genera *Engraulis* and *Cetengraulis*. Copeia (2): 422-427.

(266) Nikolsky, G.V. 1961. On same adaptations to the regulation of population density in fish species with different types of stock structure. *In* E.D. Le Cren and M.W. Holdgate (eds.) The exploitation of natural animal populations. Blackwell Scientific Publications, Oxford.

(267) Nikolsky, G.V. 1969. Theory of fish population dynamics as biological background for rational exploitation and management of fishery resources. Oliver and Boyd, London. 323 p.

268 Ñiquen, M., A. Echevarria y L. Mariátegui. 1988. Variaciones de los desembarques de anchoveta *(Engraulis ringens)* y sardina *(Sardinops sagax sagax)* en el Perú en Enero-Abril de 1987, p. 265-272. *En* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

269 Ojeda, P.F. and J. Jaksio. 1979. Utilización diferencial de recursos alimenticios por dos poblaciones simpátricas de *Scomber japonicus peruanus* y *Sarda sarda chiliensis* en el norte de Chile (Pisces: Teleostei). Media Ambiente 4(1): 19-23.

270 Oliva, J., W. Carbajal and A. Tresierra. 1986. Biología reproductiva e histología de gonadas en peces. Editorial Bioscience, Trujillo, Perú. 151 p.

271 Oliver-Schneider, C. 1943. Catálogo de los peces marinos del litoral de Concepción y Arauco. Bol. Soc. Biol. Concepción, Chile 17: 75-126.

272 Olórtegui, J. 1973. Incremento protéico del agua de cola de la anchoveta *(Engraulis ringens)* por fermentación. Anales Científico 9. Universidad Nacional Agraria La Molina, Lima, Perú.

273 Orellana, M.C. and F. Balbontin.1983. Comparative study of the larvae of Clupeiformes of the coast of Chile. Rev. Biol. Mar 19(1): 1-46.

274 Palma, G.S. 1976. Meroplancton de la región de Valparaiso. Cienc. Tecnol. Mar (2): 99-116.

275 * Palomares, M.L., P. Muck, J. Mendo, E. Chumán de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1982, p. 117-141. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

276 * Parrish, R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. FAO Fish. Rep. 291(3): 731-777.

277 * Pastor, A. and A. Málaga. 1966. Experimentos preliminares con anchovetas adultas y larvas *(Engraulis ringens)* en acuario, p. 107-109. *En* Memoria 1er Seminario Latino-Americano sobre el Océano Pacífico Oriental. Univ. Nacional Mayor San Marcos, Lima, Perú.

278 Paulik, G.J. 1970. The anchoveta fishery of Peru. Quant. Sci. Pap. (13). Center for Quantitative Science in Forestry, Fisheries and Wildlife. University of Washington, Seattle. 79 p.

279 * Paulik, G.J. 1971. Anchovies, birds and fishermen in the Peru current, p. 156-185. *In* W.W. Murdock (ed.) Environment: resources, pollution and society. Smauer Associates Inc., Stanford, Connecticut. (reprinted in 1981 p. 35-79. *In* M.H. Glantz and J.D. Thompson (eds.) Resources management and environmental uncertainty: lessons from coastal upwelling fisheries. Wiley Interscience, New York. 491 p.).

280 * Pauly, D. 1987. A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates, p. 3-74 *In* D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines; and Kuwait Institute for Scientific Research, Safat, Kuwait.

281 * Pauly, D. 1987. Managing the Peruvian upwelling ecosystem: a synthesis, p. 325-342. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

282 * Pauly, D. and M.L. Palomares. 1989. New estimates of monthly biomass, recruitment and related statistics of anchoveta *(Engraulis ringens)* off Peru (4-14°S), 1953-1985, p. 189-206. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

283 * Pauly, D. and M. Soriano. 1987. Monthly spawning stock and egg production of Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1981, p. 167-178. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

284 * Pauly, D. and M. Soriano. 1989. Production and mortality of anchoveta eggs off Peru, p. 155-167. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

285 * Pauly D. and I. Tsukayama. 1983. On the seasonal growth, monthly recruitment and monthly biomass of Peruvian anchoveta *(Engraulis ringens* J.*)* from 1961 to 1979. FAO Fish. Rep. 291(3): 987-1004.

286 * Pauly, D. and I. Tsukayama. 1987. On the implementation of management-oriented fishery research: the case of the Peruvian anchoveta, p. 1-13. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; German Agency for Technical Cooperation (GTZ), Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

287 * Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987. VPA estimates of monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

288 * Pauly, D., A. Chirinos de Vildoso, J. Mejía, M. Samamé and M.L. Palomares. 1987. Population dynamics and estimated anchoveta consumption of bonito *(Sarda chiliensis)* off Perú, 1953 to 1982, p. 248-267. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

289 * Pauly, D., A. Jarre, S. Luna, V. Sambilay, Jr., B. Rojas de Mendiola and A. Alamo. 1989. On the quantity and types of food ingested by Peruvian anchoveta, 1953 to 1985, p. 109-124. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

290 Pauly, D., I. Tsukayama and H. Tovar. 1986. Some preliminary results from an international multidisciplinary project aimed at reconstructing monthly time series on the Peruvian ecosystem for the years 1953-1982, p. 25. *In* Chapman Conference on El Niño: an International Symposium, 27-31 October 1986, Guayaquil, Ecuador. Vol. of Abstracts, 45 p.

291 Peña, N., M. Ñiquen and S. Carrasco. 1988. Principales aspectos pesqueros y biológicos de los recursos anchoveta *(Engraulis ringens)* y sardina *(Sardinops sagax sagax)* en los años 1986 y 1987 en la costa peruana, p. 59. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

292 * Peña, N., J. Mendo and J. Pellón. 1989. Sexual maturity of anchoveta *(Engraulis ringens)*, 1961 to 1987, p. 132-142. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

293 Pequeño, G. 1968. Los peces chilenos y sus nombres vulgares. Mus. Nac. Hist. Nat. Chile. Not Mens. 12(142): 7-10.

294 Peterson, W.T., D.F. Arcos, G.B. McManus, H.Dam, D. Bellantoni, T. Johnson and P. Tiselius, 1988. The nearshore zone during coastal upwelling daily variability and coupling between primary and secondary production off central Chile. Prog. Oceanogr. 20 (1): 1-40.

(295) Pimentel, H. 1962. Empleo de la anchoveta *(Engraulis ringens)* fresca en la alimentación de cerdos. Informe. Universidad Nacional Agraria La Molina, Lima, Perú.

296 * Pitcher, T.J. and P.J.B. Hart. 1982. Fisheries ecology. Croom Helm Ltd., Kent, UK. 414 p.

297 Popovici, Z. 1962. Corrientes oceánicas y la pesca peruana. Anuario de Pesca 1961-62: 162-172.

(298) Quintano, M.M. 1978. Técnica conservera. Tecnología de elaboración de conserva de anchoveta *(Engraulis ringens)*. Documenta 6(63): 6-9.

299 Ramirez, A. 1979. Preservación de la anchoveta *(Engraulis ringens* J.*)* para consumo humano directo a bordo de las embarcaciones pesqueras. Informe Inst. Mar Perú-Callao (54). 55 p.

300 * Restrepo, V.R. and J.M. Hoenig. 1988. An empirical investigation of Peruvian anchovy recruitment. Mar. Fish. Sec. Newsl. 6(2): 7.

301 * Roff, D.A. 1981. Reproductive uncertainty and the evolution of iteroparity: why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. 38(8): 968-977.

302 * Rojas de Mendiola, B. 1964. Abundancia de los huevos de anchoveta *(Engraulis ringens* J.*)*, con relación a la temperatura de mar en la región de Chimbote. Bol. Inst. Inv. Rec. Mar, Callao (25): 24 p.

(303) Rojas de Mendiola, B. 1966. Estimación de la produción fitoplanctónica en él area de Callao. Chimbote durante Agosto de 1961, p. 50-56. *En* Memoria 1er Seminario Latino-Americano sobre el Océano Pacífico Oriental. Univ. Nacional Mayor San Marcos, Lima, Perú.

304 Rojas de Mendiola, B. 1966. Relación entre la cosecha estable de fitoplankton, el desove y la alimentación de la anchoveta *(Engraulis ringens* J.*)*, p. 60-69. *En* Memoria 1er Seminario Latino-Americano Sobre el Océano Pacífico Oriental. Univ. Nacional Mayor de San Marcos, Lima, Perú.

305 Rojas de Mendiola, B. 1969. The food of the Peruvian anchovy. J. Cons. int. Explor. Mer 32(3): 433-434.

306 * Rojas de Mendiola, B. 1970. Observaciones sobre la alimentación de la anchoveta *Engraulis ringens* J. procedente de dos áreas diferentes de la costa peruana. Presented at the International Symposium on the Fertility of the Sea, Sao Paulo, Brazil, 1-6 December 1969. Informe Esp. Inst. Mar Perú-Callao IM-56:1-36. [reprinted in 1971 as: Some observations on the feeding of the Peruvian anchoveta *Engraulis ringens* J. in two regions of the Peruvian coast, p. 417-440. *In* J.D. Costlow (ed.) Fertility of the Sea. Vol. 2, 18 p. Gordon and Breach Science Publisher, New York].

307 Rojas de Mendiola, B. 1974. Food of the larval anchovy *(Engraulis ringens* J.*)*, p. 277-285. *In* J.H.S. Blaxter (ed.) The early life history of fish. Springer-Verlag, Berlin. 765 p.

308 Rojas de Mendiola, B. 1978. El alimento de la anchoveta *Engraulis ringens* J. en una área de afloramiento (San Juan). Informe Inst. Mar Perú-Callao (49). 16 p.

309 * Rojas de Mendiola, B. 1981. Summary of the studies about food and feeding habits of the anchovy *(Engraulis ringens* J.*)*. IOC Workshop Rep. 28: 221-223.

(310) * Rojas de Mendiola, B. 1989. Stomach contents of anchoveta *(Engraulis ringens)*, 1953 to 1974, p. 97-104. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

311 * Rojas de Mendiola, B. and O. Gómez. 1981. Daily otolith rings in otoliths of larval anchovy *(Engraulis ringens)*. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 178: 565-566.

312 * Rojas de Mendiola, B. and O. Gómez. 1981. Food, survival and time of inactivity of larval anchoveta *(Engraulis ringens* J.*)*. IOC Workshop Rep. 28: 275-286.

313 * Rojas de Mendiola B. and O. Gómez. 1981. Primera alimentación, sobrevivencia y tiempo de actividad de las larvas de anchoveta *(Engraulis ringens* J.*)*, p. 72-79. *In* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.

314 * Rojas de Mendiola, B. and N. Ochoa. 1973. Observations on the food and feeding habits of the anchovy *Engraulis ringens* made during Cruise 6908-09, p. 457-461. *In* R. Fraser (comp.) Oceanography of the South Pacific 1972. New Zealand National Commission for UNESCO, Wellington.

315 * Rojas de Mendiola, B. and N. Ochoa 1981. Fitoplancton y desove de la anchoveta *(Engraulis ringens* J.). IOC Workshop Rep. 28: 241-253.

316 * Rojas de Mendiola, B., N. Ochoa, R. Calienes and O. Gómez. 1969. Contenido estomacal de anchoveta en cuatro áreas de la costa peruana. Informe Inst. Mar Perú-Callao (27). 30 p.

317 * Rojas Escadillo, B. 1953. Estudios preliminares del contenido estomacal de las anchovetas. Bol. Cia. Admin. Guano 1(2): 33-42.

318 * Rojas, O., A. Mujica y M. Braun. 1988. Variación interanual de la distribución y abundancia de huevos y larvas de sardina espanola *Sardinops sagax musica* y anchoveta *Engraulis ringens* en el norte de Chile, 1983-1987, p. 33. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the Interannual Symposium on Living Resources and Fisheries in the Southeastern Pacific).

319 * Rojas, O., A. Mujica, M. Labra, G. Ledermann y H. Miles. 1983. Estimación de la abundancia relativa de huevos y larvas de peces. Corporación de Fomento de la Producción. Gerencia de Desarollo. Inst. Fom. Pesq. (Chile) AP 83-31.

320 Rojas, S.W. and C.M. Arana.1981. Metabolizable energy values of anchovy fish meal and oil for chicks. Poult. Sci. 60(10): 2274-2277.

321 * Rosenberg, A.A. and J.R. Beddington. 1987. Monte-Carlo testing of two methods for estimating growth from length-frequency data with general conditions for their applicability, p. 283-298. *In* D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines; and Kuwait Institute for Scientific Research, Safat, Kuwait.

322 * Saetersdal, G. y J.E. Valdivia. 1964. Un estudio del crecimiento, tamaño y reclutamiento de la anchoveta *(Engraulis ringens* J.*)* basado en datos de frecuencia de longitud/A study of growth, size and recruitment of the anchovy *(Engraulis ringens* J.*)* based on length-frequency data. Bol. Inst. Inv. Rec. Mar, Callao 1(4): 85-136.

323 * Saetersdal, G., I. Tsukayama y B. Alegre. 1965. Fluctuaciones de la abundancia aparente del stock de anchoveta en 1959-1962/Fluctuations in the apparent abundance of the anchovy stock in 1959-1962. Bol. Inst. Mar Perú-Callao 1(2): 33-104.

324 * Saetersdal, G., J. Valdivia, I. Tsukayama and B. Alegre. 1967. Preliminary results of studies on the present status of the Peruvian stock of anchovy *(Engraulis ringens* Jenyns*)*. Calif. Coop. Oceanic Fish. Invest. Rep. 11: 88-95.

325 Saila, S.B. 1972. Systems analysis applied to some fisheries problems, p. 331-372. *In* B.C. Patten (ed.) Systems analysis and simulations in ecology, Vol. 2. Illus. Map. Academic Press, New York. 608 p.

326 * Sameoto, D. 1981. Distribution and abundance of six species of fish larvae in Peruvian waters and their relationship with the physical and biological environment, p. 171-179. *En* L.M. Dickie and J.E. Valdivia (eds.) Investigacion Cooperativa de la Anchoveta y su Ecosistem (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.

327 * Sameoto, D. 1982. Vertical distribution and abundance of the Peruvian anchovy, *Engraulis ringens*, and sardine, *Sardinops sagax*, larvae during November 1977. J. Fish Biol. 2(21): 171-186.

328 Sánchez, J.E. 1966. General aspects of the biology and ecology of the anchovy *(Engraulis ringens)*. Gulf Caribb. Fish. Inst., Proc. 18th Ann. Ess. 84-93.

329 Sánchez, T. y E. Icochea. 1968. Evaluación preliminar de las pérdidas de sólidos en el agua de sangre (sanguaza) de anchoveta en la industria harinera de pescado. Informe Esp. Inst. Mar Perú-Callao IM-32. 85 p.

330 Sandoval de Castillo, O. 1979. Distribución y variación estacional de larvas de peces en la costa peruana. Informe Inst. Mar Perú-Callao (63): 1-32.

332 * Sandoval de Castillo, O., C. Wosnitza-Mendo, P. Muck and S. Carrasco. 1989. Abundance of hake larvae and its relationship to hake and anchoveta biomasses off Perú, p. 280-296. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

333 Santander, H. 1976. La corriente peruana. Parte II: Aspectos biológicos, p. 285-298. *En* Actas de la Reunión de trabajo sobre el fenómeno conocido como El Niño, Guayaquil, Ecuador, 4-12 Diciembre 1974. FAO Informe de Pesca 185. Informe Esp. Inst. Mar Perú-Callao (166). 32 p.

334 * Santander, H. 1981. Fluctuaciones del desove de anchoveta y algunos factores relacionados. IOC Workshop Rep. 28: 255-274.

335 * Santander, H. 1981. Patrones de distribución y fluctuaciones de desoves de anchoveta y sardina, p. 180-192. *En* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.

336 * Santander, H. 1981. The zooplankton in an upwelling area off Peru, p. 411-416. *In* F.A. Richards (ed.) Coastal upwelling. Coastal and Estuarine Sciences 1. American Geophysical Union, Washington, DC. 529 p.

337 * Santander, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru, 4-14oS, p. 179-207. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

338 * Santander, H. y J. Alheit. 1984. Producción, mortalidad y predación de huevos de anchoveta *(Engraulis ringens)* y sardina *(Sardinops sagax)*, p. 24. *En* Libro de Resúmenes: Primer Congreso Nacional de Biología Pesquera, 28 de Junio al 1 de Julio 1984, Colegio de Biologos Regional del Norte, Trujillo, Perú. 115 p.

339 * Santander, H. y R. Flores. 1983. Los desoves y distribución larval de cuatro especies pelágicas y sus relaciones con las variaciones del ambiente mari o frente al Perú. FAO Fish. Rep. 291(3): 835-867.

(340) Santander, H. y N. Ochoa. 1974. Informe del crucero Krill III a bordo del barco de investigación científica "Alexander Agassiz" de la Universidad de California y estadía en el Departamento de Oceanología de Montemar, Chile. Serie de Informes Especiales. Inst. Mar del Perú-Callao. 166:18p+6 tablas.

341 Santander, H. and B. Rojas de Mendiola. 1980. The spawning habitat of the Peruvian anchovy, *Engraulis ringens*. Deep-Sea Res. 27A: 27 p.

342 Santander, H. y O. Sandoval de Castillo. 1969. El desove de la anchoveta *(Engraulis ringens* J.*)* en los períodos reproductivos de 1961 a 1968. Informe Inst. Mar Perú-Callao (40). 15 p.

343 * Santander, H. y O. Sandoval de Castillo. 1973. Estudio sobre las primeras etapas de vida de la anchoveta. Informe Inst. Mar Perú-Callao (41). 30 p.

344 Santander, H. y O. Sandoval de Castillo. 1977. Variaciones en la intensidad del desove de la sardina *(Sardinops sagax sagax* J.*)* en la costa peruana en los años 1966-73. Bol. Inst. Mar Perú-Callao 3(3): 73-94.

345 Santander, H. y O. Sandoval de Castillo. 1979. El ictioplancton de la costa peruana. Bol. Inst. Mar Perú-Callao 4(3): 69-112.

346 Santander, H. y O. Sandoval de Castillo. 1981. Algunos indicadores biológicos del ictioplancton, p. 89-103. *En* Memorias del Seminario sobre Indicadores Biológicos del Plancton. UNESCO, Oficina Regional de Ciencia y Tecnología para America Latina y El Caribe, Montevideo, Uruguay.

347 * Santander, H. y O. Sandoval de Castillo. 1981. El ictioplancton en el área norte del Perú en Noviembre de l977, p. 233-243. *En* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.

348 * Santander, H. y O. Sandoval de Castillo. 1985. Efectos del fenómeno El Niño en la composición, distribución y abundancia del ictioplancton, p. 355-374. *En* Ciencia, tecnología y agresión ambiental: el fenómeno El Niño. Congreso Nacional de Biología Pesquera, 28 de Junio al 1 de Julio 1984. Colegio de Biólogos Regional del Norte, Trujillo, Perú.

349 Santander, H. and O. Sandoval de Castillo. 1986. The El Niño phenomenon and the resources and ichthyoplankton off Perú, p. 24-25. *In* Chapman Conference on El Niño: an International Symposium, 27-31 October 1986, Guayaquil, Ecuador. Vol. of Abstracts, 45 p.

350 Santander, H. and I. Tsukayama. 1984. The anchoveta and sardine and some events associated with recruitment. IOC Workshop Rep. 33(Annex IV): 11-14.

351 * Santander, H. y J. Zuzunaga. 1984. Cambios en algunos componentes del ecosistema marino frente al Perú durante el fenómeno El Niño 1982-1983. Rev. Com. Perm. Pacif. Sur 15: 311-331.

352 Santander, H. and J. Zuzunaga. 1984. Impact of the 1982 to 83 El Niño on the pelagic resources of Perú. Trop. Ocean Atmos. Newsl. (20): 9-10.

353 * Santander, H, J. Alheit, and P.E. Smith. 1984. Determination of sampling effort required for estimating egg production of anchoveta, *Engraulis ringens*, off Peru. Bol. Inst. Mar Perú-Callao 7(1): 1-20.

354 * Santander, H., J. Alheit y P.E. Smith. 1984. Estimación de la biomasa de la población desovante de anchoveta peruana *Engraulis ringens* en 1981 por aplicación del "Método de Producción de Huevos". Bol. Inst. Mar Perú-Callao 8(6): 209-250.

355 * Santander, H., P. Smith y J. Alheit. 1982. Determinación del esfuerzo de muestro requerido para al estimado de producción de huevos de anchoveta *(Engraulis ringens)* frente al Perú. Bol. Inst. Mar Perú-Callao 7(1): 18.

356 Santander, H., F. Tello y J. Cisneros. 1969. Exploración del área Callao - Puerto Chala, a bordo del buque "Calypso". Informe Esp. Inst. Mar Perú-Callao (36). 17 p.

357 * Santander, H., J. Alheit, A.D. MacCall and A. Alamo. 1983. Egg mortality of the Peruvian anchovy *(Engraulis ringens)* caused by cannibalism and predation by sardines *(Sardinops sagax)*. FAO Fish. Rep. 291(3): 1011-1025.

358 * Schaefer, M. 1967. Dinámica de la pesquería de la anchoveta *(Engraulis ringens)* en el Perú. Bol. Inst. Mar Perú-Callao 5(1): 189-304.

359 * Schaefer, M. 1970. Investigaciones adicionales de la dinámica de las pesquerías de la anchoveta *(Engraulis ringens)* en el Perú. Informe Inst. Mar Perú-Callao (31). 32 p.

360 * Schaefer, M.B. 1970. Men, birds and anchovies in the Perú current - dynamic interactions. Trans. Am. Fish. Soc. 99: 461-467.

361 Schneider, O.G. 1943. Catálogo de los peces marinos del litoral de Concepción y Arauco. Museo de Concepción, Chile.

362 * Schneider, S.H. and R. Londer. 1984. The coevolution of climate and life. Sierra Club Books, San Francisco. 563 p.

363 * Schweigger, E. 1964. El litoral peruano (segunda edición). Universidad Nacional "Federico Villareal", Lima, Perú. 435 p.

364 * Sears, M. 1954. Notes on the Peruvian coastal current. I. An introduction to the ecology of Pisco Bay. Deep-Sea Res. 1: 141-169.

365 * Segura, E.L. 1973. Optimal fishing effort in the Peruvian anchoveta fishery, p. 57-64. *In* A.A. Sokoloski (ed.) Ocean fishery management; discussions and research. NOAA Tech. Rep. NMFS Circ-371. U.S. Department of Commerce; National Oceanic and Atmospheric Administration; National Marine Fisheries, Seattle, Washington, DC. 173 p.

366 * Senocak, T. 1988. Verteilung und dichteabhaengige Sterblichkeit der Eier von *Engraulis ringens* vor des Küste Perus. Inst. für Meereskunde, Kiel, Federal Republic of Germany. 74 p. Thesis.

367 * Senocak, T., D. Schnack and D. Pauly. 1989. Mean monthly distribution, abundance and production of anchoveta eggs off Perú (4-14°S) from 1964 to 1971 and 1972 to 1986, p. 143-154. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

368 Serra, J.R. 1978. La pesquería de sardina común *(Clupea (Strangomera) bentincki)* y anchoveta *(Engraulis ringens)* de Talcahuano: análisis de su desarollo y situación actual. Inv. Pesq. (29): 1-21.

369 Serra, J.R. 1981. Situación de los recursos pelágicos de la zona norte. IIIer Jornadas en Pesquerías Chilenas. Universidad Católica de Valparaiso. Escuela Ciencias del Mar. 34 p.

370 * Serra, J.R. 1983. Changes in the abundance of pelagic resources along the Chilean coast. FAO Fish. Rep. 291(2): 255-284.

371 * Serra, J.R. 1986. Patrones de captura y tendencias: Chile, p. 63-70. *En* O.A. Mathisen and I. Tsukayama (eds.) Bases biológicas y marco conceptual para el manejo de los recursos pelágicos en el Pacífico Suroriental, BID/SELA/OLDEPESCA, Documento de Pesca 1, Lima, Perú. 196 p.

(372) Serra, J.R. 1986. Desarollo de la pesquería de anchoveta *(Engraulis ringens*, Jenyns*)* y los cambios de su abundancia. Invest. Pesq. (Chile) 33: 13-24.

373 * Serra, J.R. 1987. Impact of the 1982 to 83 El Niño/southern oscillation on the southeastern Pacific fisheries, with an emphasis on Chilean fisheries, p. 24-29. *In* M. Glantz, R. Katz and M. Kenz (eds.) The societal impacts associated with the 1982-83 worldwide climate anomalies. National Center for Atmospheric Research, Boulder, Colorado. 105 p.

374 Serra, J.R. y E. Gil. 1975. Marcación de anchoveta en la zona norte de Chile. Metología y resultados preliminaires. Rev. Com. Perm. Pacif. Sur (3): 3-19.

375 Serra, J.R. y E. Gil. 1977. Experimentos de recuperación de marcas de anchoveta *(Engraulis ringens)* en la industria reductora del norte de Chile. Bol. Inst. Fom. Pesq. (Chile). 15 p.

376 Serra, J.R. y A. Zuleta. 1982. La pesquería pelágica chilena: antecedentes. Rev. Monogr. Biol. (Chile) 2: 19-37.

377 Serra, J.R., M. Aguayo, O. Rojas, J.R. Cañon y F. Inostroza. 1979. Anchoveta *Engraulis ringens* (Jenyns) Teleostomi Clupeiformes Engraulidae. Corporación de Fomento de la Producción (AP 79-18). Inst. Fom. Pesq. Chile. 52 p.

378 * Sharp, G.D. 1981. Report of the workshop on effects of environmental variation on survival of larval pelagic fishes. IOC Workshop 28: 15-59.

379 Simpson, J.G. and R. Buzeta. 1966. Relaciones entre la longitud y el peso de la anchoveta *(Engraulis ringens*, Jenyns*)* en Chile. Bol. Cient Inst. Fom. Pesq. Santiago, Chile 2: 1-67.

380 Simpson, J.G. y R. Buzeta. 1967. El crecimiento y la edad de la anchoveta *(Engraulis ringens* J.*)* en Chile, basado en estudios de frecuencia de longitud. Bol. Inst. Fom. Pesq. (Chile) (3). 53 p.

381 Simpson, J.G. y E. Gil. 1967. Maduración y desove de la anchoveta *(Engraulis ringens* J.*)* en Chile. Bol. Cient. Inst. Fom. Pesq. (Chile) 4: 1-21.

382 Simpson, J.G. y H. Simon. 1966. Algunas observaciones sobre las características electroforéticas de la hemoglobina de anchoveta, *Engraulis ringens*, J., en Chile. Inv. Zool. Chilenas 13: 21-45.

383 * Smith, P.E., H. Santander and J. Alheit. 1983. Comparison of egg sample probability distributions of the anchovy *(Engraulis ringens)* and sardine *(Sardinops sagax)* off Peru and the anchovy *(E. mordax)* and the sardine *(Sardinops caerulea)* off California. FAO Fish. Rep. 291(3): 1027-1038.

384 Smith, P.E., H. Santander y J. Alheit. 1983. Detalles técnicos de un plan de crucero para estimar la biomasa desovante de anchoveta. Bol. Inst. Mar Perú-Callao 7(2): 19-48.

385 * Smith, S.L., K.H. Brink, H. Santander, T.J. Cowles and A. Huyer. 1981. The effect of advection on variation in zooplankton at a single location near Cabo Nazca, Perú, p. 400-410. *In* F.A. Richards (ed.) Coastal upwelling. Coastal and Estuarine Sciences 1. American Geophysical Union, Washington, DC. 529 p.

386 Solis, V. y J. Ducato. 1977. Utilización de la anchoveta *(Engraulis ringens)* para consumo humano, salada-seca. Universidad Nacional Agraria La Molina, Lima, Perú. Tesis.

387 Sorokin, Y.I. 1978. Characteristics of the ecosystem of the Peruvian upwelling. Dokl. Akad. Nauk. SSSR Ser. Biol. 236(1-6): 339-342.

388 * Sotelo, R.J., J. Csirke, and I. Tsukayama. 1978. Dynamics of the fishery for the anchoveta *Engraulis ringens*, off Peru. Bol. Inst. Mar Perú-Callao 1(5): 189-304.

389 * Stephenson, M. R. and H. R. Hicks. 1975. Bibliography of El Niño and associated publications. Inter-Amer. Trop. Tuna Comm. Bull. 16(6): 451-501.

390 Talavera, V.,A. Bacigalupo and J. Shonberg. 1971. Study of the presence of thiaminase in the anchovy *Engraulis ringens*. Bol. Soc. Quim. Perú 37(2): 63.

391 * Tello Zevallos, F. 1966. Contenido de grasa a la anchoveta peruana *Engraulis ringens* J., en relación con algunos aspectos biológicos. Univ. Nacional Mayor de San Marcos, Lima, Perú. 49 p. Tesis.

392 * Thompson, J.D. 1981. Climate, upwelling, and biological productivity: some primary relationships, p. 13-33. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York.

393 * Thurow, F. 1982. Sustained fish supply. An introduction to fishery management. Arch. Fischwiss. 33(1/2): 1-42.

394 Tilic, I. 1962. Capacidad de producción de la industria de la harina de pescado en el Perú. Bol. Inst. Inv. Rec. Mar, Callao Informe (4). 38 p.

395 Tilic, I. 1962. La ubicación de la industria peruana de harina de pescado. Bol. Inst. Inv. Rec. Mar, Callao (3). 20 p.

396 Tilic, I. 1963. Costos y beneficios de la industria de la pesca de la anchoveta 1962. Bol. Inst. Inv. Rec. Mar, Callao 21. 64 p.

397 Tilic, I. 1963. Información estadística sobre embarcaciones utilizadas en la pesca industrial en el Perú 1953-62. Bol. Inst. Inv. Rec. Mar, Callao 8. 30 p.

398 Tilic, I. 1963. Material estadístico sobre la industria peruana de harina de pescado. Bol. Inst. Inv. Rec. Mar, Callao 14. 24 p.

399 * Tomczak, M., Jr. 1981. Prediction of environmental changes and the struggle of the third world for national independence: the case of the Peruvian fisheries, p. 401-435. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York. 491 p.

400 * Tovar, H. 1983. Fluctuaciones de poblaciones de aves guaneras en el litoral peruano. FAO Fish. Rep. 291(3): 957-976.

401 * Tovar, H.S. y V. Guillén. 1988. Composición por especies del contenido estomacal de guanay *(Phalacrocorax bougainvillii* Lesson*)*, p. 83. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

402 * Tsukayama, I. 1965. El número de branquispinas como carácter diferencial de sub-poblaciones de anchoveta *Engraulis ringens* Jenyns, en la costa del Perú. Universidad Nacional Mayor de San Marcos, Lima, Perú. 56 p. Tesis.

403 Tsukayama, I. 1966. El número de branquispinas como carácter diferencial de sub-poblaciones de anchoveta *(Engraulis ringens* Jenyns*)* en la costa del Perú, p. 139-145. *En* Memoria 1er Seminario Latino-Americano Sobre el Océano Pacífico Oriental. Universidad Nacional Mayor de San Marcos, Lima, Perú.

404 Tsukayama, I. 1969. Una nueva medida de la pesca por unidad de esfuerzo en la pesquería de anchoveta *(Engraulis ringens* J.*)*, en el Perú. Bol. Inst. Mar Perú-Callao 2(4): 129-156.

405 Tsukayama, I. 1982. Investigaciones de los recursos marinos y su explotación, p. 1-14. *En* Seminario sobre investigación y uso de los recursos naturales en el Perú, 14-16 Julio 1982, Lima, Perú.

406 Tsukayama, I. 1983. Recursos pelágicos y sus pesquerías en Perú. Rev. Com. Perm. Pacif. Sur 13: 25-63.

407 * Tsukayama, I. 1986. Patrones de captura y tendencias: Perú, p. 59-63. *En* O.A. Mathisen and I. Tsukayama (eds.) Bases biológicas y marco conceptual para el manejo de los recursos pelágicos en el Pacífico Suroriental, BID/SELA/OLDEPESCA, Documento de Pesca 1, Lima, Perú. 196 p.

408 * Tsukayama, I. 1989. Dynamics of the fat content of Peruvian anchoveta *(Engraulis ringens)*, p. 125-131. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

409 * Tsukayama, I. y M.A. Alvarez. 1981. Fluctuaciones en el stock de anchovetas desovantes durante las temporadas reproductivas de primavera 1964-1978. IOC Workshop Rep. 28:233-240. (reprinted in 1981 as p. 50-54. *En* L.M. Dickie and J.M. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. del Mar del Perú-Callao. Volumen Extraordinario. 288 p.).

410 * Tsukayama, I. and M.L. Palomares. 1987. Monthly catch and catch composition of Peruvian anchoveta *(Engraulis ringens)* (northern-central stock, 4-14oS), 1953 to 1982, p. 89-108. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

411 * Tsukayama, I. y G. Sanchez de Benitez. 1981. Estimado de consumo de alimento en anchovetas adultas, p. 254-257. *En* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.

412 Tsukayama, I. y H. Santander. 1987. Cambios bióticos y efectos sobre los recursos pesqueros y las pesquerías en Perú, p. 97-156. *En* R. Jordán (ed.) El fenómeno El Niño 1982-83 con particular referencia a sus efectos sobre los recursos pesqueros y las pesquerías en el Pacífico Sudeste. Rev. Com. Perm. Pacif. Sur 16.

413 Valdivia de Camarena, O. 1964. Anatomía macroscópica de las gonadas de "anchoveta" *Engraulis ringens* Jenyns. Facultad de Ciencias, Universidad Nacional Mayor de San Marcos, Lima, Perú. BSc. Thesis.

414 Valdivia de Camarena, O. 1965. Longitud y peso de las gonadas de *Engraulis ringens* Jenyns "Anchoveta" en los diversos estadios sexuales. Universidad Nacional Mayor de San Marcos, Lima, Perú. 55 p. Tesis.

415 * Valdivia, J.E. 1978. The anchoveta and El Niño. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 173: 196-202.

416 * Valdivia, J.E. 1976. Aspectos biológicos del fenómeno "El Niño, 1972-1973. Parte II. La población de la anchoveta. Actas Reunión de Trabajo sobre el Fenómeno Conocido como El Niño. FAO Fish. Rep. 185:80-93. (reprinted in 1980 as "Biological aspects of the 1972-1973 "El Niño" - Part 2: The anchovy population", p. 73-81. *In* Proceedings of the Workshop on the Phenomenon known as "El Niño, 4-12 December 1974, Guayaquil, Ecuador. UNESCO, Paris. 284 p.)

417 * Valdivia, J.E. 1980. "Biological aspects of the 1972-73 El Niño - Part 2: The anchovy population", p. 73-81. *In* Proceedings of the Workshop on the Phenomenon known as "El Niño", 4-12 December 1974, Guayaquil, Ecuador. UNESCO, Paris. 284 p.

418 * Valiela, I. 1984. Marine ecological processes. Springer-Verlag, Berlin, 546 p.

419 Vásquez, I. y A. Paz. 1969. La pesquería marítima peruana durante 1968. Informe Inst. Mar Perú-Callao (30). 93 p.

420 Vásquez, I. y I. Tsukayama. 1964. La pesca de la anchoveta. Estadística de pesca y esfuerzo durante los meses de Enero a Junio de 1963. Bol. Inst. Inv. Rec. Mar, Callao 24. 39 p.

421 Vásquez, I., A. Paz y R. Hidalgo. 1970. La pesquería marítima peruana durante 1969. Informe Inst. Mar Perú-Callao (32). 85 p.

422 Vásquez, I., R. Hidalgo y E. Perez. 1972. Resumen de la pesquería de anchoveta durante el año 1971. Informe Esp. Inst. Mar Perú-Callao IM-101. 35 p.

423 * Vegas-Vélez, M. 1972. Contribution a l'étude de l'appareil digestif des téléostéens - Rapports avec l'éthologie alimentaire. Université d'Aix-Marseille, France. 206 p. Thesis.

424 * Vegas-Vélez, M. 1981. Los filtradores en la cadena alimenticia del mar Peruano. Bol. de Lima (13):1-8.

425 * Vegas-Vélez, M. 1983. El fenómeno del Niño. Cielo Abierto 9(25): 54-61.

426 * Vegaz-Vélez, M. 1987. Ictiología. Texto Universitario, Universidad Nacional Agraria La Molina, Lima, Perú. 271 p.

427 Vegas-Vélez, M. y V. Paredes. 1974. La alimentación de algunos peces marinos del Perú. Documenta Lima 3: 40-44.

428 Vela López, J., L.A. Flores y H. Fuentes. 1980. Campaña de marcación de anchoveta, Abril-Mayo 1979. Informe Inst. Mar Perú-Callao (70). 23 p.

429 Vestnes, G. y G.S. Saetersdal. 1964. Informe sobre la prospección de anchoveta en el norte de Chile, entre Marzo y Junio de 1964, realizada con el B.M. "Stella Maris". Bol. Inst. Fom. Pesq. 5: 1-11.

430 Vestnes, G. y G.S. Saetersdal. 1965. Informe sobre la prospección de anchoveta en el norte de Chile, entre Agosto y Octubre, 1964, realizado con el B/I "Carlos Darwin". Bol. Inst. Fom. Pesq. 3: 1-6.

431 Vílchez, R. y P. Muck. 1988. Variaciones en la biomasa y en la distribución de los principales recursos pelágicos del Perú 1983-1987, p. 58. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

432 * Vílchez, R., P. Muck y A. Gonzales. 1988. Variaciones en la biomasa y en la distribución de los principales recursos pelágicos del Perú entre 1983 y 1987, p. 255-264. *En* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

(433) Villamar, A. et al. 1979. Análisis y propuesta nacional sobre la administración de la pesquería de anchoveta. Depto. de Pesca, Dir. Gral. del Inst. Nacl. de la Pesca, Programa de Anchoveta, Septiembre de 1979. 244 p.

434 Villanueva, R., R. Jordán y A. Burd. 1969. Informe sobre el estudio de comportamiento de cardúmenes de anchoveta. Informe Esp. Inst. Mar, Perú-Callao (45). 12 p.

435 * Villavicencio, Z. 1981. Investigación preliminar de los requerimientos energéticos de anchoveta adulta (metabolismo estandar y actividad), p. 193-205. *En* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.

436 * Villavicencio, Z. y P. Muck. 1983. Costos metabólicos de *Engraulis ringens* y *Sardinops sagax* en relación al peso temperatura y nivel de actividad. Bol. Inst. Mar Perú-Callao 7(3):49-68. (reprinted in 1983 as "Metabolic costs of *Engraulis ringens* and *Sardinops sagax* regarding weight, temperature and activity level". Can. Trans. Fish. Aquat. Sci. 5017. 20 p.).

437 * Villavicencio, Z. y P. Muck. 1983. La ración de mantenimiento, la densidad de mantenimiento y la eficencia de crecimiento de *Engraulis ringens* y *Sardinops sagax* como una medida de su potencia ecológica. Bol. Inst. Mar Perú-Callao 7(4):69-108. (reprinted in 1983 as Maintenance ration, maintenance density and growth efficiency of *Engraulis ringens* and *Sardinops sagax* as a measure of their ecological potential. Can. Trans. Fish. Aquat. Sci. 5021. 31 p.).

438 * Villavicencio de Muck, Z. y P. Muck. 1985. La importancia del cambio de la temperatura y de la biomasa planctonica para la producción y mortalidad de anchoveta *(Engraulis ringens)* y sardina *(Sardinops sagax)*, p. 119-128. *En* W. Arntz, A. Landa and J. Tarazona (eds.) "El Niño", su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 222 p.

439 * Vondruska, J. 1981. Postwar production, consumption, and prices of fish meal, p. 285-316. *In* M.H. Glantz and J.D. Thompson (eds.) Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York. 491 p.

440 * Walsh, J.J. 1975. A spatial simulation of the Peru upwelling ecosystem. Deep-Sea Res. 22: 1-13.

441 * Walsh, J.J. 1976. Models of the sea, p. 388-407. *In* D.H. Cushing and J.J. Walsh (eds.) The ecology of the seas. Blackwell Scientific Publications, Oxford. 467 p.

442 * Walsh, J.J. 1978. The biological consequences of interaction of the climatic, El Niño, and event scales of variability in the eastern tropical Pacific. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 173: 182-192.

443 * Walsh, J.J. 1981. A carbon budget for overfishing off Peru. Nature 290: 300-304.

444 * Walsh, J.J., T.E. Whitledge, W.E. Esaias, R.L. Smith, S.A. Huntsman and H. Santander. 1980. The spawning habitat of the Peruvian anchovy, *Engraulis ringens* J. Deep-Sea Res. 27A: 1-27.

445 * Ware, D.M. and I. Tsukayama. 1981. A possible recruitment model for the Peruvian anchovy, p. 55-61. *In* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar. Perú-Callao. Volumen Extraordinario. 288 p.

446 * Ware, D.M., B. Rojas de Mendiola and D.S. Newhouse. 1979. Behaviour of first feeding peruvian anchoveta larvae, *(Engraulis ringens)*. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 178:467-474. (reprinted in 1981 as p. 80-87. *En* L.M. Dickie and J.E. Valdivia (eds.) Investigación Cooperativa de la Anchoveta y su Ecosistema (ICANE) entre Perú y Canadá. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 288 p.).

447 Whitehead, P.J.P. 1973. The clupeoid fishes of the Guianas. Bull. Br. Mus. Natl. Hist. (Zool.), Suppl. 5: 1-227.

448 * Whitledge, T.E. 1978. Regeneration of nitrogen by zooplankton and fish in the northwest Africa and Perú upwelling ecosystems, p. 90-100. *In* R. Boje and M. Tomczak (eds.) Upwelling ecosystems. Springer-Verlag, Berlin. 303 p.

449 * Whitledge, T.E. and R.C. Dugdale. 1972. Creatine in seawater. Limnol. Oceanogr. 17(2): 309-314.

450 * Whitledge, T.E. and T. Packard. 1971. Nutrient excretion by anchovies and zooplankton in Pacific upwelling regions. Inv. Pesq. 35(1): 243-250.

451 * Wooster, W.S. 1978. Upwelling research and ocean affairs, p. 291-300. *In* R. Boje and M. Tomczak (eds.) Upwelling ecosystems. Springer-Verlag, Berlin.

452 * Yañez, E. 1988. Fluctuaciones de los principales recursos pelágicos explotados en la zona norte Chile y variaciones ambientales asociadas, p. 27. *En* Libro de Resúmenes. Simposio sobre recursos vivos y pesquerías en el Pacífico Sudeste, Viña del Mar, Chile, 9-13 Mayo 1988. (Volume of abstracts of the International Symposium on Living Resources and Fisheries in the Southeastern Pacific).

(453) Yañez, E. y L. Maritaño. 1983. Análisis histórico (1971-1980) de la pesquería pelágica de la zona norte de Chile (18°20'S-24°00'S) y estimación del estado de los recursos explotados, p. 161-177. *En* P. Arana (ed.) Análisis de pesquerías Chilenas. Universidad Católica, Valparaiso, Chile.

(454) Yañez, E.R., M.A.B. Barbieri y O.A. Barra. 1986. Evaluación de los principales recursos pelágicos explotados en la zona norte de Chile entre 1957 y 1985, p. 183-194. *En* P. Arana (ed.) La pesca en Chile. Escuela de Ciencias del Mar, Universidad Católica de Valparaiso, Chile.

455 * Zuta, S. y W. Urquizo. 1972. Temperatura promedio de la superficie del mar frente a la costa peruana período 1928-1969. Bol. Inst. Mar Perú-Callao 2(8): 459-520.

456 * Zuta, S., I. Tsukayama y R. Villanueva. 1983. El ambiente marino y las fluctuaciones de las principales poblaciones pelágicas de la costa peruana. FAO Fish. Rep. 291(2): 179-254.

457 * Zuzunaga, J. 1985. Cambios del equilibrio poblacional entre la anchoveta *(Engraulis ringens)* y la sardina *(Sardinops sagax)* en el sistema de afloramiento frente al Perú, p. 107-117. *En* W. Arntz, A. Landa and J. Tarazona (eds.) El Niño, su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 222 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; and Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany.

458 * Zuzunaga, J. 1986. Interactions between the populations of the anchovy and sardine along the Perú coast from 1970 to the present - a period of great changes, p. 26. *In* Chapman Conference on El Niño: an International Symposium, 27-31 October 1986, Guayaquil, Ecuador. Vol. of Abstracts. 45 p.

Addendum

Aguilera, E.L., G.C. Herrera y G. Castillo. 1985. Tasa de crecimiento de larvas de *Engraulis ringens* determinadas para el área de Talcahuano mediante lectura de anillos diarios en otolitos, p. 20. *In* Resúmenes V. Jornadas de Ciencias del Mar, Octubre 1985, Coquimbo, Chile.

Alvarado, E. 1966. Estudio micológico durante el proceso de elaboración de la harina de pescado en el Perú, p. 95-96. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Avila, A. 1954. Potencia deyectiva del guanay. Bol. Cient. Cia. Adm. Guano 1(2): 22-49.

Avila, E. 1966. Radioisotópos y elementos estables en el plancton, harina de anchoveta y guano del Perú, p. 96-97. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Butler, J.L. and B. Rojas de Mendiola. 1985. Growth of larval sardines off Peru. Calif. Coop. Oceanic Fish. Invest. Rep. 26: 113-118.

Cabrera, D. 1966. Situación actual de las aves guaneras en el litoral peruano, p. 103-105. *En* Libro de Resúmenes y Concluciones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Csirke, J. 1989. Changes in the catchability coefficient in the Peruvian anchoveta *(Engraulis ringens)* fishery, p. 207-219. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú, Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

DeVries, T.J. 1979. Nekton remains, diatoms and holocene upwelling off Peru. Dept. of Oceanography, University of Oregon. MS thesis.

Fernandez, J. 1966. Aspectos biológicos de utilización económica de la anchoveta en la producción de harina y guano, p. 106. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Fuentes, H. y H. Tovar. 1966. Las poblaciones de aves guaneras en Febrero de 1965, p. 103. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Garland, D.E. 1985. Anillos de crecimiento diario en otolitos de post-larvas de anchovetas *(Engraulis ringens)* y cabrilla *(Paralabrax humeralis)*, p. 32. *En* Resúmenes V. Jornadas de Ciencias del Mar, Octubre 1985, Coquimbo, Chile.

Hellevang, N. 1970. Recent developments in the peruvian anchoveta fishery. Technical Conference on Fish Finding, Purse Seining and Aimed Trawling. FAO, FII:FF/70/12.

Instituto del Mar del Perú. 1988. Informe del crucero de evaluación acústica BIC/SNP-1, BIC/HUMBOLDT 8805-07. y diagnóstico de la situación de los recursos pelágicos a Julio 1988. Inst. Mar Perú, Callao Informe Esp. IM-194. 19 p.

MacCall, A.D. 1983. Informe del grupo de trabajo sobre investigación y monitoreo de recursos. FAO Fish. Rep. 291(1): 9-42.

Málaga, A. 1966. El desove de la anchoveta *Engraulis ringens* J. en acuario, p. 90-91. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Martínez, C. y G. Böhm. 1980. Evaluación de las pesquerías pelágicas. CORFO/Inst. Fom. Pesq. (AP 80-3). Santiago, Chile. 183 p.

Martínez, C., C. Salazar, G. Böhm, A. Aranis, J. Mendieta y A. Torres. 1984. Análisis de las pesquerias pelágicas 1978-1983. CORFO/Inst. Fom. Pesq. (AP 84-26). Santiago, Chile. 133 p.

Martínez, C., C. Salazar, J. Mendieta y A. Aranis. 1986. Desarrollo y perspectivas de la pesquería pelágica en el Norte de Chile (Arica-Coquimbo), p. 165-182. *En* P. Arana (ed.) La pesca en Chile. Escuela de Ciencias del Mar, Universidad Católica de Valparaiso, Chile.

Martínez, C., C. Salazar, G. Böhm, A. Aranis, C. Estrada, V. Erbs, E. Estay, A. Torres, J. Mendieta, M. Reyes, H. Steffens y V. Bocic. 1986. Diagnóstico de las principales pesquerías nacionales pelágicas zona norte. I. Estado de situación del recurso. Corporación de Fomento de la Producción. Gerencia de Desarrollo. Inst. Fom. Pesq. Santiago, Chile. 259 p.

Mathisen, O.A. 1989. Adaptations of the anchoveta *Engraulis ringens* to the Peruvian upwelling system, p. 220-234. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18,438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú, Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Méndez, R. 1987. Cambios bioticos y efectos sobre los recursos pesqueros y pesquerías en Chile, p. 7-96. *En* R. Jordán (ed.) Fenómeno de El Niño 1982-1983 con particular referencia a sus efectos sobre los recursos y las pesquerías en el Pacífico Sudeste. Rev. Com. Perm. Pacífico Sur (16).

Miñano, J. 1966. Fecundidad de la anchoveta *(Engraulis ringens* J.*)* en la zona de Chimbote, p. 89. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biologiá, Lima, Perú, 31 Julio al 5 Agosto 1966.

Muck, P. 1989. Relationships between anchoveta spawning strategies and the spatial variability of sea surface temperature off Perú, p. 168-173. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú, Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pastor, A. 1966. Desarrollo y eclosión de huevos de anchoveta *(Engraulis ringens* J.*)* en condiciones experimentales a bordo del B.A.P. "Unanue", p. 93. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Pauly, D. 1989. Interactions and dynamics of the Peruvian upwelling system: a postscript, p. 404-407. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pellón, J., N. Peña y J. Mendo. 1988. Reporte de datos de madurez sexual de la anchoveta peruana *(Engraulis ringens)* durante el período 1961-1987. Informe Inst. Mar Perú-Callao (92). 77 p.

Santander, H. y O. Sandoval de Castillo. 1966. Observaciones en huevos de anchoveta de apariencia anormal en el crucero 6408, p. 93-95. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Santander, H., O. Sandoval de Castillo y F. Vásquez. 1966. El desove de la anchoveta en el periódo 1964-1965 y 1965-1966, p. 89-90. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biologiá, Lima, Perú, 31 Julio al 5 Agosto 1966.

Sears, M. 1954. Notas sobre la corriente constanera del Perú. I. Introducción a la ecología de la Bahía de Pisco. Bol. Cient. Cia. Adm. Guano 1(2): 133-179.

Tsukayama, I. 1966. Estractura de la población de anchoveta *Engraulis ringens* Jenyns, por el análisis del número de radios dorsales, p. 98-99. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Valdivia, J. 1966. El factor de condición relativo de anchoveta 1964-1965, p. 101-102. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Valdivia, J. I. Tsukayama y J. Miñano. 1966. Estimado del reclutamiento de la anchoveta *Engraulis ringens*, Jenyns, p. 99-100. *En* Libro de Resúmenes y Conclusiones 1er Congreso Nacional de Biología, Lima, Perú, 31 Julio al 5 Agosto 1966.

Villanueva, R. 1970. The peruvian Eureka programme rapid acoustic surveys using fishing vessels. Technical Conference on Fish Finding, Purse Seining and Aimed Trawling. FAO, FII:FF/70/5. 12 p.

Villavicencio de Muck, Z. 1989. Tetracycline labelling for age and growth studies in fishes, with emphasis on the Peruvian anchoveta, p. 174-178. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Yáñez, E.R. 1988. Principales recursos pelágicos explotados en Chile y su relación con cambios del medio ambiente, p. 14-15. *En* VII Jornadas en Pesquerías Chilenas: Perspectivas de la Actividad Pesquería en Chile, 29-31 Augusto 1988. Escuela del Ciencias del Mar, Universidad Católica del Valparaiso. Volume of Abstracts, 55 p.

Yáñez, E. and M.A. Barbieri. 1986. Principal pelagic resources exploited in northern Chile and their relationship to environmental variations, p. 197-219. *In* T. Wyatt and M.G. Larrañeta (eds.) Long-term changes in marine fish population. A symposium held in Vigo, Spain, 18-21 November 1986, Vigo.

Yáñez, E., M.A. Barbieri y O. Barra. 1986. Un análisis sobre las causas del colapso de la pesquería de anchoveta (*Engraulis ringens*) realizada en la zona Norte de Chile, p. 43. *In* Chapman Conference on El Niño: an International Symposium, 27-31 October 1986, Guayaquil, Ecuador, Vol. of Abstracts, 45 p.

Zuta, S. and L.A. Flores. 1980. Oceanography development in Peru, p. 642-655. *In* M. Sears and D. Merriman (eds.) Oceanography: the past. Springer-Verlag, Berlin.

Abundance of Hake Larvae and Its Relationship to Hake and Anchoveta Biomasses off Peru*

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Abstract

An analysis of 43 maps of hake larvae *(Merluccius gayi)* distribution off the Peruvian coast, from survey areas between 3°30' and 18°S for 1966 to 1987, was performed and an index of larval abundance was calculated. This index, plotted against anchoveta biomass, showed an inverse relationship, suggesting a negative impact of anchoveta on hake eggs and larvae and on the distribution area of the hake larvae. The latter increased two- to fourfold in the period of low anchoveta biomass from 1972 to 1983. The hake larvae abundance index plotted against spawning stock biomass showed the expected positive relationship. The seasonal and interyear changes of the distribution of both larvae and adult stocks are discussed with reference to abiotic and biotic factors.

Resumen

Se efectuó un análisis de 43 mapas de distribución de larvas de merluza *(Merluccius gayi)* frente a la costa peruana, obtenidos de cruceros realizados de 3°30' hasta 18°S para el periódo entre 1966 y 1987 y se calculó un índice de abundancia larval. Este índice graficado contra la biomasa de la anchoveta, mostró una relación inversa, sugiriendo un impacto negativo de la anchoveta sobre los huevos y larvas de merluza y en el área de distribución de las larvas. Esta última se incrementó dos a cuatro veces durante el período de baja biomasa de la anchoveta, en los años de 1972 a 1983. El índice de abundancia de larvas graficado contra la biomasa del stock desovante indicó la relación positiva esperada. Los cambios estacionales e interanuales de la distribución de ambos, larvas y adultos, se discuten con referencia a factores bióticos y abióticos.

Introduction

The interactions in the 1970s between the major pelagic fish of the Peruvian upwelling ecosystem, i.e., anchoveta *(Engraulis ringens)*, sardine *(Sardinops sagax)*, mackerel *(Scomber japonicus)* and horse mackerel *(Trachurus murphyi)* on the one hand and the main demersal

*PROCOPA Contribution No. 94.

species, hake *(Merluccius gayi)* on the other hand, resulted in a great abundance and area extension by the sardine and apparently also by horse mackerel and hake. This requires that we include the early life history stages of these species in our investigations of the dynamics of the Peruvian upwelling ecosystem, and that we should look for relationships between the abundance of eggs/larvae and adult biomasses.

Until some years ago, the demersal species have been neglected in discussions on interspecific relationships in the Peruvian ecosystem. Hake is the most abundant demersal species in the Peruvian coastal ecosystem. Normally, it is distributed from the Peru/Ecuador border down to 10°S. However, following the "El Niño" events of 1982-1983, the habitat of hake extended to 17°38'S (Velez and Zeballos 1983).

Previous studies on the reproduction of hake off Peru and Chile include Fischer (1959), Miranda (1966), Saetersdal and Villegas (1968), Fischer and Balbontin (1970), Balbontin and Fischer (1981), and Alheit (1986). Fig. 1 depicts hake larvae of various stages, such as discussed in this contribution.

Previous studies on hake recruitment (Wosnitza-Mendo and Espino 1986) suggested an influence of pelagic fish species, mainly anchoveta, on the early stages of hake, e.g., through predation of adult anchoveta on hake eggs (and larvae?) and interlarval (anchoveta/hake) competition. The analysis of data from 43 surveys, conducted off Peru from 1966 to 1987 provided information on hake larval abundances and on the latitudinal distribution of spawning area.

Although these surveys were not specially designed as larval survey, the data obtained allow to demonstrate some relationships between hake larvae and biomasses of hake and anchoveta.

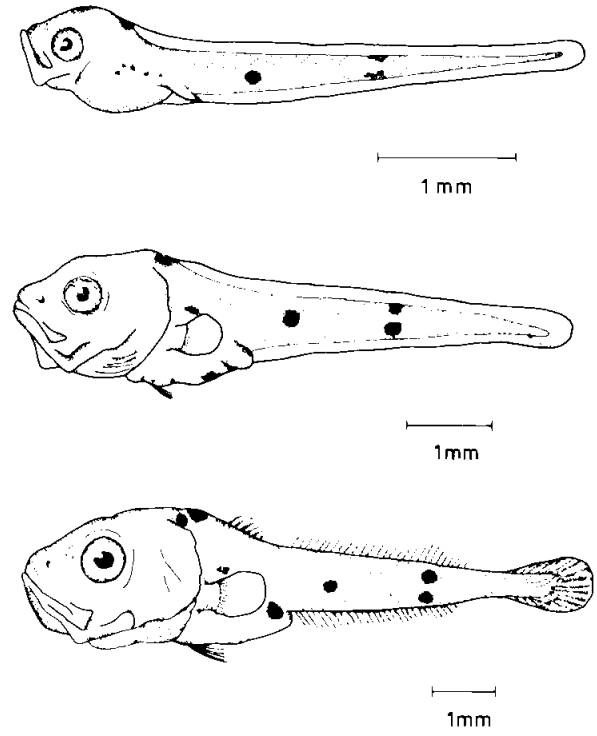

Fig. 1. Larvae of Peruvian hake *(Merluccius gayi)* (from Sandoval de Castillo 1979).
Fig. 1. Desarrollo de la larva de la merluza peruana (Merluccius gayi) *(tomado de Sandoval de Castillo 1979).*

Materials and Methods

The data used stem from 43 surveys conducted from 1966 to 1987 (Table 1), the same as used by Santander (1987) to discuss anchoveta egg distributions. Sampling was performed as described for anchoveta eggs by Santander and Sandoval de Castillo (1969) and Santander (1987), who also described the sampling gear. The surveys ranged from 10 nautical miles (n.m.) to 220 n.m. offshore and from 3°30'S to the Chilean border.

Table 1. Key statistics of the ichthyoplankton surveys considered in this contribution.[a]
Tabla 1. Datos estadísticos de los cruceros de ictioplancton considerados en esta contribución.

Fig. no./ Map no. in Santander (1987)	Year	Month	Lat. range of sampling area	Larval abundance (No/m2)	Lat. range of distr. area (n.m.)	Weighted larval abundance	Hake spawning area
6/12	1966	8/9	04°00'-18°43'	2.73	122	333.06	06°48'-08°50'
6/15	1967	8/9	04°15'-20°49'	1.96	165	323.40	04°15'-07°00'
7/16		11/12	04°00'-19°05'	0.13	42	5.46	05°28'-06°10'
7/18	1968	9/10	04°04'-19°19'	2.28	50	114.00	06°30'-07°20'
7/22	1969	8/9	06°56'-12°18'	0.47	145	68.15	06°00'-09°25'
7/28	1971	8/9	04°00'-17°40'	0.85	70	59.50	06°00'-07°10'
-/30	1972	2/3	03°16'-18°13'	0.13	1[b]	0.13	11°19'-11°21'
8/34		8/9	05°10'-18°25'	0.31	535	165.85	06°00'-14°55'
8/44	1973	9	06°02'-18°36'	1.24	678	840.72	06°02'-17°20'
8/45		11	05°15'-18°20'	0.25	698	174.50	05°27'-17°05'
8/46	1974	2	04°05'-13°55'	0.11	50	5.50	06°12'-07°02'
9/49		9	05°45'-18°25'	2.35	355	834.25	05°50'-11°45'
9/50		11	04°30'-18°15'	0.16	170	27.20	05°00'-07°50'
9/51	1975	2	06°05'-18°20'	0.16	115	18.40	06°35'-08°30'
9/53		9	04°25'-18°33'	0.96	502	481.92	05°00'-13°22'
10/54		11/12	04°00'-12°00'	0.85	72	61.20	04°40'-05°52'
10/57	1976	8	05°00'-18°12'	0.48	415	199.20	06°20'-13°15'
10/58		10/11	03°30'-18°18'	0.87	508	441.96	03°32'-12°00'
10/59	1977	3	04°00'-18°00'	0.22	332	73.04	06°28'-12°00'
11/62		8	05°10'-18°00'	3.49	470	1,640.30	05°28'-13°18'
11/64		10/11	05°30'-18°30'	1.19	348	414.12	06°02'-11°50'
11/66	1978	3/4	05°50'-18°17'	1.21	312	377.52	06°38'-11°50'
11/67		7	05°00'-18°20'	10.58	377	3,988.66	05°18'-11°35'
12/69		11/12	04°00'-18°00'	0.35	132	46.20	04°38'-06°50'
12/70	1979	2	03°30'-18°17'	0.13	100	13.00	06°40'-08°20'
12/72		9	03°30'-18°17'	2.96	510	1,509.60	03°30'-12°00'
12/73		11/12	03°45'-18°21'	0.38	85	32.30	04°30'-05°55'
13/74	1980	2	04°30'-18°17'	0.26	217	56.42	04°38'-08°15'
13/75		9	03°00'-18°20'	0.74	358	264.92	04°00'-09°58'
-/78	1981	8/9	06°14'-14°00'	0.28	60[c]	16.80	06°30'-07°30'
13/79		10	04°50'-18°20'	0.85	330	280.50	03°40'-09°10'
13/80	1982	2/3	03°40'-18°10'	0.98	205	200.90	03°50'-07°15'
14/81		9	03°30'-18°20'	5.46	385	2,102.10	03°35'-10°00'
14/-	1983	8	08°12'-14°27'	0.26	180	46.80	08°30'-11°30'
-/84	1984	8/9	04°00'-14°00'	0.09	1[b]	0.09	04°49'-04°51'
-/85		11/12	03°27'-08°58'	0.58	120[b]	69.60	03°40'-05°40'
-/86	1985	2/3	03°54'-13°43'	0.06	60[c]	3.60	05°00'-06°00'
14/87		3/4	05°04'-08°51'	6.08	180	1,094.40	03°00'-06°00'
-/88		7/8	04°58'-18°00'	0.08	60[c]	4.80	05°00'-06°00'
14/89		8/9	03°35'-14°02'	0.08	180	14.40	03°00'-06°00'
-/90	1986	4	03°30'-12°59'	0.05	180[c]	9.00	05°20'-08°20'
15/-	1987	1/2	03°27'-09°36'	7.18	333	2,390.94	03°27'-09°00'

[a]See Table 3 in Santander (1987) and Pauly and Soriano (this vol.) for cross-reference to anchoveta eggs collected in these surveys.
[b]Map not available.
[c]Map superfluous (2 or 3 stations only).

Monthly anchoveta biomasses were taken from Pauly et al. (1987) and hake biomasses from Espino and Wosnitza-Mendo (this vol.). The relative larval abundance (No/m2) was weighed by the latitudinal distribution area of hake larvae to provide an index of total abundance (A_L).

Results and Discussion

Hake spawn during the whole year (Fig. 2), but a major peak usually occurs in August/September (Fig. 3). In general, about 5 to 15% (in 1972 up to 25%) of the females are ready to spawn in any given month.

Table 1 suggests that the highest extension of spawning area generally occurs during the austral winter (July-September) (Santander and Sandoval de Castillo 1981). For interyear comparisons, we used only the winter cruises, during which larval abundance fluctuates between 0.28 and 10.6 larvae/m2 (Table 2). These numbers, weighed by the latitudinal distribution area, were plotted against anchoveta biomass. As might be seen from Fig. 4, low weighed hake larvae abundances (A_L) occur when anchoveta are very abundant.

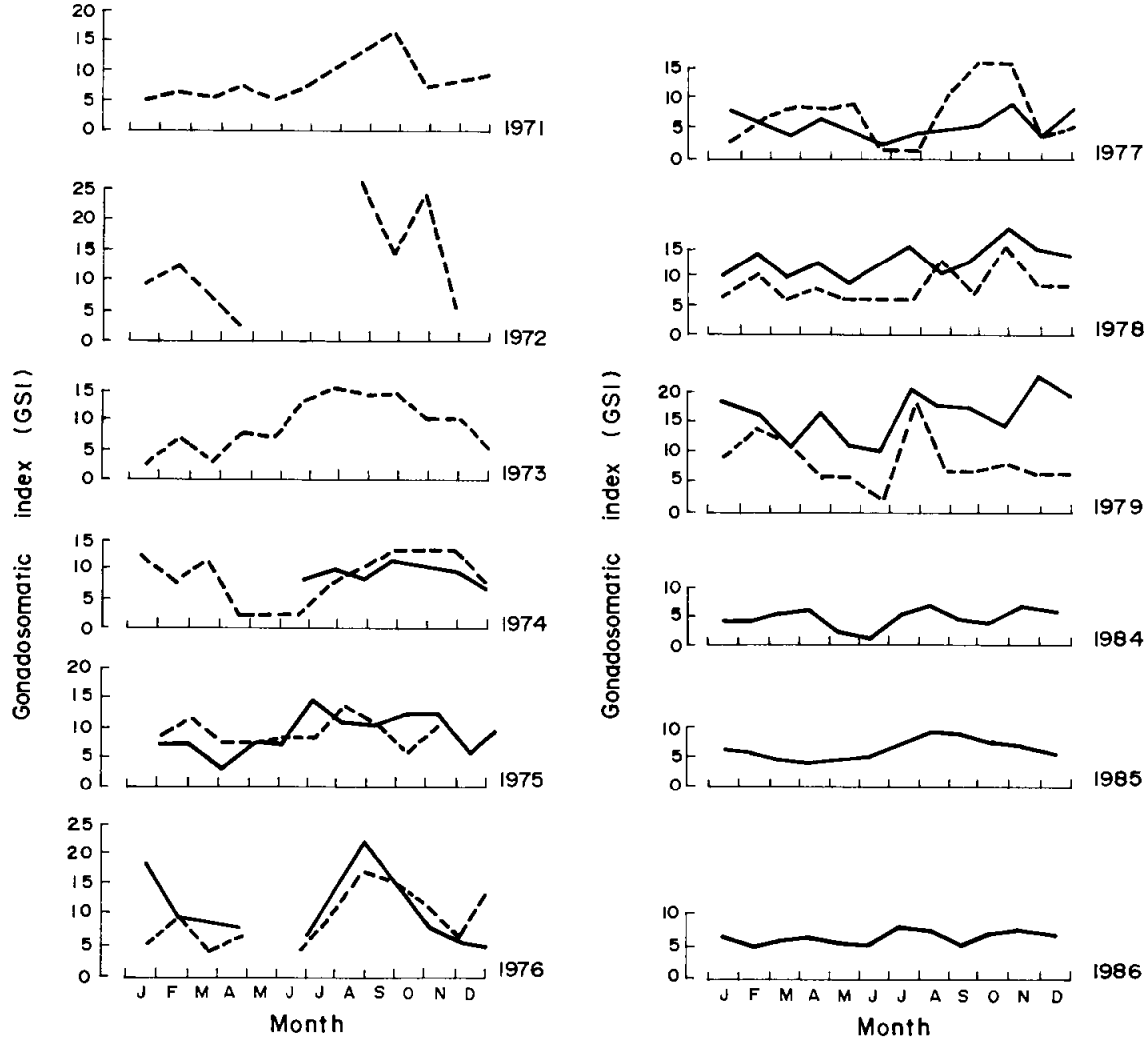

Fig. 2. Annual spawning cycle of Peruvian hake *(Merluccius gayi)* as expressed by its gonadosomatic index (_____) and/or the percentage of maturity stages V and VI (-----) (modified from Canal 1988).

Fig. 2. Ciclo anual de desove de la merluza peruana (Merluccius gayi) *expresada por su índice gonadosomático (_____) y/o el porcentaje de los estados de madurez V y VI (-----) (modificado de Canal 1988).*

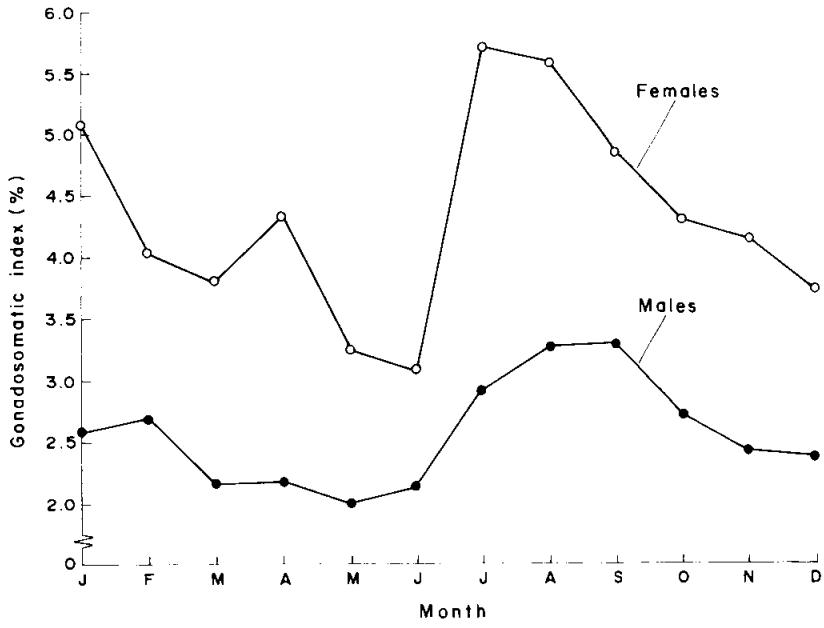

Fig. 3. Mean monthly gonadosomatic index of Peruvian hake from 1971 to 1980.
Fig. 3. Promedio mensual del índice gonadosomático de la merluza peruana en el período 1971-1980.

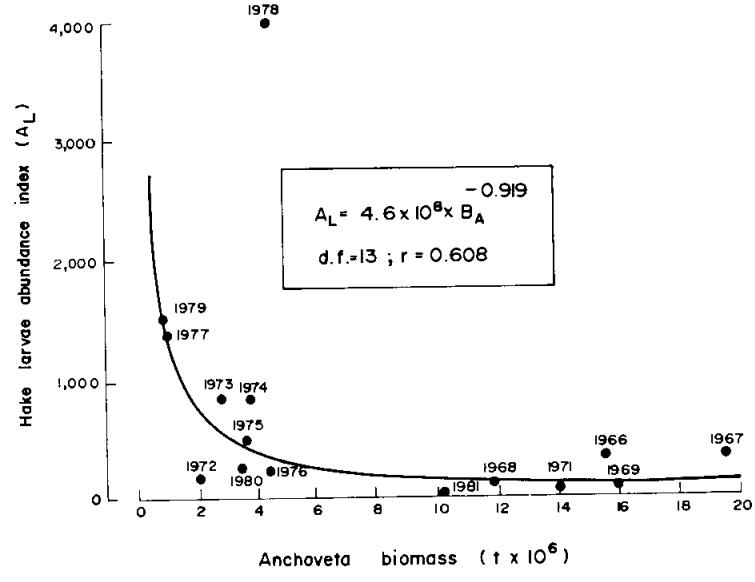

Fig. 4. Relationship between abundance of hake larvae and anchoveta biomass off Peru (based on data in Table 2).
Fig. 4. Relación entre la abundancia de larvas de merluza y la biomasa de anchoveta frente al Perú (basada en datos de Tabla 2).

This inverse relationship is mainly due to an extension of the distribution area of hake larvae. Before 1972 and after 1983, hake larvae normally did not extend to more than 8-9°S (i.e., an extension of 3 degrees). From 1972 to 1983 and in several years thereafter, hake larvae extended their distribution, in winter by 6-12 degrees), i.e., two- to fourfold (see also Santander and Sandoval de Castillo 1981).

The relation between hake larvae and hake biomass is given in Fig. 5. A stock-recruitment relationship for hake (spawning stock against two-year-old recruits) was described by Wosnitza-Mendo and Espino (1986) and Espino and Wosnitza-Mendo (1988), the latter including density-dependence (i.e., cannibalism) by means of a Ricker function. However, cannibalism on hake younger than two years does not occur, so the relationship between hake biomass and hake larval abundance continues to increase at high hake biomass levels. The values of our hake larval abundance index were estimated independently from the hake biomass estimates, which were obtained by cohort analysis, and we can exclude statistical artifacts as the cause for the

Table 2. Data used to estimate parameters of curves in Figs. 4 and 5 and of Equation (1).
Tabla 2. Datos usados para estimar los parámetros de las curvas en las figuras 4 y 5 y de la ecuación (1).

Year	Month	Hake larval[a] abundance of No/m2	Anchoveta[b] biomass (x 10^3 t)	Hake biomass (t)[c]	Weighted larval abundance (A_L)[d]
1966	8/9	2.73	15,479	180,415	333.06
1967	8/9	1.96	19,530	194,659	323.40
1968	9/10	2.28	11,873	182,012	114.00
1969	8/9	0.47	15,897	173,040	68.15
1971	8/9	0.85	14,018	200,796	59.50
1972	8/9	0.31	2,047	262,260	165.85
1973	9	1.24	2,822	407,941	840.72
1974	9	2.35	3,854	382,542	834.25
1975	9	0.96	3,609	361,096	481.92
1976	8	0.48	4,422	502,632	199.20
1977	8	3.49	1,171	613,403	1,640.30
1978	7	10.58	4,519	670,788	3,988.66
1979	9	2.96	1,064	363,600	1,509.60
1980	9	0.74	3,447	315,946	264.92
1981	8/9	0.28	10,261	179,923	16.80

[a]From Table 1.
[b]From Pauly et al. (1987).
[c]From Espino and Wosnitza-Mendo (this vol.).
[d]See text for definition.

relationship in Fig. 5. Thus, the relationship between hake biomass and hake larvae is confirmed. No relationship, on the other hand, seems to exist between hake larval abundance and the number of subsequent two-year old hake recruits. Thus, between the larval stages of hake and their recruitment to the fishery two years later, mortality is determined by processes not accounted for here.

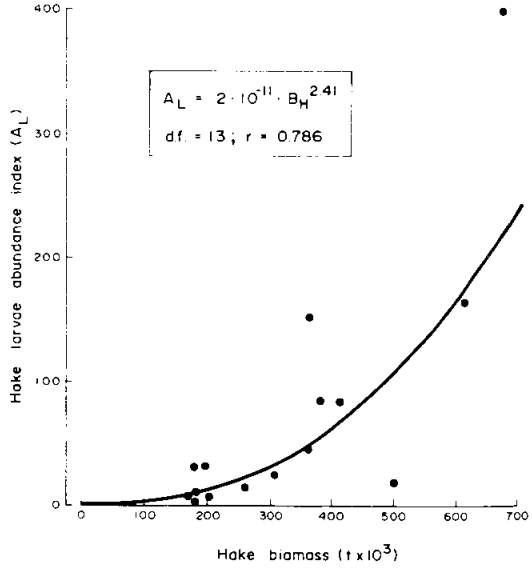

Fig. 5. Relationship between abundance of hake larvae and hake biomass off Peru (based on data in Table 2).
Fig. 5. Relación entre la abundancia de larvas y biomasa de merluza frente al Perú (basada en datos de Tabla 2).

Finally, a multiple linear regression between our hake larval abundance index (A_L), anchoveta biomass (B_A) and hake biomass (B_H) was computed, based on the data in Table 2. This resulted in:

$$\log_{10}A_L = -9.7-0.0681 \log_{10}B_A+2.31 \log_{10}B_H \qquad ...1)$$

whose slopes have the expected signs and which, with R =0.787 and d.f.=12, is significant ($P<0.01$). The slope associated with anchoveta biomass (i.e., -0.0681) has, however, a very high standard error (0.406) suggesting that anchoveta may have no effect on the abundance of hake larvae once the (negative) correlation between anchoveta and hake biomass is accounted for.

The aim of the present study was to analyze: a) the influence of anchoveta biomass on larval hake abundance and b) the relationship between adult and larval hake.

Although statistically significant relationships were identified, the most striking result is the increment of the larval distribution area of hake from 1972 to 1983.

Espino and Wosnitza-Mendo (1988) discuss the size of adult hake distribution area as a function of environmental conditions (mainly the oxygen content of deeper water layers), which increase in austral summer and autumn and decrease in austral winter and spring. During "El Niño" events, the distribution area of hake increases extraordinarily, depending on their intensity and duration of the warm anomaly (see also Muck, this vol.).

On the other hand, hake larvae usually cover a greater area in austral winter than in summer and maintained a two- to fourfold area extension over a 12-year period (1972-1983). This is probably not caused by the range extension of adult hake; rather, it can be attributed to the drastic reduction of anchoveta biomasses which occurred in 1972, as was suggested by Santander and Sandoval de Castillo (1981).

This suggests that, for hake, winter spawning plus higher survival rate is more important than summer spawning alone. Also, the reduced biomass of anchoveta now allow hake to "rear" their larvae over a greater area with reduced predation. Figs. 6 to 15 illustrate this range extension over the period from 1966 to 1987.

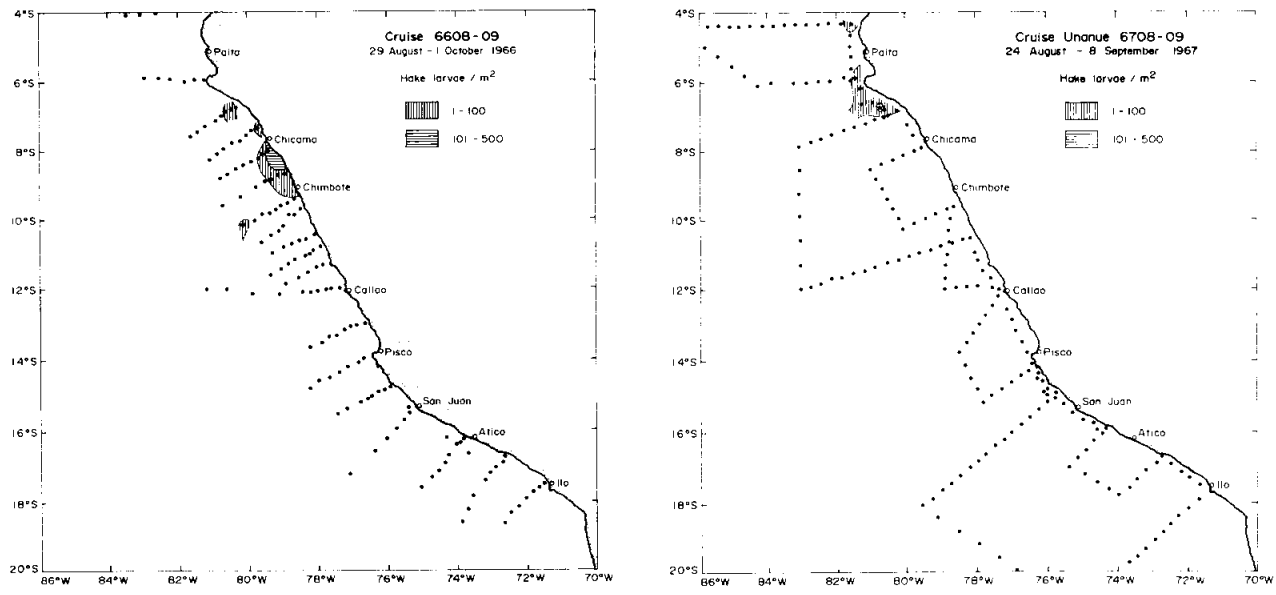

Fig. 6. Distribution of hake larvae along the Peruvian coast (see also Table 1). *Left:* 29 August-1 October 1966; *right:* 24 August-8 September 1967.

Fig. 6. Distribución de larvas de merluza fuera de la costa peruana (ver tambien Tabla 1). Izquierda: 29 de Agosto-1 de Octubre 1966; derecha: 24 de Agosto-8 de Septiembre 1967.

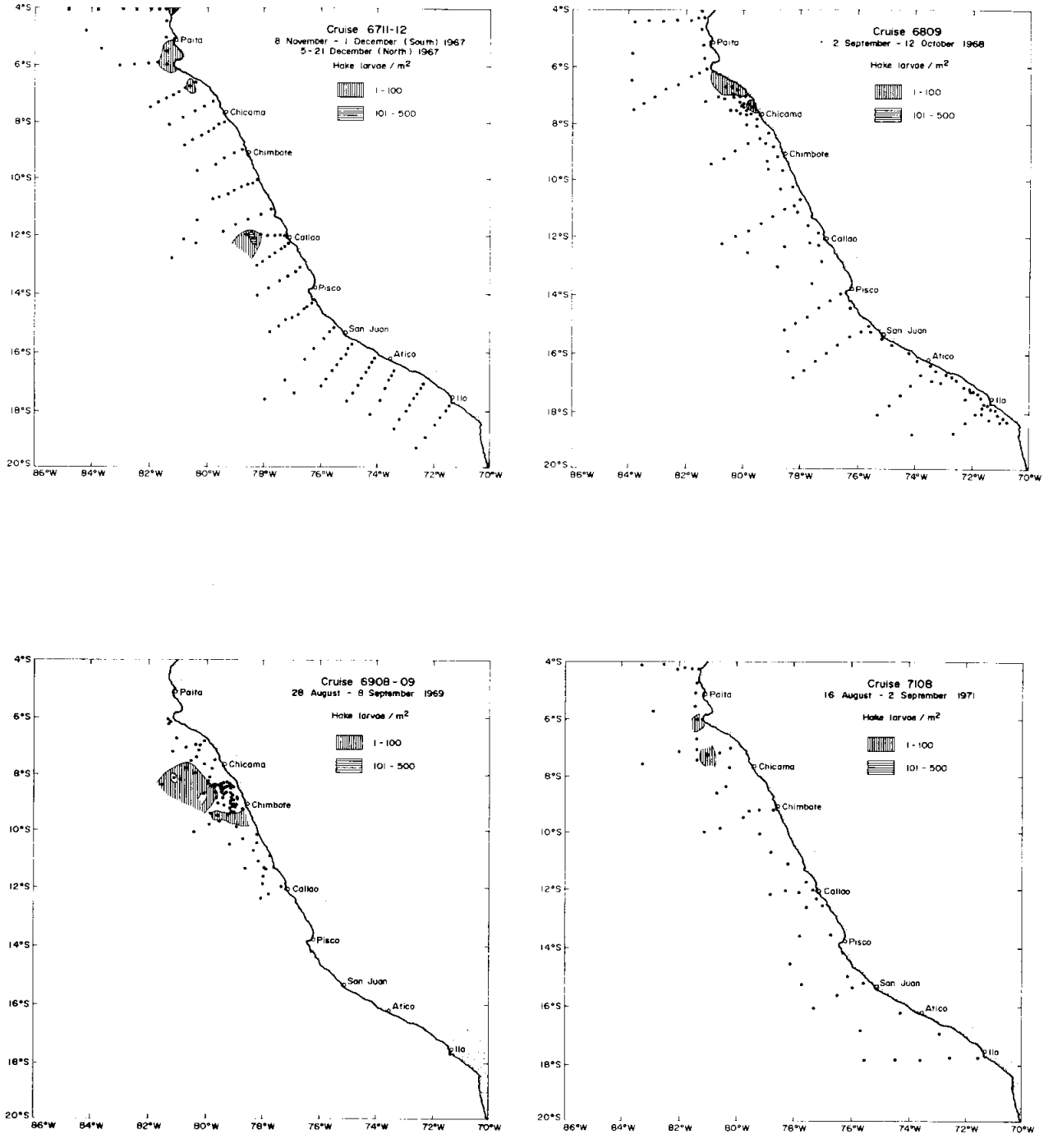

Fig. 7. Distribution of hake larvae along the Peruvian coast (see also Table 1). Upper graphs - left: 8 November-21 December 1967; right: 2 September-12 October 1968. Lower graphs - left: 28 August-8 September 1969; right: 16 August-2 September 1971.

Fig. 7. Distribución de larvas de merluza fuera de la costa peruana (ver también Tabla 1). Cuadros superiores - izquierda: 8 de Noviembre-21 de Diciembre 1967; derecha: 2 de Septiembre-12 de Octubre 1968. Cuadros inferiores - izquierda: 28 de Agosto-8 de Septiembre 1969; derecha: 16 de Agosto-2 de Septiembre 1971.

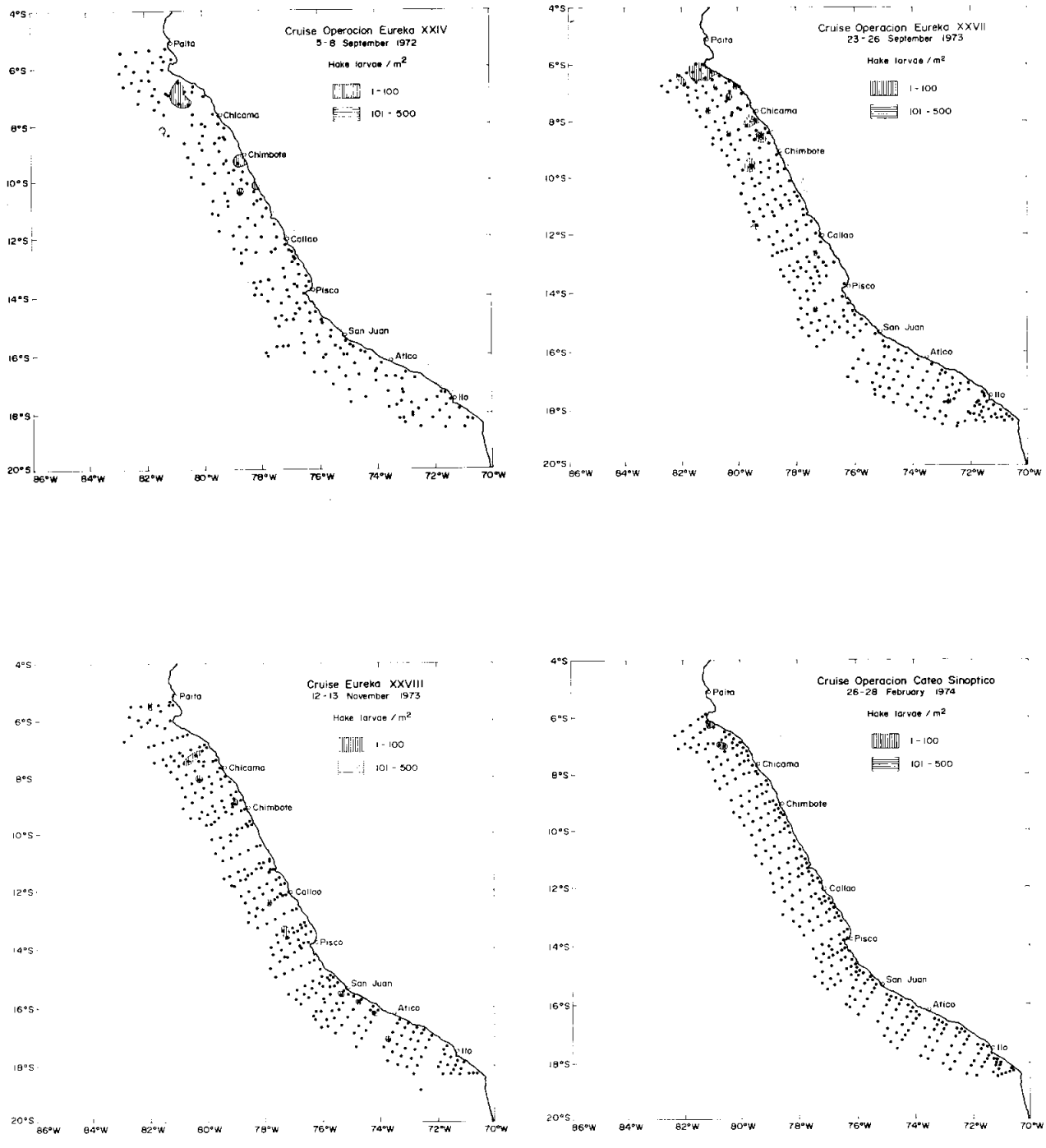

Fig. 8. Distribution of hake larvae along the Peruvian coast (see also Table 1). Upper graphs - left: 5-8 September 1972; right: 23-26 September 1973. Lower graphs - left: 12-13 November 1973; right: 26-28 February 1974.

Fig. 8. Distribución de larvas de merluza fuera de la costa peruana (ver también Tabla 1). Cuadros superiores - izquierda: 5-8 de Septiembre 1972; derecha: 23-26 de Septiembre 1973. Cuadros inferiores - izquierda: 12-13 de Noviembre 1973; derecha: 26-28 de Febrero 1974.

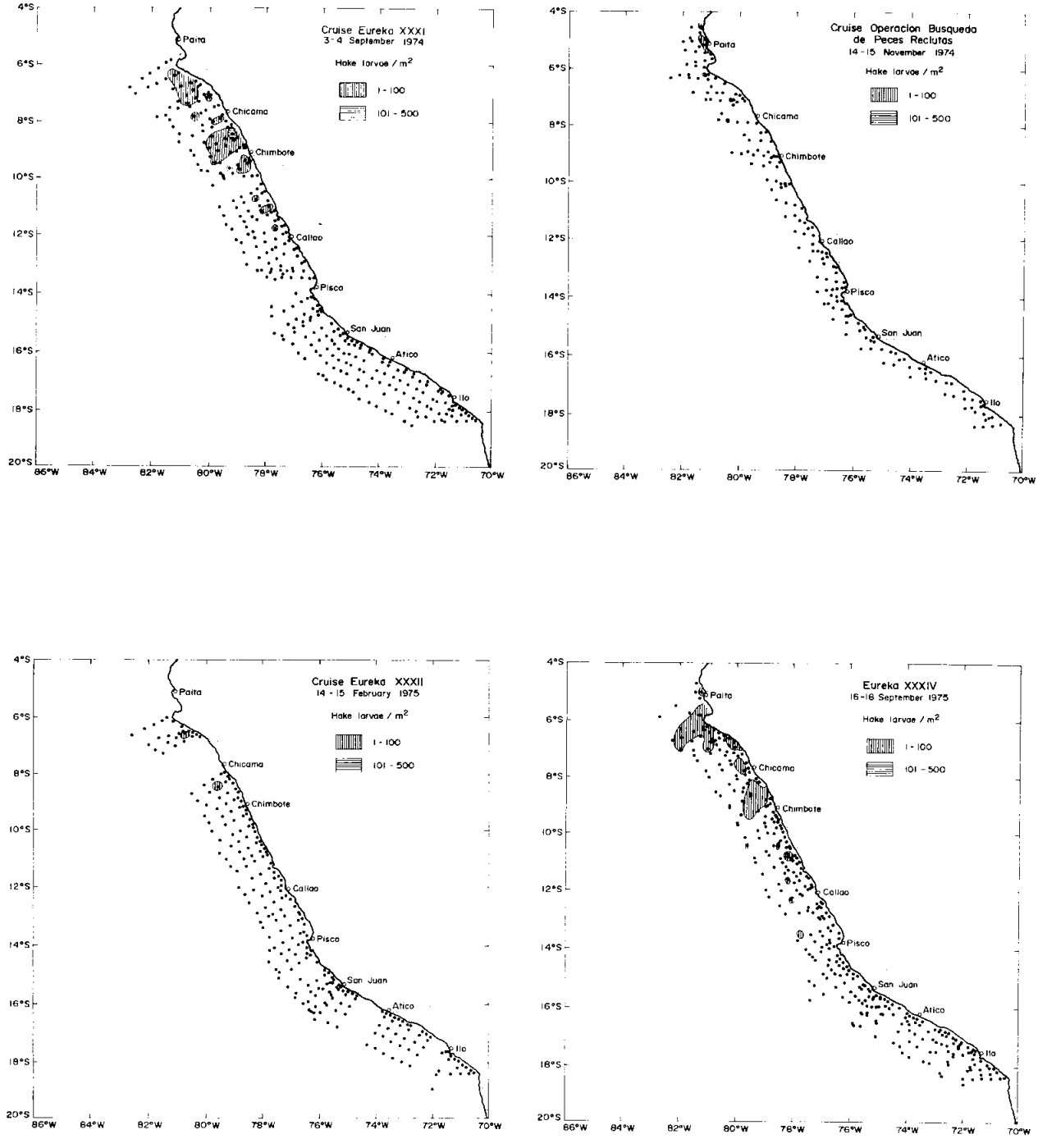

Fig. 9. Distribution of hake larvae along the Peruvian coast (see also Table 1). Upper graphs - left: 3-4 September 1974; right: 14-15 November 1974. Lower graphs - left: 14-15 February 1975; right; 16-18 September 1975.

Fig. 9. Distribución de larvas de merluza fuera de la costa peruana (ver también Tabla 1). Cuadros superiores - izquierda: 3-4 de Septiembre 1974; derecha: 14-15 de Noviembre 1974. Cuadros inferiores - izquierda: 14-15 de Febrero 1975; derecha: 16-18 de Septiembre 1975.

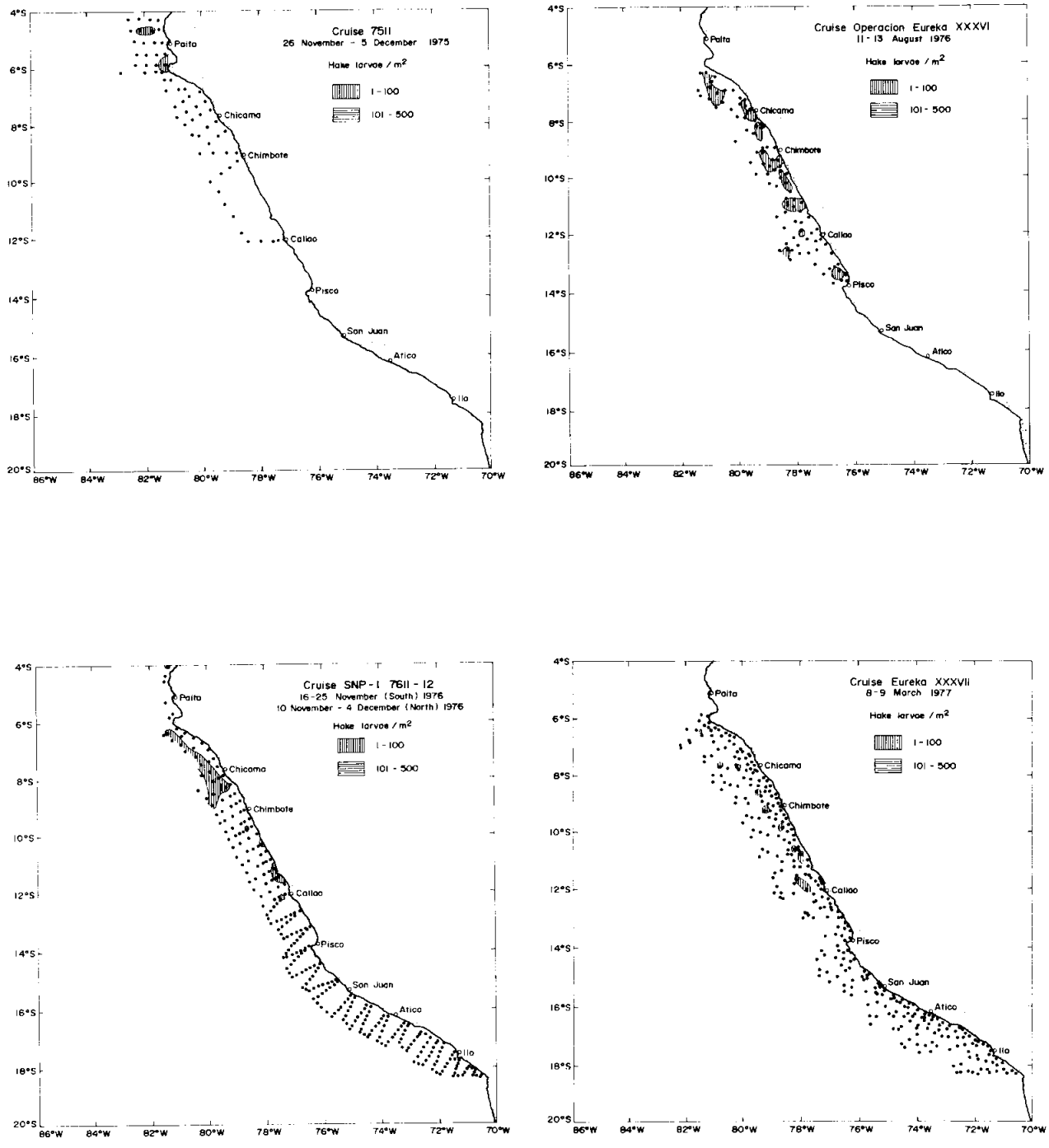

Fig. 10. Distribution of hake larvae along the Peruvian coast (see also Table 1). Upper graphs - left: 26 November-5 December 1975; right: 11-13 August 1976. Lower graphs - left: 16 November-4 December 1976; right: 8-9 March 1977.

Fig. 10. Distribución de larvas de merluza fuera de la costa peruana (ver también Tabla 1). Cuadros superiores - izquierda: 26 de Noviembre-5 de Diciembre 1975; derecha: 11-13 de Agosto 1976. Cuadros inferiores - izquierda: 16 de Noviembre-4 de Diciembre 1976; derecha: 8-9 de Marzo 1977.

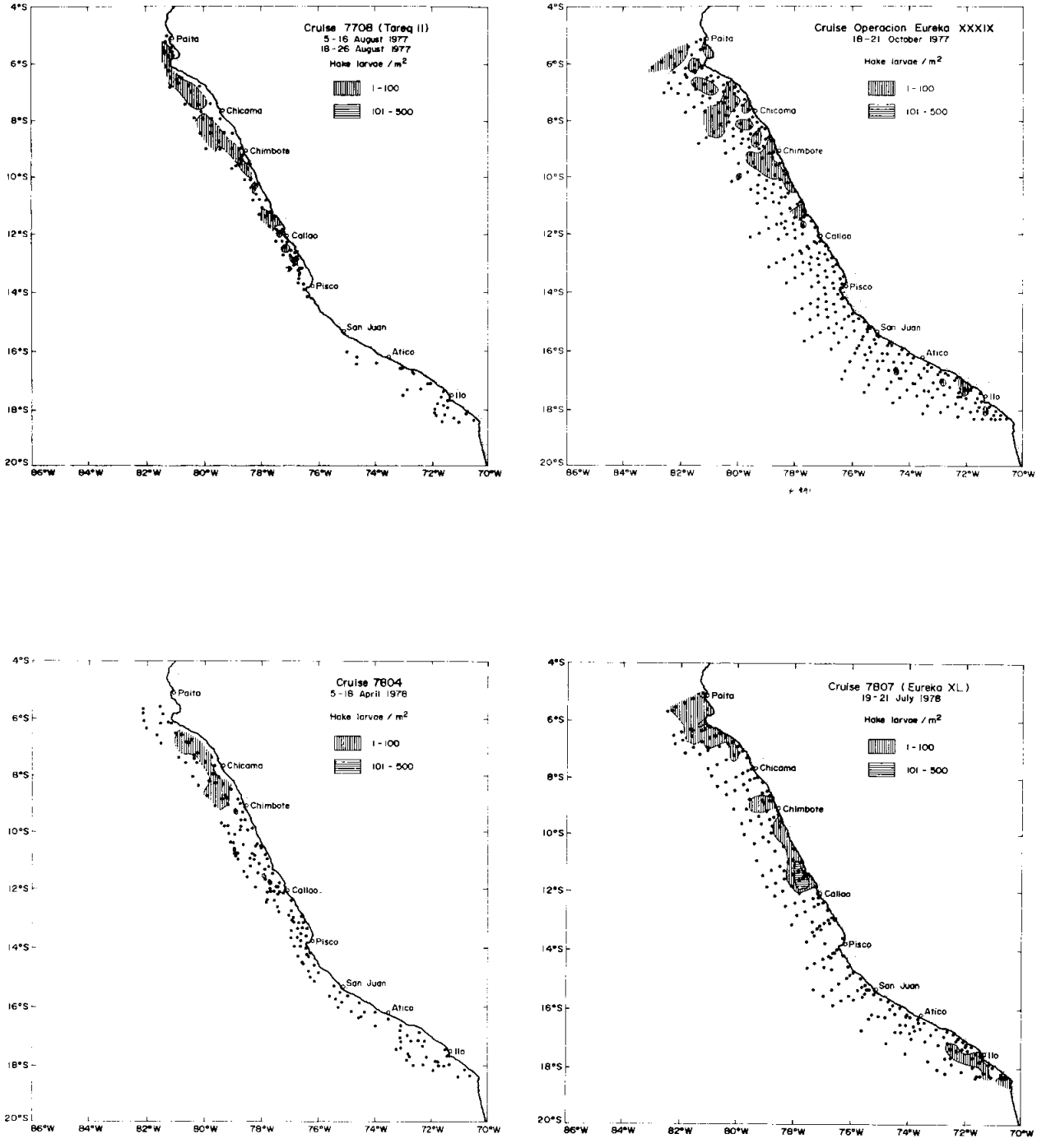

Fig. 11. Distribution of hake larvae along the Peruvian coast (see also Table 1). Upper graphs - left: 5-26 August 1977; right: 18-21 October 1977. Lower graphs - left: 5-18 April 1978; right: 19-21 July 1978.

Fig. 11. Distribución de larvas de merluza fuera de la costa peruana (ver también Tabla 1). Cuadros superiores - izquierda: 5-26 de Agosto 1977; derecha: 18-21 de Octubre 1977. Cuadros inferiores - izquierda: 5-18 de Abril 1978; derecha: 19-21 de Julio 1978.

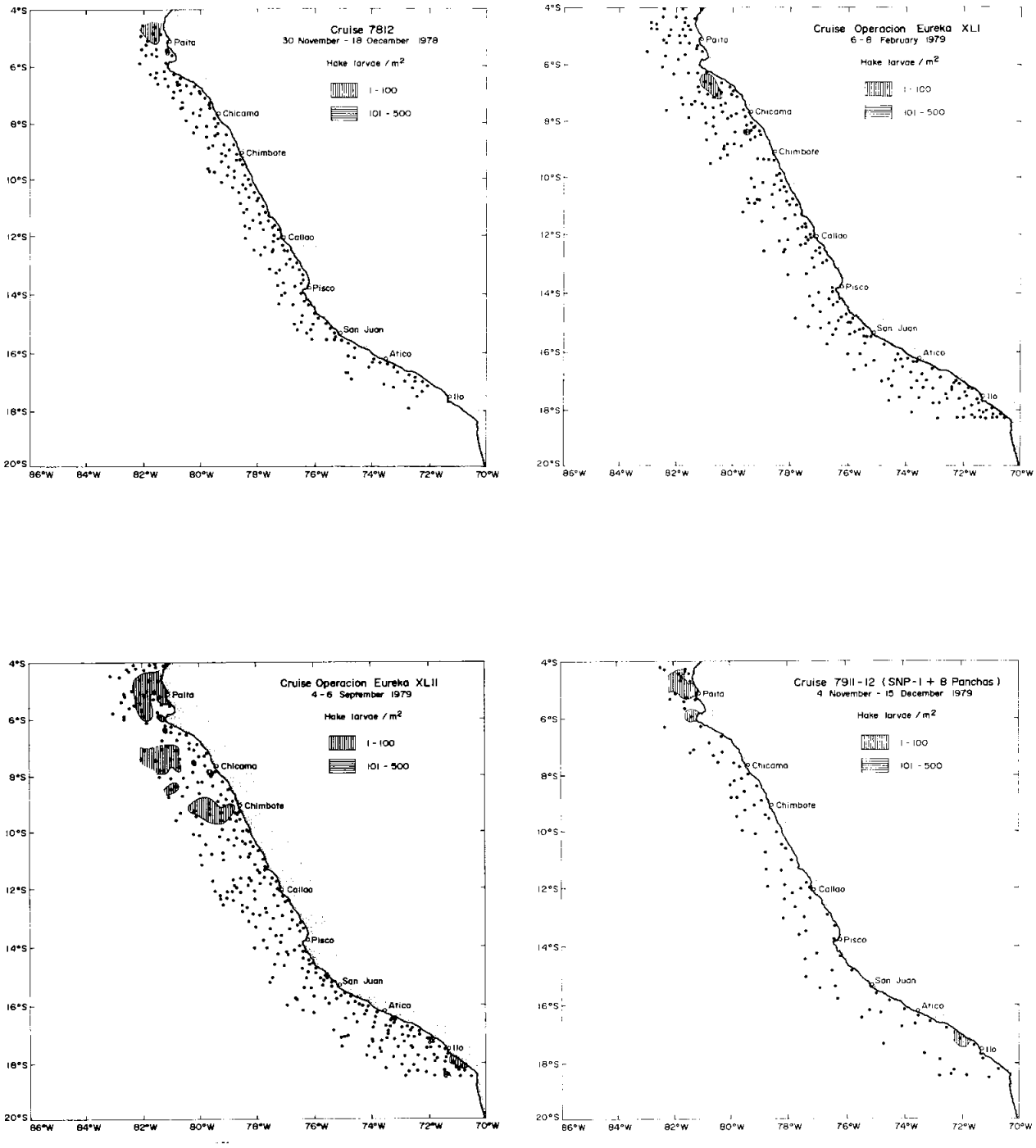

Fig. 12. Distribution of hake larvae along the Peruvian coast (see also Table 1). Upper graphs - left: 30 November-18 December 1978; right: 6-8 February 1979. Lower graphs - left: 4-6 September 1979; right: 4 November-15 December 1979.

Fig. 12. Distribución de larvas de merluza fuera de la costa peruana (ver también Tabla 1). Cuadros superiores - izquierda: 30 de Noviembre-18 de Diciembre 1978; derecha: 6-8 de Febrero 1979. Cuadros inferiores - izquierda: 4-6 de Septiembre 1979; derecha: 4 de Noviembre-15 de Diciembre 1979.

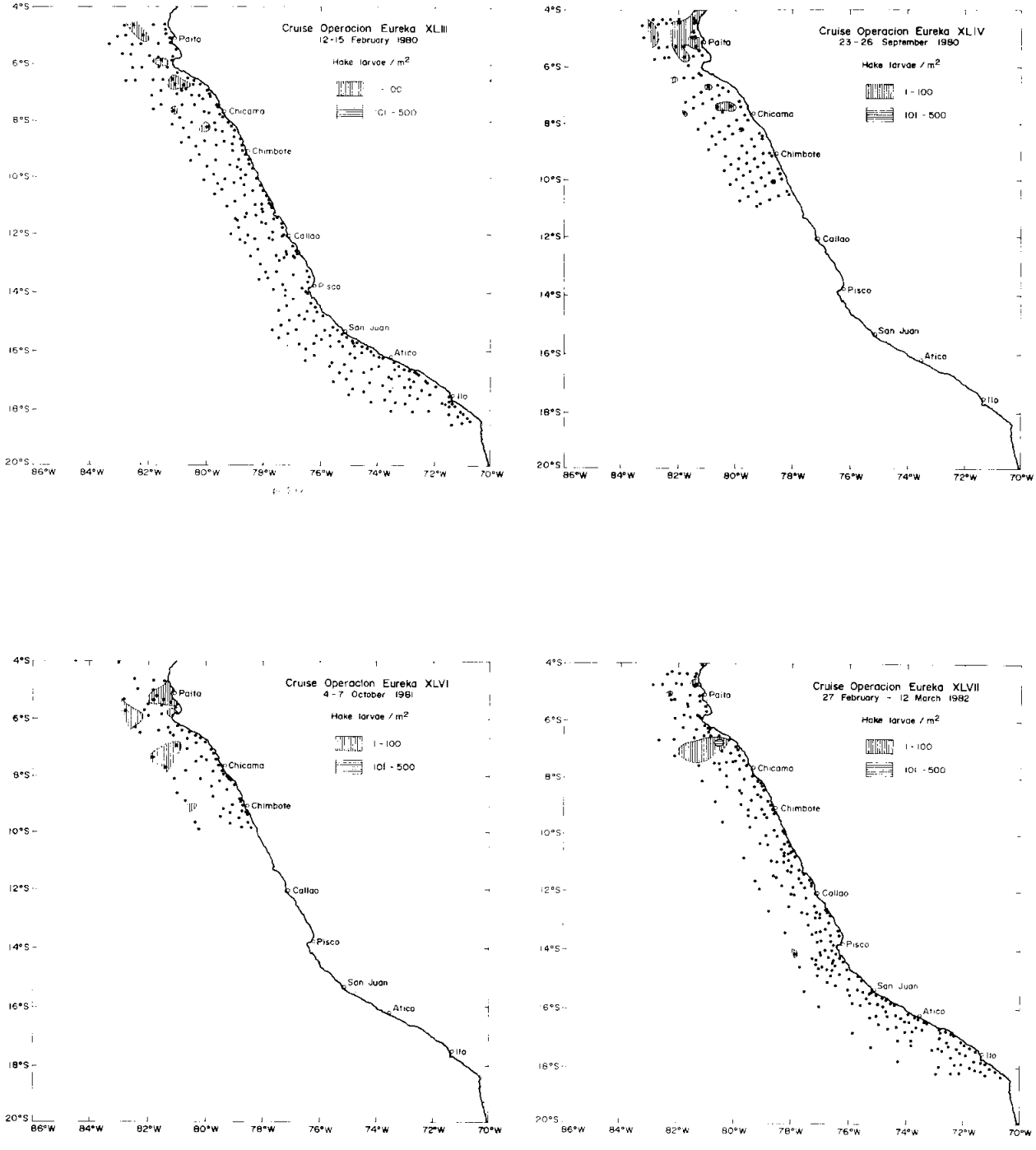

Fig. 13. Distribution of hake larvae along the Peruvian coast (see also Table 1). Upper graphs - left: 12-15 February 1980; right: 23-26 September 1980. Lower graphs - left: 4-7 October 1981; right: 27 February-12 March 1982.

Fig. 13. Distribución de larvas de merluza fuera de la costa peruana (ver también Tabla 1). Cuadros superiores - izquierda: 12-15 de Febrero 1980; derecha: 23-26 de Septiembre 1980. Cuadros inferiores - izquierda: 4-7 de Octubre 1981; derecha: 27 de Febrero-12 de Marzo 1982.

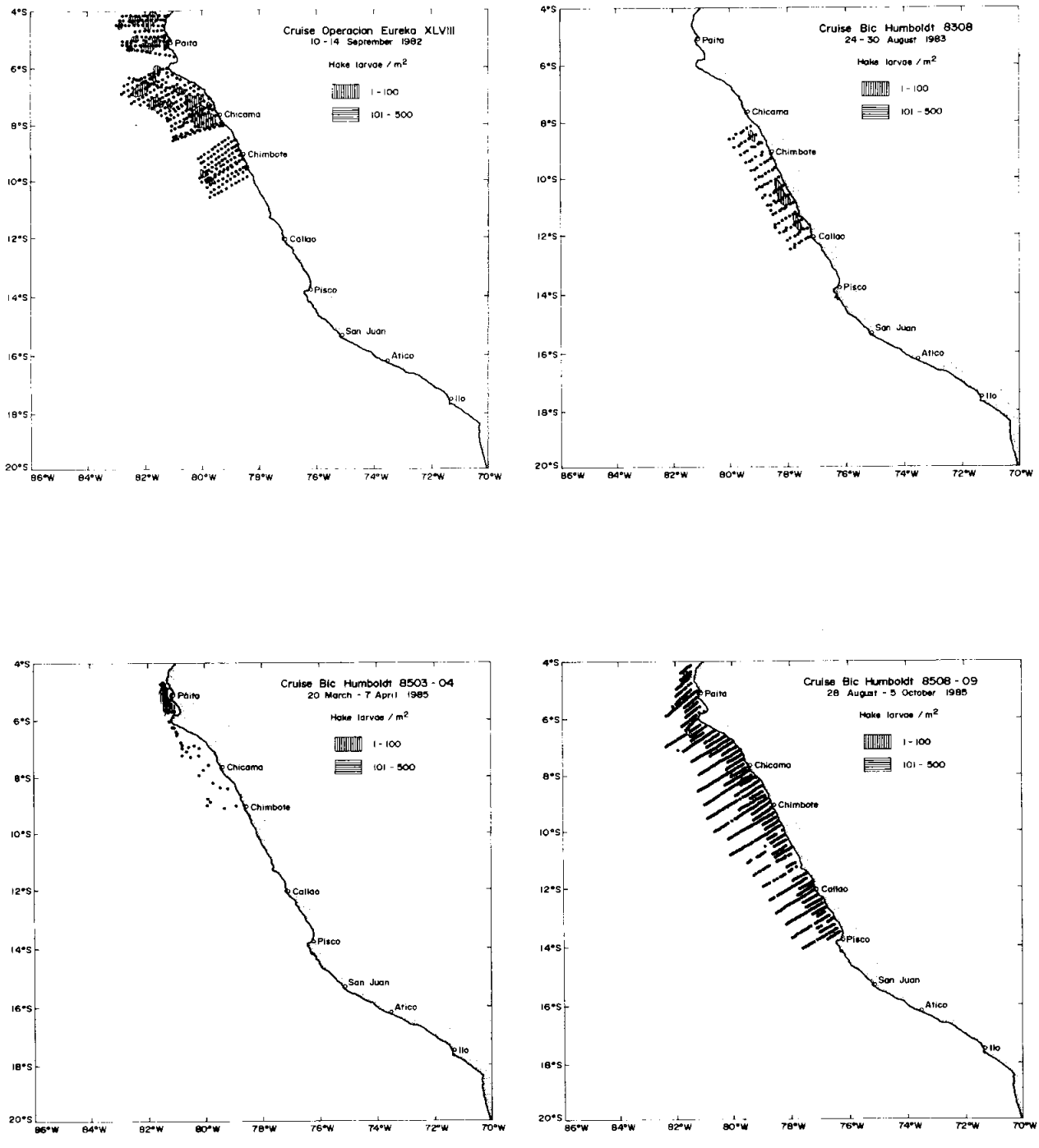

Fig. 14. Distribution of hake larvae along the Peruvian coast (see also Table 1). Upper graphs - left: 10-14 September 1982; right: 24-30 August 1983. Lower graphs - left: 20 March-7 April 1985; right: 28 August-5 October 1985.

Fig. 14. Distribución de larvas de merluza fuera de la costa peruana (ver también Tabla 1). Cuadros superiores - izquierda: 10-14 de Septiembre 1982; derecha: 24-30 de Agosto 1983. Cuadros inferiores - izquierda: 20 de Marzo-7 de Abril 1985; derecha: 28 de Agosto-5 de Octubre 1985.

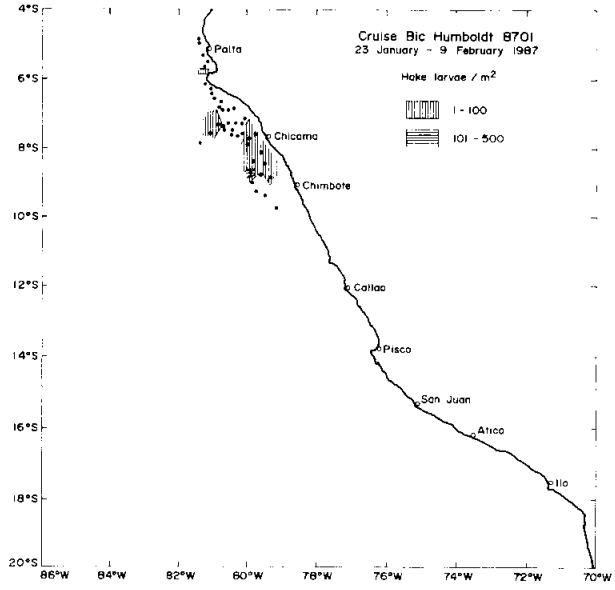

Fig. 15. Distribution of hake larvae along the Peruvian coast 23 January-9 February 1987 (see also Table 1).
Fig. 15. Distribución de larvas de merluza fuera de la costa peruana, 23 de Enero-9 de Febrero 1987 (ver también Tabla 1).

References

Alheit, J. 1986. A new method for determining batch fecundity of hake (genus: *Merluccius*). CIEM, Cons. Meet. C.M. 1986/G:62. Demersal Fish Cttee. 9 p.

Balbontin, F. and W. Fischer. 1981. Cicló sexual y fecundidad de la merluza, *Merluccius gayi gayi*, en la costa de Chile. Rev. Biol. Mar. Inst. Oceanol. Univ. Valparaiso 17(3): 285-334.

Canal, R. 1988. Reproducción de la merluza *(Merluccius gayi peruanus)* frente a Paita, Perú, entre 1971 y 1988, p. 231-238. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento Peruano. Bol. Inst. Mar. Perú-Callao. Volumen Extraordinario. 382 p.

Espino, M. and C. Wosnitza-Mendo. 1988. Efecto de la concentración en la mortalidad natural y su aplicación en el análisis de cohortes, p. 235-252. *In* T. Wyatt M.G. Larrañeta (eds.) Long term changes in marine populations. A symposium held in Vigo, Spain, 18-21 November 1986. Vigo.

Fischer, W. 1959. Huevos, crias y prelarvas de la merluza *Merluccius gayi* Guichenot. Rev. Biol. Mar. Valparaiso 9: 229-249.

Fischer, W. and F. Balbontin. 1970. On the investigation of ovarial cycle and fecundity of fish with special reference to partial spawners. Ber. dt. Wiss. Komm. Meeresforsch. 21(1-4): 56-77.

Miranda, O. 1966. Sobre el ciclo de desarrollo sexual de la merluza frente a la zona de Valparaíso (Gadidae, *Merluccius gayi gayi*). Estud. Oceanol., Chile 2: 41-43.

Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987. VPA estimates of the monthly population, length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE) Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Saetersdal, G. and L. Villegas. 1968. Estudio del tamaño, crecimiento y madurez de la merluza (*Merluccius gayi*) en aguas Chilenas. Publ. Inst. Fom. Pesq. 34: 1-14.

Sandoval, O. 1979. Distribución y variación estacional de larvas de peces en la costa Peruana. Informe Inst. Mar Perú-Callao 6. 32 p.

Santander, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru, 4-14°S, p. 179-207. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Santander, H. and O. Sandoval de Castillo. 1969. Desarrollo y distribución de huevos y larvas de merluza, *Merluccius gayi* (Guichenot) en la costa peruana. Bol. Inst. Mar. Perú-Callao 2(3): 80-107.

Santander, H. and O. Sandoval de Castillo. 1981. Algunos indicadores biológicos del ictioplancton, p. 89-103. *In* Memorias del Seminario sobre indicadores biologicos del plancton. Seminario realizado en el Instituto del Mar del Perú, Callao-Perú, 8-11 Setiembre de 1980. UNESCO Oficina Regional de Ciencia y Tecnologia para America Latina y el Caribe, Montivideo, Uruguay.

Velez, J. and J. Zeballos. 1985. Ampliación de la distribución de algunos peces e invertebrados durante el fenómeno "El Niño" 1982-1983, p. 173-180. *In* W. Arntz, A. Landa and J. Tarazona (eds.) El Niño: su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao, Volumen Extraordinario.

Wosnitza-Mendo, C. and M. Espino. 1986. The impact of "El Niño" on recruitment in the Peruvian hake *(Merluccius gayi peruanus)*. Meeresforsch. 31 (1): 47-51.

Biomass of Hake *(Merluccius gayi)* off Peru, 1953-1987

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Abstract

The population, in numbers and weight of hake *Merluccius gayi* off Peru, were reconstructed for the years 1953 to 1987 using J. Pope's cohort analysis. The analyses were performed with a natural mortality (M) assumed to vary with distribution area, itself varying with oceanographic conditions, especially sea surface temperature off Peru, and with a calibration based on fishery and survey data. The estimated annual biomasses of hake show an inverse relationship with those of the Peruvian anchoveta.

Resumen

Usando el análisis de cohortes de J. Pope se reconstruyó la población en número y peso de la merluza peruana *(Merluccius gayi)* en el período 1953 a 1987. Se asumió que la mortalidad natural (M) varió en función al tamaño del área de distribución, que a su vez depende de las condiciones oceanográficas especialmente la temperatura superficial del mar frente a Perú. Además se efectuó una calibración al último año con información de la pesquería y cruceros de evaluación. Las biomasas anuales halladas muestran una relación inversa con aquellas de la anchoveta peruana.

Introduction

Merluccius gayi (Guichenot), family Merluccidae, is the main hake species off the western coast of South America, where it occurs in two forms: *M. gayi peruanus* off Peru and *M. gayi gayi* off Chile (Ginsburg 1954). Off Peru, *M. gayi* is most abundant in the north where it has been commercially exploited since the mid-1960s. Earlier contributions on the distribution, biology and dynamics of *Merluccius gayi* include Solar et al. (1965), Vestnes et al. (1965a, 1965b, 1966), Stroem et al. (1966), Saetersdal and Villegas (1968), and Jones (1974).

PROCOPA Contribution No. 87.

Studies on hake have been one area of emphasis of the Instituto del Mar del Peru (IMARPE) and of the Peruvian-German Cooperative Program of Fisheries Investigation (PROCOPA), leading to a number of publications which have largely clarified the status of this resource off Peru (see Armstrong 1981; Dioses 1984; Espino et al. 1984, 1986; Espino and Wosnitza-Mendo 1984a, 1984b, 1984c, 1986, 1988; Wosnitza-Mendo et al. 1985 and references therein; Wosnitza-Mendo and Espino 1986a, 1986b).

Particularly, a positive relationship was identified between sea surface temperature (SST) and the range of hake distribution off the Peruvian coast (Espino and Urquizo 1986). This relationship, along with an associated density-dependent mechanism affecting the natural mortality (M) of younger hake (via cannibalism, see references above), was used here to reconstruct the biomasses of hake off the Peruvian coast, from 1953 to 1987, based on cohort analysis (Pope 1972) and field data collected mainly in the late 1970s and early 1980s (see Table 1).

Table 1. Basic information on Peruvian hake fishery, and on data used to run cohort analyses (see also text).
Tabla 1. Información básica sobre la pesquería de merluza peruana y de los datos usados en el análisis de cohortes (ver tambien texto).

Year	REMARKS
1987	Survey data used for initiating analysis
1986, 1985[a], 1984, 1983, 1982	Low catches due to "El Niño" and absence of high sea trawlers; quarterly age-length keys and length distributions available; F_t = 0.5 year^{-1}.
1981[a], 1980, 1979, 1978, 1977, 1976, 1975, 1974, 1973, 1972, 1971	High catches, stock fully exploited, central data to calibrate earlier and later data with less information; quarterly age-length keys and length distributions available; F_t = 0.5 year^{-1}.
1970, 1969, 1968, 1967, 1966, 1965, 1964, 1963, 1962, 1961, 1960, 1959, 1958, 1957, 1956, 1955, 1954, 1953	Low catches, absence or limited effect of trawler fleet, which begins in 1965 with converted purse-seiners; age-length key taken from 1987 cruise and a mean length distribution for the 1964-1970 period; three options of F_t investigated: 0.0001; 0.00025 and 0.0005 year^{-1} (see Fig. 1).

[a]Years for which survey data were available for comparison with results of cohort analysis (see Fig. 1).

Since the 1980s the investigation of Peruvian hake have been oriented mainly to the implementation and application of direct evaluation models such as swept-area and analytical models such as cohort analysis (Pope 1972).

A description of the population dynamics of Peruvian hake in the years from 1971 to 1982 is presented in Espino and Wosnitza-Mendo (1986). Due to near zero catches after 1982 brought about by an El Niño and the termination of international fishing agreements, a cohort analysis up to 1986 was not possible without taking the risk of introducing a great error by selecting an

erroneous value of terminal fishing mortality (F_t) (we recall here that use of cohort analysis is only recommendable if a considerable portion of the stock is taken by the fishery (Jones 1982)). However, by integrating information from demersal research cruises on stock numbers per age group in the cohort analysis, the 1983 to 1987 segment of the biomass estimates could be determined and used for calibration (Espino and Wosnitza-Mendo 1988, Espino et al. 1988).

An analysis of hake stomach contents for the period of 1976 to 1986, in relation to its possible role as predator on anchoveta (*Engraulis ringens*) showed that, in case of coincidence of distribution area of the two species, hake could consume a considerable amount of anchoveta (Muck et al. 1988; Muck et al., this vol.). To complete the study over the 30-year period considered in the book "The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change" (Pauly and Tsukayama 1987), an effort is presented here to reconstruct hake numbers and biomasses from 1953 to 1987.

Materials and Methods

To reconstruct population numbers, the catch data presented in Table 2 were used. Between 1953 and 1964 hake fishery catches were negligible. Quarterly length-frequency distribution and age-length keys were available for the years from 1971 to 1986.

For the period from 1953 to 1970, the mean length-frequency distribution for the years between 1964 and 1970 was applied. The age-length key taken as representative of the years

Table 2. Annual catch of Peruvian hake and estimates of biomass of population ("Pop.") and of two-year old recruits ("Recr."), given three levels of terminal fishing mortality (F_t, year^{-1}); all weights are in tonnes.

Tabla 2. Captura anual de la merluza peruana y estimados de la biomasa de la población ("Pop.") y de los reclutas de dos años ("Recr."), dados tres niveles de mortalidad por pesca introducida (F_t, año^{-1}); todos los pesos son en toneladas.

		F_t=0.0001		F_t=0.00025		F_t=0.0005	
Year	Annual catch	Pop.	Recr.	Pop.	Recr.	Pop.	Recr.
1953	25	268,807	680	268,807	680	268,807	680
1954	12	263,623	2,207	263,623	2,207	263,623	2,207
1955	17	225,587	6,618	225,587	6,618	225,587	6,618
1956	7	208,465	22,831	208,465	22,831	208,465	22,831
1957	13	247,056	66,542	247,056	66,543	247,056	66,543
1958	18	260,368	1,534	259,618	783	259,367	533
1959	1	188,134	5,038	184,548	2,551	183,352	1,722
1960	1	206,342	13,504	193,974	6,020	189,851	3,525
1961	1	238,558	44,254	197,346	18,727	183,609	10,218
1962	1	395,714	158,694	249,061	64,983	200,176	33,746
1963	1	444,675	8,412	258,379	8,412	196,280	8,412
1964	1	490,358	28,129	281,482	28,129	211,856	28,129
1965	1,291	468,896	17,017	268,072	17,017	201,131	17,017
1966	685	445,200	19,233	246,612	19,233	180,415	19,233
1967	19,621	426,023	12,860	252,500	12,860	194,659	12,860
1968	17,867	368,803	21,995	228,710	21,995	182,012	21,995
1969	15,281	315,600	23,224	208,680	23,224	173,040	23,224
1970	17,218	281,933	28,257	208,177	28,257	183,592	28,257
1971	26,187	200,796	90,133	200,796	90,133	200,796	90,133
1972	12,585	262,260	72,396	262,260	72,396	262,260	72,396
1973	132,856	407,941	90,989	407,941	90,989	407,941	90,989
1974	109,318	382,542	93,981	382,542	93,981	382,542	93,981
1975	84,898	361,096	81,612	361,096	81,612	361,096	81,612
1976	92,802	502,632	229,191	502,632	229,191	502,632	229,191
1977	106,799	613,403	104,617	613,403	104,617	613,403	104,617
1978	303,495	670,788	112,763	670,788	112,763	670,788	112,763
1979	92,954	363,600	78,976	363,600	78,976	363,600	78,976
1980	159,376	315,946	12,681	315,946	12,681	315,946	12,681
1981	69,293	179,923	55,163	179,923	55,163	179,923	55,163
1982	26,454	154,409	54,694	154,409	54,694	154,409	54,694
1983	4,378	243,952	44,256	243,952	44,256	243,952	44,256
1984	9,410	353,965	52,473	353,965	52,473	353,965	52,473
1985	16,855	500,701	148,565	500,701	148,565	500,701	149,565
1986	2,534[a]	70,1974	192,882	70,1974	192,882	701,974	192,882
1987	n.a.	765,951	2,378[b]	765,951	2,378[b]	765,951	2,378[b]

[a] Preliminary estimate
[b] Underestimate

1953-1970 stems from the January 1987 survey reported in Anon. (1987), but the otoliths used for age determination stem from the earlier period. The reason for this approach was that we assumed similar stock conditions for the two periods, because both the 1953-1970 and the 1982-1986 periods experienced low exploitation rates. Thus, the structure of the population was probably similar.

The stock (in numbers) was calculated by means of a modified cohort analysis using a quarterly catch-in-number matrix. Natural mortality, formerly estimated as $M = 0.3$ year^{-1} (Espino and Wosnitza-Mendo 1986), was made variable depending on SST through the equation

$$M = \exp{-0.0624} + (2.0588/(1 + \exp{-0.28522(T^{o}-18.16)})) \qquad ...1)$$

where T^{o} is the mean SST in Puerto Chicama. This states that there is an inverse relationship between intensity of cannibalism and water temperature, which is also related to the changes in the size of distribution area (Espino and Wosnitza-Mendo 1988).

The cohort analysis run was initiated with a terminal population size obtained by the swept-area method (Espino and Wosnitza-Mendo 1984b; Espino et al. 1988). Thus, we avoided having to choose a terminal F which would have been very low in relation to M.

The population estimates obtained for 1981 and 1985 were verified using the population sizes estimated through the surveys. The 1971 to 1982 results from a former analysis (Espino and Wosnitza-Mendo 1986) were also used to calibrate the population estimates obtained from the cohort analysis.

In the processing of information from 1970 backwards, three different terminal F's were used for age group 10: 0.0001, 0.00025 and 0.0005 year^{-1}, since we know that the catches were very small but do not know their exact value (see Table 1).

For the comparison of the hake stock with the anchoveta population, the anchoveta biomasses were taken from Pauly et al. (1987). The relation between Peruvian hake biomass (B_M) and anchoveta biomass (B_A) was then expressed by the power function

$$B_M = a \cdot B_A^{b}$$

where a and b are fitted parameters.

Results and Discussion

Variation of Hake Population

Tables 2 and 3 give the estimated yearly populations (in weight and numbers, respectively) of Peruvian hake over the period considered here. Fig. 1 shows the three types of curves resulting from the three F_t values used for the 1970 to 1953 run. The values obtained for F_t = 0.0001 year^{-1} are well above those obtained for the other F_t values and do not seem realistic. In general, we would expect a more stable stock situation in the years before 1970 due to reasons presented further below. We are inclined to accept that hake biomass in the years from 1960 to 1970 varied between 2×10^5 and 3×10^5 tonnes. The years before 1960, due to the convergence of cohort estimates, do not show any differences related to the different F_t values.

We can divide the time series into three periods: the first with very low to low exploitation rates; the second, with population under full exploitation; and the third, with reoccurrence of low exploitation rates.

In the first period, from 1953 to 1972, the population does not show great fluctuations and stays at a low level, while the anchoveta biomass is at its maximum level (see Pauly et al. 1987). During this period, the high biomasses of the anchoveta might have stabilized the hake population. In its early life and up to 1 year, hake is pelagic and feeds principally on copepod larvae, copepods and euphausids (Carrasco 1986). Thus, young hakes compete for food with the anchoveta, which in the northern area (i.e., in the main distribution area of hake) also feed particularly on copepods and euphausids (A. Alamo, IMARPE, pers. comm.). The hypothesis of competition between anchoveta and hake in the early phase of the latter's life, is further

Table 3. Population of Peruvian hake *(Merluccius gayi)* in numbers x 10^3 for 1953 to 1987, as reconstructed using $F_t = 0.0005$ year^{-1} (see text and Fig. 1).[a]
Tabla 3. Población de la merluza peruana (Merluccius gayi) *en números x 10^3), entre 1953 a 1987, reconstruidos usando $F_t = 0.0005$ año^{-1} (ver texto y Fig. 1).*

Age group	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970
1	16,060	53,467	181,741	514,986	3,727	12,674	26,351	79,766	259,620	211,751	211,751	134,444	137,308	98,351	173,690	182,858	206,350	735,870
2	3,674	11,928	35,771	123,411	359,691	2,883	9,307	19,054	55,230	182,410	45,469	152,046	91,982	103,961	69,511	118,891	125,537	15,274
3	851	2,728	7,953	24,290	86,196	278,226	2,116	6,729	13,193	38,805	126,157	32,649	104,024	69,578	73,443	46,641	80,760	9,216
4	182	629	1,815	5,394	16,963	66,669	204,303	1,530	4,659	9,269	26,838	90,586	22,337	78,272	48,926	43,229	25,508	54,079
5	238,238	131	412	1,221	3,763	13,111	48,945	147,725	1,058	3,273	6,410	19,270	61,974	15,992	54,851	20,261	17,452	8,174
6	36,804	177,671	85	277	852	2,908	9,625	35,390	102,285	743	2,263	4,602	13,184	46,699	11,188	34,323	10,927	10,305
7	8,470	27,333	118,469	57	193	658	2,135	6,960	24,504	71,866	514	1,625	3,149	9,921	32,975	6,784	22,758	7,380
8	2,117	6,290	18,225	80,446	40	149	483	1,544	4,819	17,217	49,703	369	1,112	2,343	6,991	21,987	4,114	27,483
9	534	1,572	4,194	12,375	56,187	30	109	1,069	1,069	3,386	11,907	35,689	253	814	1,642	4,393	14,735	2,727
10	102	397	1,048	2,848	8,643	43,462	22	242	242	751	2,342	8,550	24,417	187	573	1,059	1,956	10,855

Age group	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987b
1	584,287	646,306	745,938	657,159	1,866,576	766,949	864,710	623,574	95,000	419,232	425,416	315,530	361,661	1,184,622	1,556,444	18,070	1,623
2	487,206	391,327	491,835	508,003	441,144	1,238,869	565,495	609,532	426,896	68,548	298,176	295,641	239,221	283,640	803,054	1,042,606	12,853
3	100,308	326,273	297,793	334,788	340,999	291,962	912,968	395,030	414,397	307,289	46,987	207,216	224,132	187,614	191,464	536,528	739,090
4	54,913	65,377	248,154	189,878	209,459	212,547	206,334	613,380	150,980	248,110	146,495	28,624	156,094	174,279	121,954	118,338	364,064
5	24,339	16,060	39,243	42,480	183,334	29,498	37,582	24,889	22,709	20,483	17,772	4,306	20,458	120,535	114,052	74,331	75,228
6	2,612	7,176	8,587	3,305	9,335	2,847	3,951	15,058	7,636	7,973	2,837	797	3,119	15,565	79,901	74,593	50,358
7	6,064	899	4,774	893	584	5,890	2,074	2,044	8,461	3,047	353	642	568	2,217	9,780	52,795	51,387
8	4,376	3,764	532	0	0	167	4,277	584	0	5,210	0	245	470	380	1,214	6,300	36,811
9	0	0	2,862	0	0	0	1	0	0	0	0	0	0	368	184	642	3,973
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	123	456

[a] Zero entries refer to values $<10^3$
[b] Age group 11 = 88 x 10^3

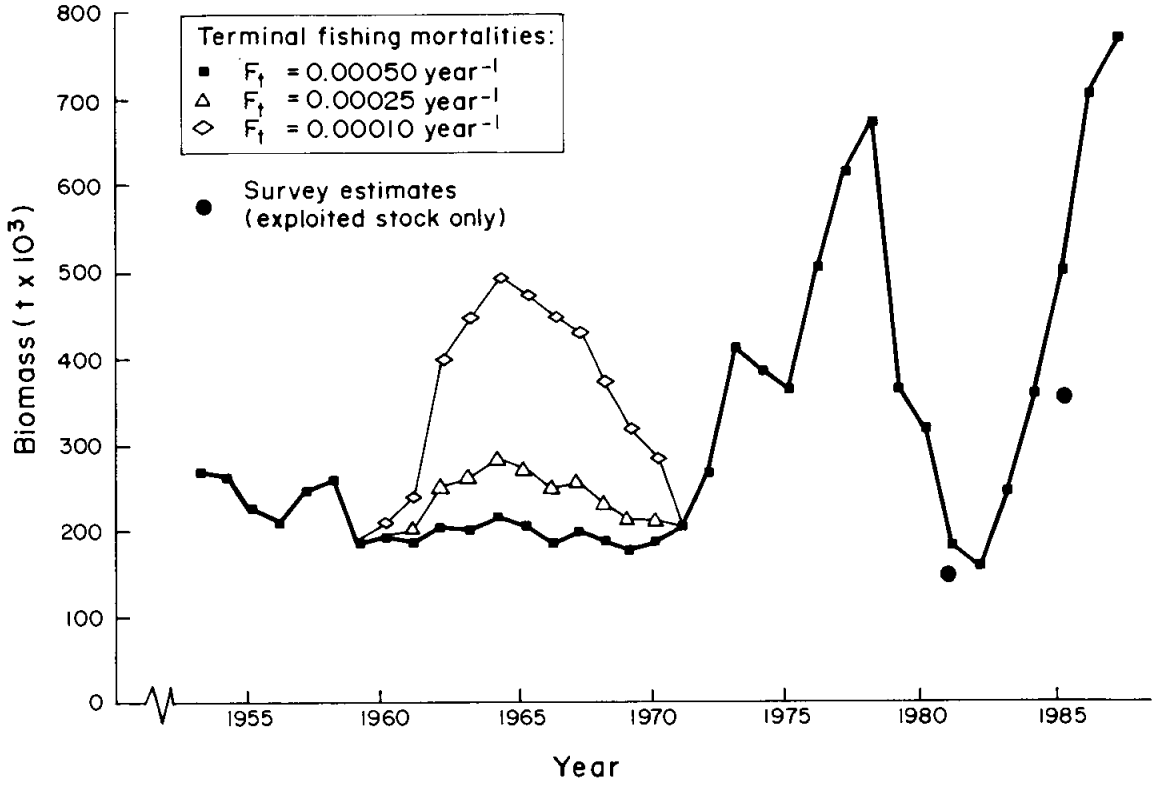

Fig. 1. Biomass of Peruvian hake *Merluccius gayi*, as reconstructed using cohort analysis and different terminal fishing mortalities for the period 1970-1980. Note closeness of survey estimates (1981 and 1985) and see Table 1 and text for details.
Fig. 1. Biomasa de la merluza peruana (Merluccius gayi), *reconstruida usando análisis de cohortes y diferentes mortalidades por pesca terminal para el período entre 1970-1980. Notar la proximidad de los estimados de los cruceros (1981 y 1985) y ver Tabla 1 y texto para detalles.*

illustrated by Fig. 2 which shows the biomass of the two-year-old hake recruits. Clearly, recruitment levels were much lower in the years before 1970,which could be explained by competition with anchoveta.

In the second period, from 1973 to 1981, the stock was fully exploited. International agreements permitted the operation of foreign high sea trawlers. Thus, we have to include the influence of fishing pressure in our considerations.

We note an increase of hake biomass in this period until 1978, with a marked decrease later on.

The biomass increase might have been due to three groups of factors, all acting simultaneously:

a) A reduction of cannibalism might have taken place. Hake become cannibals at about 50 cm, i.e., at about 5 years of age (Espino and Mendieta 1978). Initially, the fishing pressure was mainly acting on older cannibalistic individuals. This will have reduced the natural mortality of young hake, and hence increased recruitment and biomass.
b) As described in Wosnitza-Mendo and Espino (1986b), the "El Niño" event of 1972/73 appears to have had a positive effect on the recruitment of hake (the same occurred after the 1982/83 event). The reason for this was the increase of the potential distribution area due to higher O_2 levels near the sea bottom.
c) Finally, perhaps a major factor might be, from 1972 on, the marked reduction of anchoveta biomass which stayed at a low level, and which led to a reduced consumption of hake eggs and larvae and a reduced food competition for young hakes.

The reduction of hake biomass from 1979 to 1981 is attributed to overfishing (Espino et al. 1986).

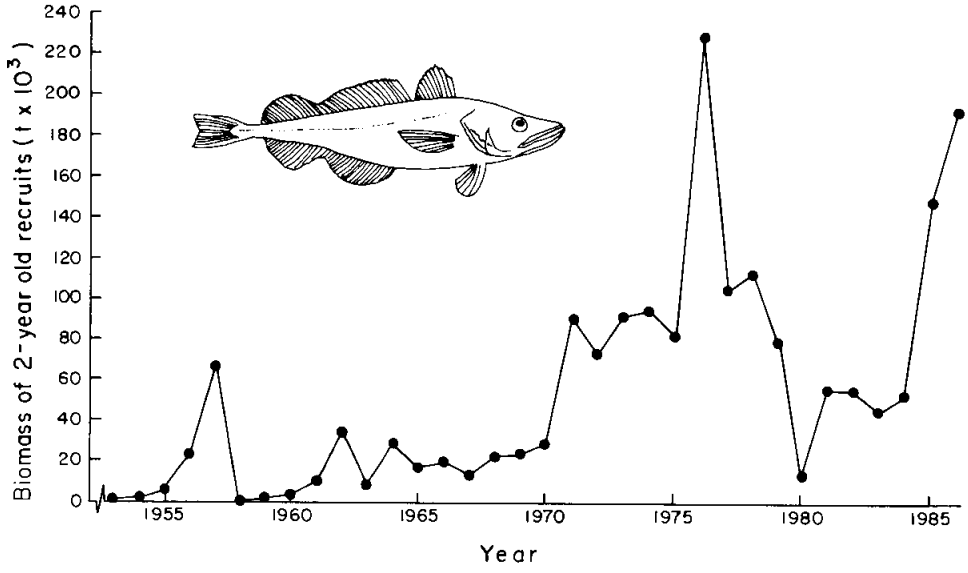

Fig. 2. Biomass of 2-year old hake *Merluccius gayi* recruits off Peru for period 1953 to 1987.
Fig. 2. Biomasa de reclutas de 2 años de la merluza peruana (Merluccius gayi) *para el periódo entre 1953 y 1987.*

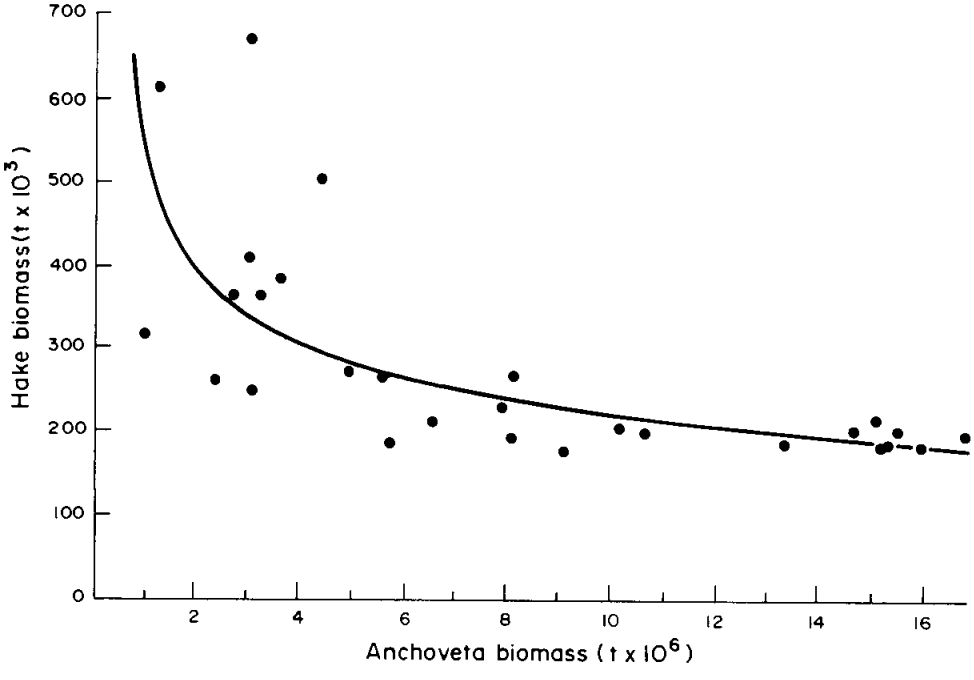

Fig. 3. Biomass of hake *Merluccius gayi vs* anchoveta *Engraulis ringens* biomasses off Peru, 1953 to 1987. Note strong suggestion of an inverse relationship.
Fig. 3. Biomasas de la merluza (Merluccius gayi) *versus biomasa de anchoveta* (Engraulis ringens) *frente a Perú, entre 1953 y 1987. Notar fuerte indicación de una relación inversa.*

In the third period (1982-1986), the catches diminished because of two facts: first, an El Niño event dispersed the stock, rendering it inaccessible to trawling; second, the international fishing agreements ended, bringing about a reduction of the fleet.

This latter item, in combination to the recruitment-enhancing effect of "El Niño", indeed helped to prevent the stock from collapsing. In 1982, the biomass had declined to about 1.5×10^5 t, but recovered rapidly, to over 7×10^5 t (=15 t km^{-2}), a level never observed before. All of this occurred, however, in the absence of anchoveta. The preceding El Niño events of 1953, 1957/58, 1965 and 1969 did not have as strong a positive impact as the 1972/73 and 1982/83 events.

The comparison of the cohort analysis with the cruise data from 1981 and 1985 (Fig. 1) shows the same tendencies and a remarkably good fit, taking into account that the swept-area method only estimates the exploited part of the stock and underestimates the stock of younger fishes. Former cruise estimates, for the years before 1980, are highly inflated, due to the fact that the area covered by densest hake concentrations was only a small part of the total distribution area, and that most trawl hauls were made only on these densest concentrations. Furthermore, in some cruises, a catch efficiency factor of 0.25 only was used for the net.

The relationship between anchoveta and hake biomass (in tonnes) is described by the relationship

$$B_M = 6.95 \cdot 10^7 \, B_A^{-0.36}$$

whose linearized form has a correlation coefficient r = 0.76. Fig. 3 shows the original data points and the derived curve. These suggest a stock-controlling influence of anchoveta on hake, possibly via egg predation, as described in Muck et al. (1987) for sardine/anchoveta. The interactions between hake and anchoveta, however, are not unidirectional. During its early life, hake competes with anchoveta for food and might also suffer from the predation of adult anchoveta on hake eggs, especially since hake eggs, larvae and juveniles are distributed more southernly than the adults (see Sandoval et al., this vol.). On the other hand, adult hake feeds on anchoveta, but mainly in the north, where adult hakes are abundant. In any case, the impact of anchoveta on hake is probably greater than vice versa.

References

Anon. 1987. Situación de los stocks de peces demersales y el ambiente marino en Enero-Febrero 1987. IMARPE, Informe Interno. 15 p.

Armstrong, D. 1981. Investigación de la merluza en IMARPE. Proyecto PNUD/FAO-PER/76/022; Instituto del Mar del Perú Informe No. 79: 1-47.

Carrasco, S. 1986. Algunos copépodos en la dieta de larvas de merluza en la Perú. VIII Congreso Nacional de Biología. Arequipa-Perú, 25-31 Mayo 1986 (Resumen).

Dioses, T. 1984. Edad y crecimento de la merluza peruana *Merluccius gayi peruanus* (G.), p. 21. *In* Libro de Resúmenes. Primer Congreso Nacional de Biología Pesquera, 28 Junio-1 Julio 1984. Trujillo, Perú.

Espino, M. and C. Wosnitza-Mendo. 1986. Peruvian hake fisheries from 1971 to 1982. CalCOFI Rep. 27: 113-120.

Espino, M. and C. Wosnitza-Mendo. 1984a. La relación entre stock y reclutamiento de la merluza peruana *(Merluccius gayi peruanus)*. Bol. Inst. Mar Peru-Callao 8(5): 179-189.

Espino, M. and C. Wosnitza-Mendo. 1984b. Manuales de evaluación de peces. No. 1: Area barrida. Inf. Int. Mar Perú-Callao. No. 86. 31 p.

Espino, M. and C. Wosnitza-Mendo. 1984c. El uso del modelo Csirke-Caddy para la merluza peruana (*Merluccius gayi peruanus*). Bol. Inst. Mar Perú-Callao 8(5): 191-205.

Espino, M. and C. Wosnitza-Mendo. 1988. Efecto de la concentración en la mortalidad natural y su aplicación en el análisis de cohortes, p. 235-252. *In* T. Wyatt and M.G. Larrañeta (eds.) Long-term changes in marine fish populations. A symposium held in Vigo, Spain, 18-21 November 1986, Vigo.

Espino, M. and W. Urquizo. 1986. Effect of El Niño on the distribution and recruitment of the Peruvian hake (*Merluccius gayi peruanus*). Presented at the Chapman Conference on El Niño: an International Symposium, Guayaquil, 27-31 October 1986 (p. 41 in volume of abstracts).

Espino, M. and A. Mendieta. 1978. Algunos aspectos del régimen alimentario de merluza, *Merluccius gayi peruanus*, del área de Paita, en 1975. Primer Congreso Nacional de Pesquería, Huacho, 19-25 Marzo 1978 (Resumen).

Espino, M., C. Wosnitza-Mendo and R. Castillo. 1984. La pesca de arrastre de la flota costera de Paita entre 1970-1982. Bol. Inst. Mar Perú-Callao 8(5): 159-178.

Espino, M., C. Wosnitza-Mendo and F. Fernández. 1988. Ajuste del análisis de cohortes con información de cruceros de evaluación, p. 239-244. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento Peruano. Bol. Inst. Mar Perú-Callao, Volumen Extraordinario. 382 p.

Espino, M. and C. Wosnitza-Mendo. 1988. Efecto de la concentración en la mortalidad natural y su aplicación en el análisis de cohortes, p. 235-252. *In* T. Wyatt and M.G. Larrañeta (eds.) Long-term changes in marine fish populations. A symposium held in Vigo, Spain, 18-21 November 1986. Vigo.

Espino, M., J. Castillo, F. Fernandez, A. Mendieta, C. Wosnitza-Mendo and J. Zeballos. 1986. El stock de merluza y otros demersales en Abril de 1985 crucero Bic Humboldt (23 Marzo al 5 April, 1985). Inf. Inst. Mar Perú-Callao (89): 1-57.

Ginsburg, I. 1954. Whitings on the coasts of the American continent. Fish. Bull. Fish. Wildl. Serv. U.S. 56: 185-208.

Jones, R. 1974. World resources of hakes of the genus *Merluccius*, p. 139-166. *In* F.R. Harden Jones (ed.) Sea fisheries research. Elek Science, London.

Jones, R. 1982. El uso de datos de composición por tallas en la evaluación de poblaciones de peces (con notas sobre VPA y análisis de cohortes). FAO Circ. Pesca 734. 61 p.

Muck, P., M. Espino, H. Fuentes, C. Wosnitza-Mendo and M. Esquerre. 1988. La importancia de la merluza peruana en la mortalidad de la anchoveta, p. 249-253. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento Peruano. Bol. Inst. Mar Perú-Callao, Volumen Extraordinario. 382 p.

Muck, P., O. Sandoval de Castillo and S. Carrasco. 1987. Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Peru, p. 268-275. In D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D. and I. Tsukayama. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D., M. L. Palomares and F. C. Gayanilo. 1987. VPA estimates of the monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.). The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM. Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

Pope, J. G., 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. Northeast Atl. Fish. Res. Bull. 9:65-74.

Saetersdal, G. and L. Villegas. 1968. Estudio del tamaño, crecimiento y madurez de la merluza (*Merluccius gayi*) en aguas chilenas. Publ. Inst. Fom. Pesq. 34. 52 p.

Solar, E. del, J. Sánchez and A. Piazza. 1965. Exploración de las áreas de abundancia de merluza (*Merluccius gayi peruanus*) en el costa peruana a bordo del "Betina". Inf. Inst. Mar Peru 8. 28 p.

Stroem, A., G. Vestnes, L. Villegas and J. Parker. 1966. Informe sobre investigaciones exploratorias en la zona de Chiloe Abril-Junio 1966, realizadas con el B/I "Carlos Darwin". Publ. Inst. Fom. Pesq. 19. 19 p.

Vestnes, G., A. Stroem, G. Saetersdal, L. Villegas and H. Trujillo. 1966. Report on an exploratory survey with the M/S "Carlos Darwin" in the Talcahuanao-Valdivia area, October-November 1965. Publ. Inst. Fom. Pesq. 16. 17 p.

Vestnes, G., A. Stroem and L. Villegas. 1965a. Report on the exploratory survey with M/S "Carlos Darwin" in the Talcahuanao-Valdivia area. December 1964 to February 1965. Publ. Inst. Fom. Pesq. 6. 25 p.

Vestnes, G., A. Stroem, G. Saetersdal and L. Villegas. 1965b. Informe sobre investigaciones exploratorias en la zona de Talcahuano-Valdivia y Puerto Montt. Junio-Julio 1965, realizada con el B/I "Carlos Darwin". Publ. Inst. Fom. Pesq. 10. 21 p.

Wosnitza-Mendo, C. and M. Espino. 1986a. La construcción de curvas de rendimiento sostenible (Shepherd 1982) para la merluza peruana. Bol. Inst. Mar Perú-Callao 10(7):167-183.

Wosnitza-Mendo, C. and M. Espino. 1986b. The impact of "El Niño" on recruitment in the Peruvian hake (*Merluccius gayi peruanus*). Meeresforsch. 31(1):47-51.

Wosnitza-Mendo, C., M. Espino, T. Dioses, E. Sánchez and A. Pereda. 1985. Rendimiento de equilibrio de la merluza peruana (*Merluccius gayi peruanus*) y propuestas para su manejo. Bol. Inst. Mar. Perú-Callao 9(2):67-92.

Anchoveta Consumption of Peruvian Hake: A Distribution and Feeding Model*

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Abstract

A model is presented which describes the north-south distribution of hake *(Merluccius gayi)* along the coast in terms of sea surface temperature changes, themselves indicators of changes of the oxygen content in deeper water layers. This model is used, along with available information on biomass of anchoveta and hake, and on the diet of hake to estimate the overlap between the stock of anchoveta *(Engraulis ringens)* and that of hake, and the likely anchoveta consumption of hake from 1953 to the mid-1980s.

Resumen

Se presenta un modelo el cual describe la distribución norte-sur de la merluza *(Merluccius gayi)* a lo largo de la costa en relación a los cambios de la temperatura superficial del mar, indicadores también de cambios en el contenido de oxígeno en las capas profundas de aguas. Este modelo es usado con la información disponible sobre biomasa de anchoveta y merluza, y sobre la dieta de merluza para estimar el traslape entre el stock de anchoveta *(Engraulis ringens)* y el de merluza y el consumo de anchoveta por merluza desde 1953 a mediados de la década del 80.

Introduction

Mortality due to predation or caused by fishing is one of the most important processes affecting anchoveta population dynamics off Peru.

As shown for sea birds (Muck and Pauly 1987), pinnipeds (Muck and Fuentes 1987) and pelagic fishes (Pauly et al. 1987b; Muck and Sánchez 1987), the total consumption of anchoveta by various predators is (i) of the same order of magnitude as the fishery catches, and (ii) varies with the physical characteristics of the upwelling system off Peru.

With the present contribution on anchoveta consumption by semi-pelagic Peruvian hake, the "cycle" of major anchoveta predators is completed.

The Distribution Model

The size of hake distribution area is dependent of the oxygen condition in the deeper water layers (100-200 m), which shows seasonal and inter-annual variations (Espino and Urquizo 1986; Espino and Wosnitza-Mendo 1988).

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While the offshore distribution of hake is more or less constant and largely limited to the east-west extension of the continental shelf, the north-south distribution varies notably, apparently as a function of the oxygen content of the deeper water layers, which is increased when warm, oxygen-rich waters intrude, from the north, into the Peruvian upwelling ecosystem (e.g., during El Niño events).

The dynamics of the oxygen minimum zone can be expressed as a function of the mean sea surface temperature (SST), which allows the estimation of the total area of hake distribution, as described in Espino and Wosnitza-Mendo (1988).

Modifying equation (1) given by these authors, by adding as a mean offshore extension a constant "C" (=70 km), the alongshore extension of hake distribution (Ext., in km) can be approximated by:

$$\text{Ext.} = \frac{10^5}{C * (1 + e^{-0.2852 * (SST-18.16)})} \qquad ...1)$$

During cold years, hake is most abundant in the north of Peru, within 2-7°S, with a density maximum at 5°S. This distribution pattern can be approximated by a normal distribution curve with mean ($\overline{X}$) = 5 and standard deviation (s.d.) = 1.25 (Fig. 1), or

$$Y = \frac{1}{s.d. * \sqrt{2\pi}} * e^{-0.5 * (Lat. - \overline{X}/s.d.)^2} \qquad ...2)$$

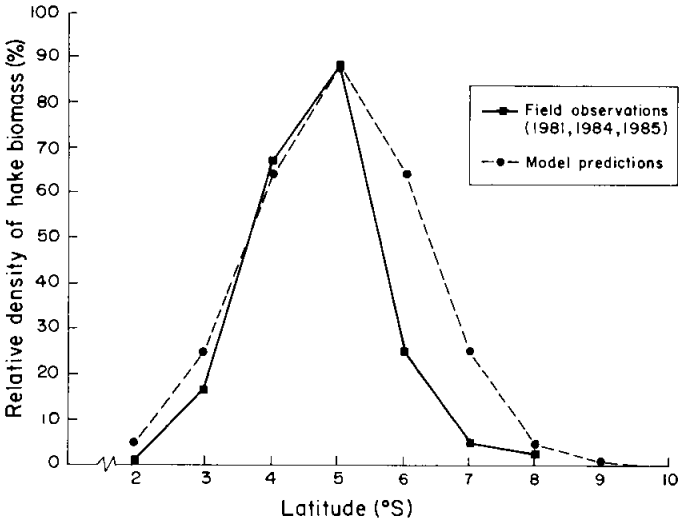

Fig. 1. Observed (in 1981, 1984 and 1985) and estimated relative density of hake biomass along the Peruvian coast.
Fig. 1. Densidad relativa estimada y observada (en 1981, 1984, 1985) de la biomasa de la merluza a lo largo de la costa peruana.

Thus, if we assume that the northern limit of hake distribution is more or less constant (i.e., 2°S, see Espino and Wosnitza-Mendo 1988), and that the southern extension of hake distribution in 1982/83 was the maximum ever, since it occurred during the very strongest El Niño on record (during which SST = 26.6°C in autumn 1983, for 4-14°S), the north-south extension estimated through equation (1) would be 1,310 km, implying a southern limit of hake distribution near 14°S (Fig. 2).

Thus, the density maximum (D_{max}, in °S, i.e., $\overline{X}$ in equation 2) of the latitudinal distribution of hake can be expressed as an SST-related variable:

$$D_{max} = -0.227 + 0.309 * SST \qquad ...3)$$

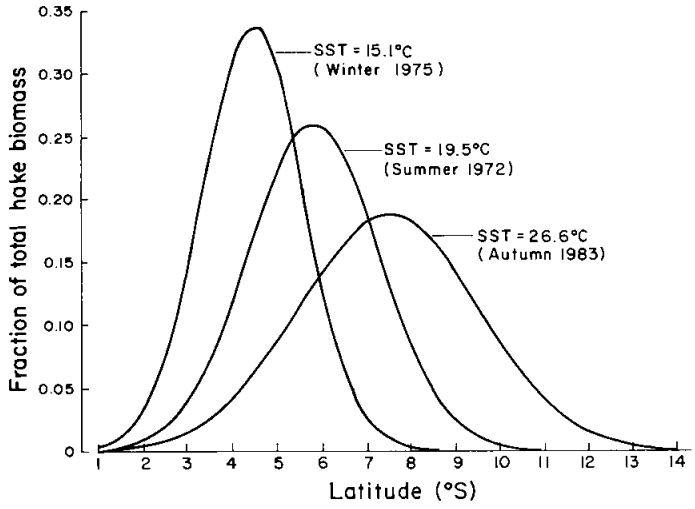

Fig. 2. Total biomass of Peruvian hake estimated to occur off 1-14°S, from three different SST regimes.
Fig. 2. Biomasa total de la merluza peruana frente a 1-14°S estimada de 3 diferentes regímenes de TSM.

and equation (2) may be rewritten as

$$Y = \frac{1}{D_{max}*0.25*\sqrt{2\pi}} * e^{-0.5*\left(Lat. - D_{max}/0.25*D_{max}\right)^2} \qquad ...4)$$

Fig. 2 shows model results (equations 3 and 4) for hake density distribution under three different SST-regimes:

SST = 15.1°C(winter 1975)
SST = 19.5°C (summer 1972)
SST = 26.6°C (autumn 1983)

The percentage of total hake population (POP%) which is distributed, for a given SST, south of a given latitude, corresponds to the area under the normal distribution. This is defined, in the standardized normal distribution, by the variable Z. In this case:

$$z = (Lat. - D_{max})/D_{max} * 0.25 \qquad ...5)$$

The corresponding area (= POP%) for different values of Z are tabulated in most statistic texts and can also be calculated using

$$POP\% = \frac{1}{\sqrt{2\pi}} \int_{z}^{\infty} e^{-0.5v^2} dv \qquad ...6)$$

and the polynom

$$POP(\%) = f(x)(b_1v + b_2v^2 + b_3v^3 + b_4v^4 + b_5v^5) * 100 \qquad ...7)$$

where

$$f(x) = \frac{1}{\sqrt{2\pi}} e^{-0.5Z^2} \qquad ...8)$$

and

$$v = \frac{1}{1 + 0.23164 * z} \qquad ...9)$$

and where the constants

$b_1 = 0.31938$
$b_2 = -0.35656$
$b_3 = 1.78148$
$b_4 = -1.82126$
$b_5 = 1.33027$

(For negative values of z, the output of equation (7) is subtracted from 100.)

Table 1 gives the latitude (D_{max}) corresponding to the density maximum of hake population for different values of SST, and the percentage of the total hake population (POP%) occurring south of a given latitude.

Thus, during a warm period (e.g., SST = 23°C) D_{max} = 6.9°S, i.e., about 26% of the total hake population is distributed south of 8°S and the subpopulation within, e.g., 8-9°S is about 15% of the total hake population (Table 2).

The data given in Table 2, together with the VPA biomass estimates of Espino and Wosnitza-Mendo (this vol.) thus allows quantification of the hake biomass within each degree of latitude along the coast of Peru in relation to SST.

The Feeding Model

The total daily food intake of a population ($R_{tot.}$) can be expressed as the sum of the intake by each age (or weight) group (R_t):

$$R_{tot} = \sum_{t=n}^{t_{max}} N_t * R_t \qquad ...10)$$

where N_t is the number of individuals of age t and R_t the mean daily ration of an individual of age t.

The daily anchoveta consumption (R_a) can be expressed as a fraction of total consumption by:

$$R_a \sum_{t=n}^{t_{max}} = R_t * A \qquad ...11)$$

where A (>0, <1) quantifies the availability of anchoveta to the predator. This availability can be viewed as a function of the biomass and the vulnerability of anchoveta (Muck and Pauly 1987); Muck and Fuentes 1987; Muck and Sanchez 1987).

Stomach content analyses show that anchoveta availability to hake depends on predator size and varies between different areas off the Peruvian coast (Muck et al. 1988; Fuentes et al., in press). Fig. 3 shows annual means of the fraction of anchoveta (P%-anch.) in the stomach contents of adult hake (35-45 cm) for the period 1975-1986.

Table 1. Percentage of total hake population south of a given latitude along the Peruvian coast, as related to SST.

Tabla 1. Porcentaje total de la población de merluza al sur de una latitud dada a lo largo de la costa peruana, relacionada a la TSM.

		Southern latitude													
SST	Dmax	1°	2°	3°	4°	5°	6°	7°	8°	9°	10°	11°	12°	13°	14°
15.0	4.4	99.903	98.537	89.800	64.060	29.120	7.350	0.914	0.048	0.000	0.000	0.000	0.000	0.000	0.000
15.5	4.6	99.903	98.809	91.770	69.850	36.320	11.120	1.831	0.154	0.007	0.000	0.000	0.000	0.000	0.000
16.0	4.7	99.903	98.928	92.650	72.570	39.740	13.350	2.500	0.248	0.011	0.000	0.000	0.000	0.000	0.000
16.5	4.9	99.931	99.111	93.940	76.730	46.810	18.410	4.360	0.570	0.048	0.000	0.000	0.000	0.000	0.000
17.0	5.0	99.931	99.180	94.520	78.810	50.000	21.190	5.480	0.820	0.069	0.000	0.000	0.000	0.000	0.000
17.5	5.2	99.931	99.305	95.450	82.120	55.960	26.760	8.380	1.578	0.175	0.011	0.000	0.000	0.000	0.000
18.0	5.3	99.931	99.361	95.910	83.650	59.100	29.810	10.030	2.068	0.264	0.023	0.000	0.000	0.000	0.000
18.5	5.5	99.952	99.461	96.560	86.210	64.060	35.940	13.790	3.440	0.539	0.048	0.003	0.000	0.000	0.000
19.0	5.6	99.952	99.492	96.860	87.290	66.640	38.590	15.870	4.360	0.755	0.097	0.007	0.000	0.000	0.000
19.5	5.8	99.952	99.560	97.320	89.250	70.880	44.430	20.330	6.430	1.355	0.187	0.016	0.000	0.000	0.000
20.0	6.0	99.952	99.621	97.725	90.820	74.860	50.000	25.140	9.180	2.275	0.379	0.048	0.000	0.000	0.000
20.5	6.1	99.952	99.643	97.882	91.620	76.420	52.790	27.760	10.560	2.870	0.523	0.069	0.005	0.000	0.000
21.0	6.3	99.966	99.683	98.214	92.790	79.670	57.530	33.000	14.010	4.360	0.939	0.144	0.016	0.000	0.000
21.5	6.3	99.966	99.683	98.214	92.790	79.670	57.530	33.000	14.010	4.360	0.939	0.144	0.016	0.000	0.000
22.0	6.6	99.966	99.736	98.537	94.290	83.400	64.060	40.520	19.770	7.350	1.970	0.379	0.048	0.005	0.000
22.5	6.6	99.966	99.736	98.537	94.290	83.400	64.060	40.520	19.770	7.350	1.970	0.379	0.048	0.005	0.000
23.0	6.9	99.966	99.774	98.809	95.350	86.430	69.850	47.610	26.110	11.120	3.590	0.866	0.154	0.023	0.000
23.5	6.9	99.966	99.774	98.809	95.350	86.430	69.850	47.610	26.110	11.120	3.590	0.866	0.154	0.023	0.002
24.0	7.2	99.966	99.807	99.010	96.250	88.880	74.860	54.380	33.000	15.870	5.940	1.743	0.379	0.069	0.007
24.5	7.2	99.966	98.807	99.010	96.250	88.880	74.860	54.380	33.000	15.870	5.940	1.743	0.379	0.069	0.007
25.0	7.5	99.977	99.831	99.180	96.710	90.320	77.640	58.710	37.450	19.490	7.930	2.560	0.639	0.135	0.016
25.5	7.4	99.977	99.825	99.134	96.930	90.820	78.810	60.640	39.360	21.190	9.180	3.070	0.820	0.169	0.023
26.0	7.8	99.977	99.846	99.266	97.260	91.920	81.060	64.060	43.640	24.830	11.700	4.360	1.287	0.298	0.048
26.5	7.7	99.977	99.851	99.305	97.440	92.510	82.120	65.910	46.020	26.760	12.920	5.050	1.578	0.379	0.069
27.0	8.1	99.977	99.865	99.379	97.725	93.320	84.130	69.150	50.000	30.850	15.870	6.680	2.275	0.621	0.135
27.5	8.0	99.977	99.865	99.413	97.831	93.700	85.080	70.540	51.990	33.000	17.360	7.640	2.680	0.776	0.181
28.0	8.4	99.977	99.865	99.461	98.077	94.410	86.650	73.570	55.570	36.690	20.610	9.680	3.750	1.160	0.298
28.5	8.3	99.977	99.865	99.492	98.214	94.740	87.290	74.860	57.530	38.590	22.360	10.750	4.360	1.426	0.379
29.0	8.7	99.977	99.903	99.534	98.382	95.250	88.690	77.040	61.030	42.470	25.780	13.140	5.710	2.018	0.604
29.5	8.6	99.977	99.903	99.560	98.461	95.540	89.250	78.230	62.550	44.430	27.430	14.460	6.430	2.390	0.734
30.0	9.0	99.984	99.903	99.621	98.679	96.250	90.820	81.330	67.000	50.000	33.000	18.670	9.180	3.750	1.321

Table 2. Percentage of total hake population with 1°-interval along the Peruvian coast, as related to SST.
Tabla 2. Porcentaje total de la población de merluza a intervalos de 1° a lo largo de la costa peruana, relacionada a la TSM.

		Southern latitude												
SST	D_{max}	(1-2)	(2-3)	(3-4)	(4-5)	(5-6)	(6-7)	(7-8)	(8-9)	(9-10)	(10-11)	(11-12)	(12-13)	(13-14)
15.0	4.4	1.37	8.74	25.74	34.94	21.77	6.44	0.87	0.05	0.00	0.00	0.00	0.00	0.00
15.5	4.6	1.09	7.04	21.92	33.53	25.20	9.29	1.68	0.15	0.01	0.00	0.00	0.00	0.00
16.0	4.7	0.98	6.28	20.08	32.83	26.39	10.85	2.25	0.24	0.01	0.00	0.00	0.00	0.00
16.5	4.9	0.82	5.17	17.21	29.92	28.40	14.05	3.79	0.52	0.05	0.00	0.00	0.00	0.00
17.0	5.0	0.75	4.66	15.71	28.81	28.81	15.71	4.66	0.75	0.07	0.00	0.00	0.00	0.00
17.5	5.2	0.63	3.86	13.33	26.16	29.20	18.38	6.80	1.40	0.16	0.01	0.00	0.00	0.00
18.0	5.3	0.57	3.45	12.26	24.55	29.29	19.78	7.96	1.80	0.24	0.02	0.00	0.00	0.00
18.5	5.5	0.49	2.90	10.35	22.15	28.12	22.15	10.35	2.90	0.49	0.05	0.00	0.00	0.00
19.0	5.6	0.46	2.63	9.57	20.65	28.05	22.72	11.51	3.61	0.66	0.09	0.01	0.00	0.00
19.5	5.8	0.39	2.24	8.07	18.37	26.45	24.10	13.90	5.08	1.17	0.17	0.02	0.00	0.00
20.0	6.0	0.33	1.90	6.90	15.96	24.86	24.86	15.96	6.91	1.90	0.33	0.05	0.00	0.00
20.5	6.1	0.31	1.76	6.26	15.20	23.63	25.03	17.20	7.69	2.35	0.45	0.06	0.00	0.00
21.0	6.3	0.28	1.47	5.42	13.12	22.14	24.53	18.99	9.65	3.42	0.80	0.13	0.02	0.00
21.5	6.3	0.28	1.47	5.42	13.12	22.14	24.53	18.99	9.65	3.42	0.80	0.13	0.02	0.00
22.0	6.6	0.23	1.20	4.25	10.89	19.34	23.54	20.75	12.42	5.38	1.59	0.33	0.04	0.00
22.5	6.6	0.23	1.20	4.25	10.89	19.34	23.54	20.75	12.42	5.38	1.59	0.33	0.04	0.00
23.0	6.9	0.19	0.97	3.46	8.92	16.58	22.24	21.50	14.99	7.53	2.72	0.71	0.13	0.02
23.5	6.9	0.19	0.97	3.46	8.92	16.58	22.24	21.50	14.99	7.53	2.72	0.71	0.13	0.02
24.0	7.2	0.16	0.80	2.76	7.37	14.02	20.48	21.38	17.13	9.93	4.20	1.36	0.31	0.06
24.5	7.2	0.16	0.80	2.76	7.37	14.02	20.48	21.38	17.13	9.93	4.20	1.36	0.31	0.06
25.0	7.5	0.15	0.65	2.47	6.39	12.68	18.93	21.26	17.96	11.56	5.37	1.92	0.50	0.12
25.5	7.4	0.15	0.69	2.20	6.11	12.01	18.17	21.28	18.17	12.01	6.11	2.25	0.65	0.15
26.0	7.8	0.13	0.58	2.01	5.34	10.86	17.00	20.42	18.81	13.13	7.34	3.07	0.99	0.25
26.5	7.7	0.13	0.55	1.87	4.93	10.39	16.21	19.89	19.26	13.84	7.87	3.47	1.20	0.31
27.0	8.1	0.11	0.49	1.65	4.40	9.19	14.98	19.15	19.15	14.98	9.19	4.41	1.65	0.49
27.5	8.0	0.11	0.45	1.58	4.13	8.62	14.54	18.55	18.99	15.64	9.72	4.96	1.90	0.60
28.0	8.4	0.11	0.40	1.38	3.67	7.76	13.08	18.00	18.88	16.08	10.93	5.93	2.59	0.86
28.5	8.3	0.11	0.37	1.28	3.47	7.45	12.43	17.33	18.94	16.23	11.61	6.39	2.93	1.05
29.0	8.7	0.07	0.37	1.15	3.13	6.56	11.65	16.01	18.56	16.69	12.64	7.43	3.69	1.41
29.5	8.6	0.07	0.34	1.10	2.92	6.29	11.02	15.68	18.12	17.00	12.97	8.03	4.04	1.66
30.0	9.0	0.08	0.28	0.94	2.43	5.43	9.49	14.33	17.00	17.00	14.33	9.49	5.43	2.43

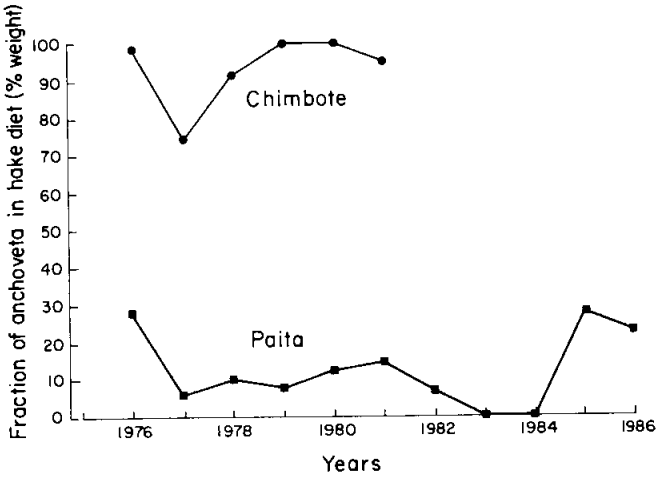

Fig. 3. Fraction of anchoveta (weight %) in stomach contents of Peruvian hake from 1976-1981 off Chimbote, and from 1976 to 1986 off Paita.

Fig. 3. Fracción de anchoveta (% peso) en el contenido estomacal de la merluza peruana desde 1976-1981 frente a Chimbote y de 1976-1986 frente a Paita.

While in the Paita area (4-6°S) in 1976-1981, anchoveta represented only ca. 10% of total stomach contents, this value was much higher (i.e.,over 90%), during the same period, off Chimbote (8-10°S).

The values of P%-anch., for hake of 35 to 45 cm caught off Paita were significantly ($r = 0.79$, d.f. 9; $P < 0.05$) positively correlated with mean annual anchoveta biomass or B_a (see also Muck, this vol., i.e.)

$$P\%\text{-anch.} = 2.03 + 5.398 * B_a \qquad ...12)$$

or, when excluding the years with less reliable anchoveta biomass estimates (i.e., 1980 to 1983)

$$P\%\text{-anch.} = -1.67 + 5.398 * B_a \qquad ...13)$$

($r = 0.86$, d.f. = 5; $P < 0.05$.) Thus, increasing anchoveta total abundance within 4-14°S results, in the Paita area, in an increasing anchoveta component in hake stomachs. (The same can be observed for hake caught off Chimbote during the period 1976-1978.)

Eliminating the intercept of equation (13) by forcing the line through the origin leads to

$$P\%\text{-anch. (Paita)} = 4.98 * B_a \qquad ...14)$$

Thus, the total anchoveta biomass estimated for the area 4-14°S (Pauly et al. 1987a) must be close to or beyond 20 t x 10^6 for the anchoveta fraction to reach 100% in the stomachs of hake of 35-45 cm, in the area of Paita.

On the other hand, in the area of Chimbote, P%-anch. values close to 100 have been found, for hake of 35-45 cm, during 1976, 1978, 1979 and 1981, when mean total anchoveta biomass was only of about 3.2 t x 10^6. This can be expressed as:

$$P\%\text{-anch. (Chimbote)} = 30.9 * B_a \qquad ...15)$$

Interpolating between Paita (5°S) and Chimbote (9°S) equations (4) and (15) can now be combined to:

$$P\%\text{-anch.} = (-27.42 + 6.48 * \text{Lat.}) * B_a \qquad ...16)$$

which quantifies the anchoveta fraction in the stomachs of hake ranging from 35-45 cm as a function of (i) anchoveta biomass and (ii) latitude south.

Multiplying equation (16) by 0.01, we obtain the anchoveta availability index (A) of equation (11):

$$A = ((-27.42 + 6.48 * Lat.) * B_a) * 0.01 \qquad ...17)$$

(In all computations, when equation (17) produced estimates of A larger then unity, A was set equal to 1.)

Fig. 4 shows the dynamics of anchoveta availability to hake for different values of anchoveta total biomass, and suggests that the north-east gradient between Paita and Chimbote is eliminated when anchoveta total biomass is higher than about 10 x 10^6 tonnes.

To generalize equation (16) for size groups of hake other than 35-45 cm, the data of Table 3 have been used (see also Fig. 5).

The increase of anchoveta in the diet of hake between 22 and 42 cm reflects the shift of these fish from a pure zooplankton diet to a fish diet, while the decreasing trend of anchoveta in the diet of hake > 42 cm is related to their transition from a diet of small fishes (i.e., anchoveta) to larger ones (sardine, hake).

Fig. 6 shows the size related changes in preferred prey item for the area of Paita. This figure suggests that hake below 20 cm and above 70 cm do not feed on anchoveta. Fig. 7 shows the size-frequency distribution of anchoveta in the stomachs of hake of 20-70 cm.

The VPA-estimates of hake biomass in Espino and Wosnitza-Mendo (this vol.) refer to *age* group while the stomach content analyses data refer to *size* groups (of 5 cm width).

To convert size to age, the inverse of the von Bertalanffy formula was used:

$$t = t_o - 1/K * \ln (1 - L_t/L_\infty) \qquad ...18)$$

The constants for hake are (Dioses 1985):

$K = 0.139$ year^{-1}
$L_\infty = 99$ cm
$t_0 = -0.278$ year

The results of the length/age conversion are shown in Table 3 along with P% anch. values put on an age basis. The frequency distribution of the latter can be approximated by:

$$Y = e^{-0.5 * \left[\frac{t * 0.5 - 1.5}{0.4}\right]^2} \qquad ...19)$$

where "t" refers to hake age groups 1-7, i.e., to those age groups which feed on anchoveta. Thus, we can generalize equation (17) to:

$$A = ((-27.42 + 6.48 * Lat.) * B_A) * e^{-0.5 * \left[\frac{t * 0.5 - 1.5}{0.4}\right]^2} * 0.01 \qquad ...20)$$

which allows the estimation of anchoveta availability for each age group of hake as a function of anchoveta biomass and latitude south.

The total daily ration of an individual of the age group t (R_t) can be estimated using the mean total stomach weight per age group (STW_t) as suggested in Durbin et al. (1983):

$$R_t = STW_t * a * e^{(b * temp.)} * 24 \qquad ...21)$$

Table 3. Summary of analyses of hake stomach content for the area off Paita, 1976-1986.[a]
Tabla 3. Resumen del análisis del contenido estomacal de la merluza en el área de Paita, 1976-1986.

Total Length (cm)	Age class (years)	Age group used for VPA	Weight of total stomach content (g)	(s.d.)	(n)	Fish weight in total stomach contents (%)	Anchoveta weight in total stomach content (%)	(s.d.)	(rel.)
20 - 25	1.3 - 1.8	I	1.1	2.0	135	7.5	0.44	1.3	0.04
> 25 - 30	>1.8 - 2.3	II	2.3	4.3	1351	79.5	3.91	15.7	0.31
> 30 - 35	>2.3 - 2.8								
> 35 - 40	>2.8 - 3.5	III	4.6	3.6	11478	77.0	12.52	23.1	1.00
> 40 - 45	>3.5 - 4.0								
> 45 - 50	>4.0 - 4.7	IV	11.9	26.9	4222	83.7	5.24	15.3	0.42
> 50 - 55	>4.7 - 5.5								
> 55 - 60	>5.5 - 6.4	V	52.7	39.7	1189	96.0	1.17	7.2	0.09
> 60 - 65	>6.4 - 7.3	VI	59.3	27.9	1097	87.0	0.15	0.1	0.01
> 65 - 70	>7.3 - 8.5	VII	63.1	28.1	656	92.0	0.009	0.022	0.0007

[a]These results take account of empty stomachs (47.1% of total).

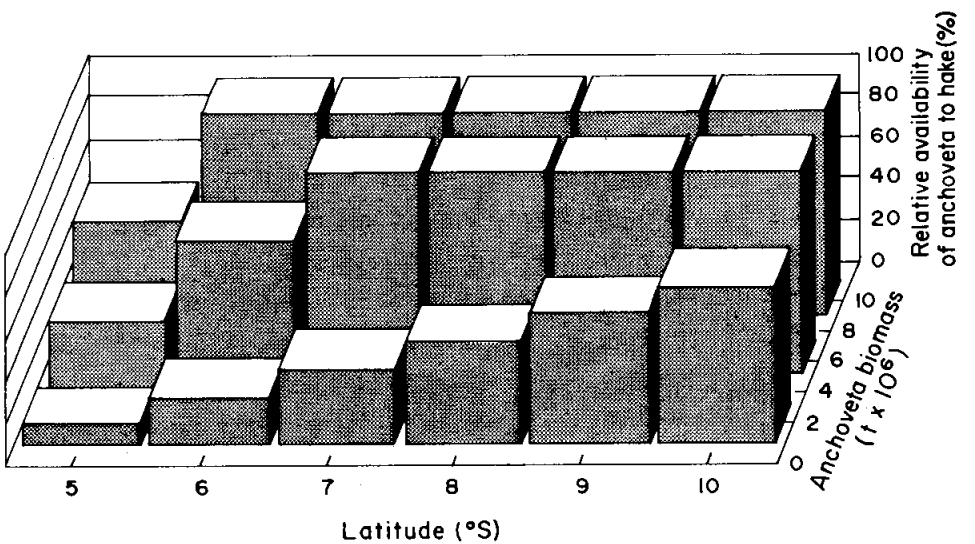

Fig. 4. Relative availability of anchoveta to Peruvian hake as a function of anchoveta biomass and latitude (5-10°S).
Fig. 4. Disponibilidad relativa de anchoveta para la merluza peruana como una función de la biomasa de anchoveta y la latitud (5-10°S).

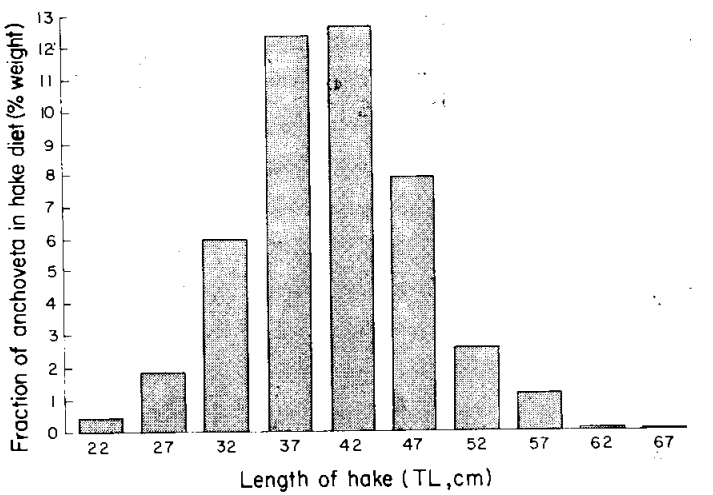

Fig. 5. Weight fraction of anchoveta in the diet of Peruvian hake of 22 to 67 cm total length.
Fig. 5. Fracción del peso de la anchoveta en la dieta de la merluza peruana de 22 a 67 cm de longitud total.

where "a" and "b" are constants relating food type and environmental temperature (temp.) to gastric evacuation rate.

As proposed in Durbin et al. (1983), "a" should vary, when R_t is expressed in per fish per day, from 0.04 (for non-fish food) to 0.004 (for fish food). The value of "b" was set here at 0.111, while "temp." was set at a constant value of 14.5°C, pertaining to the deeper layers of the Peruvian upwelling system.

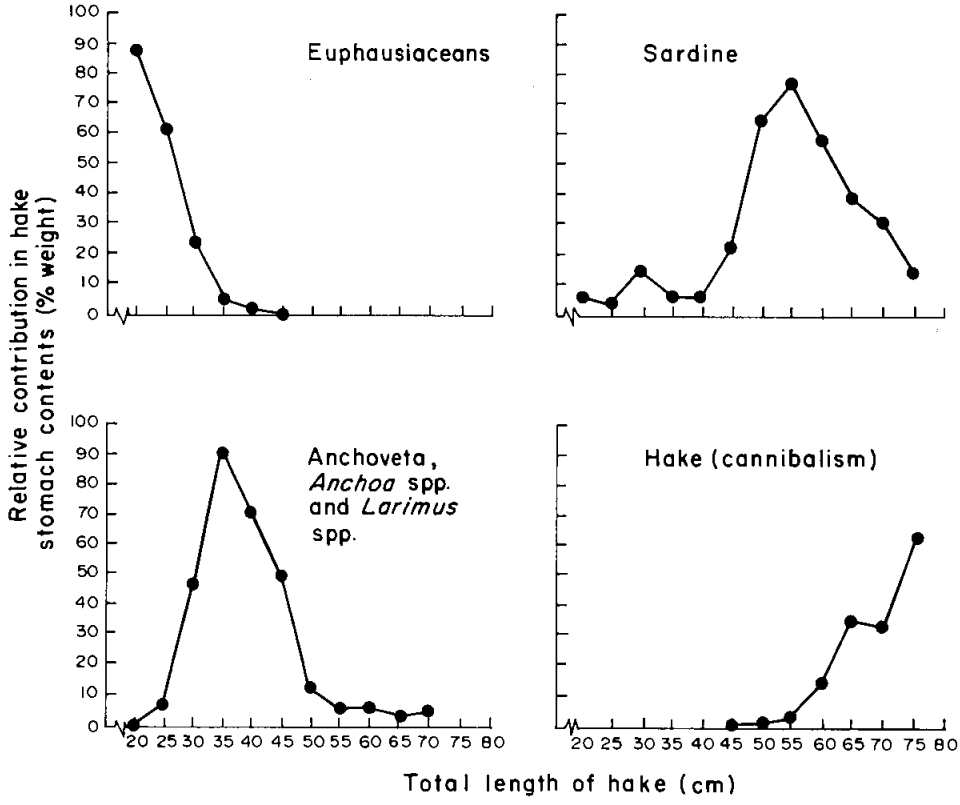

Fig. 6. Relationship between hake size and the proportion of various preferred prey items in their stomachs (based on samples collected off Paita, Peru).

Fig. 6. Relación entre el tamaño de la merluza y la proporción de varios items de presas preferidas en sus estómagos (basados en muestras colectadas de Paita, Perú).

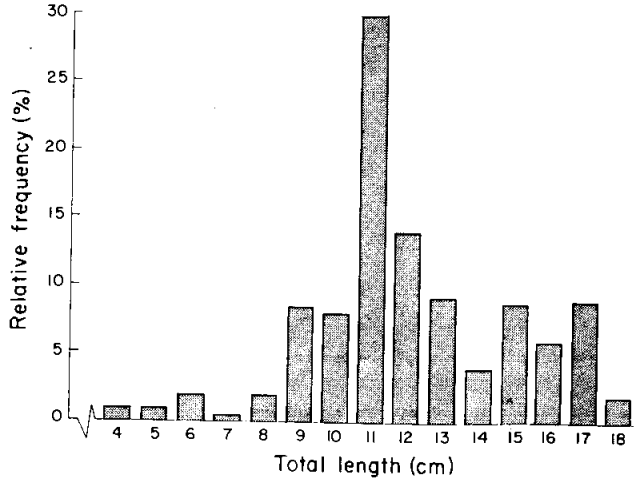

Fig. 7. Size composition of anchoveta in the stomach of Peruvian hake of 20-70 cm.

Fig. 7. Composición por tallas de la anchoveta en el estómago de la merluza peruana de 20-70 cm.

As shown in Fig. 6 the percentage of fish in hake stomach is related to predator size. Recalculating the data given in Fig. 6 and converting hake size to age (Table 3) suggest that the change from zooplankton diet to an almost pure fish diet occurs during the first 3 years (Fig. 8). This can be approximated by:

$$\% \text{ fish in hake diet} = \frac{95}{1 + e^{(5 - 2.5 * t)}} \qquad ...22)$$

Similarly, the term "a" of equation (21) can be made to vary from 0.004 (for hake age groups feeding on fish) to 0.04 (for hake age groups feeding on zooplankton) using:

$$a_t = \frac{0.33}{\left[\dfrac{95}{1 + e^{(5 - 2.5 * t)}}\right]} \qquad ...23)$$

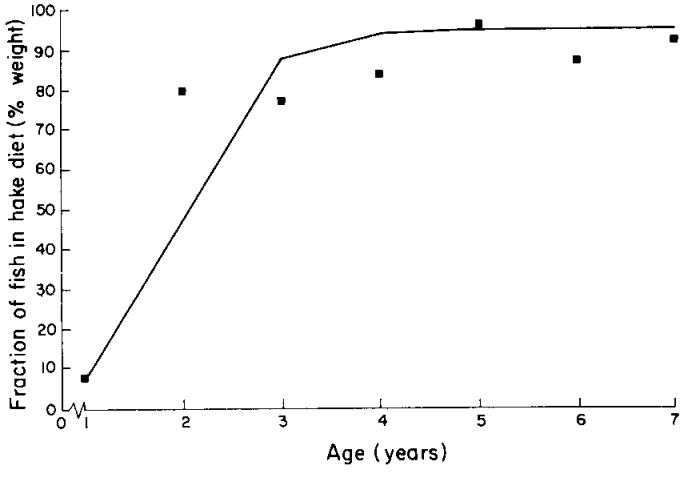

Fig. 8. Relationship between the age of Peruvian hake and the fraction of fish in their diet.
Fig. 8. Relación entre la edad de la merluza peruana y la fracción de peces en su dieta.

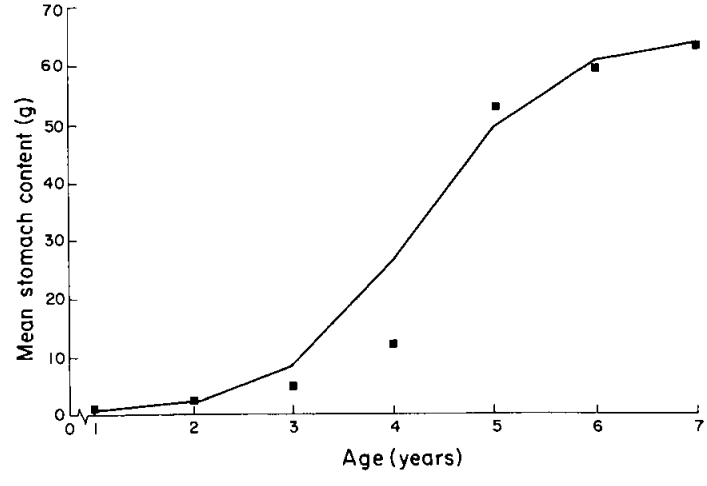

Fig. 9. Relationship between mean stomach content weight and age of Peruvian hake.
Fig. 9. Relación entre el peso promedio del contenido del estómago y la edad de la merluza peruana.

The mean stomach content weight (in g wet weight) of individual hake increases with hake age (or size, see Table 3 and Fig. 9), i.e.,

$$STW_t = \frac{65}{1 + e^{0.77(8.5 - 2t)}} \qquad ...24)$$

Thus, the complete equation for calculating the daily anchoveta consumption (in tonnes/day) by the hake population (i.e., by age group 1-7) within 4-14°S for different SST regimes and anchoveta biomasses (B_a, in millions of tonnes) is

$$\text{daily anchoveta consumption by hake population} = \sum_{lat.=4}^{lat.=14} \sum_{t=1}^{t=7} N_{t1\,lat.} * \frac{65}{1 + e^{0.77(8.5-2t)}}$$

$$* \frac{1/95}{1 + e^{(5 - 2.5t)}} * 0.33 * 24$$

$$* e^{0.111 * 14.5} * (-27.4 + 6.48 * lat.)$$

$$* B_a * e^{-0.5\left(\frac{t*0.05-1.5}{0.4}\right)^2} * 0.01 \qquad ...25)$$

Results and Discussion

The estimates of anchoveta consumption by Peruvian hake within 4-14°S are given on a monthly basis in Table 4 and on an annual basis in Fig. 10. These estimates may be used to assess the impact of hake on the natural mortality of anchoveta (see Pauly and Palomares, this vol).

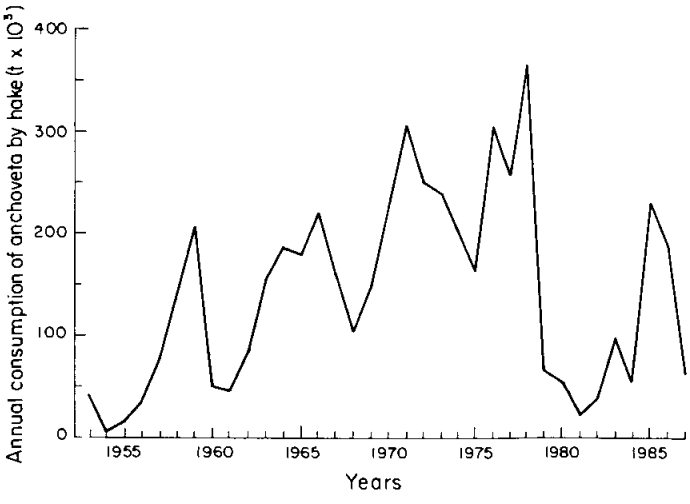

Fig. 10. Time series of annual consumption of anchoveta by hake off Peru (4-14°S), 1953 to 1987.
Fig. 10. Series de tiempo del consumo anual de la anchoveta por la merluza frente al Perú (4-14°S), 1953 a 1987.

Table 4. Monthly consumption, in tonnes, of anchoveta *(Engraulis ringens)* by hake *(Merluccius gayi)* off Peru, 4-14°S, 1953 to 1986.[a]
Tabla 4. Consumo mensual en toneladas de anchoveta (Engraulis ringens) *por la merluza* (Merluccius gayi) *frente al Perú, 4-14°S, 1953-1986.*

Year/Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	4,833	4,833	4,745	4,657	4,569	3,899	3,228	2,558	2,406	2,255	2,104	1,631
1954	1,157	684	611	539	467	407	348	288	295	302	308	896
1955	1,484	2,072	1,863	1,655	1,446	1,243	1,039	836	794	753	711	2,201
1956	3,691	5,181	4,585	3,988	3,392	2,930	2,467	2,005	1,687	1,370	1,053	3,181
1957	5,309	7,438	7,650	7,862	8,075	7,151	6,228	5,304	5,011	4,717	4,424	8,300
1958	12,176	16,052	14,201	12,350	10,499	10,125	9,751	9,377	10,334	11,292	12,249	15,917
1959	19,586	23,254	22,512	21,770	21,028	16,888	12,749	8,609	10,936	13,264	15,591	11,967
1960	8,343	4,720	4,696	4,671	4,647	4,309	3,972	3,634	3,575	3,516	3,458	3,999
1961	4,541	5,082	4,821	4,560	4,299	3,884	3,469	3,054	2,923	2,791	2,659	5,168
1962	7,676	10,184	9,251	8,319	7,387	6,897	6,408	5,919	5,380	4,841	4,303	7,795
1963	11,288	14,781	14,374	13,968	13,561	13,214	12,868	12,521	11,959	11,396	10,834	15,780
1964	20,726	25,673	22,487	19,300	16,114	14,393	12,672	10,951	10,392	9,832	9,273	10,949
1965	12,625	14,302	15,324	16,346	17,368	16,164	14,959	13,755	13,832	13,909	13,986	18,713
1966	23,439	28,166	25,218	22,270	19,323	17,029	14,734	12,440	12,702	12,963	13,225	15,776
1967	18,328	20,880	18,861	16,843	14,824	13,118	11,412	9,706	9,087	8,467	7,847	10,156
1968	12,465	14,773	12,589	10,405	8,221	7,613	7,004	6,396	6,040	5,685	5,330	8,190
1969	11,049	13,909	14,433	14,956	15,479	13,653	11,827	10,001	9,925	9,850	9,775	15,778
1970	21,781	27,784	25,482	23,180	20,878	18,604	16,330	14,057	13,474	12,892	12,310	20,560
1971	28,810	37,061	34,850	32,639	30,428	27,731	25,034	22,337	18,925	15,513	12,102	19,654
1972	27,207	34,759	28,812	22,865	16,918	15,953	14,988	14,023	15,099	16,176	17,252	27,362
1973	37,472	47,583	36,728	25,874	15,020	12,609	10,198	7,786	8,142	8,498	8,854	14,444
1974	20,034	25,624	24,260	22,896	21,532	18,306	15,079	11,853	10,480	9,107	7,735	12,383
1975	17,031	21,679	18,604	15,530	12,455	10,585	8,714	6,844	9,040	11,237	13,434	27,058
1976	40,683	54,307	47,214	40,121	33,028	25,056	17,084	9,112	7,845	6,578	5,312	9,120
1977	12,929	16,738	17,617	18,497	19,376	19,446	19,516	19,586	22,936	26,285	29,635	41,198
1978	54,761	67,324	56,607	45,890	35,174	28,289	21,404	14,519	11,245	7,971	4,698	5,925
1979	7,152	8,379	7,274	6,169	5,064	4,534	4,004	3,474	3,918	4,363	4,807	5,647
1980	6,487	7,327	6,759	6,190	5,622	4,760	3,899	3,037	2,698	2,359	2,020	2,310
1981	2,599	2,889	2,600	2,310	2,021	1,712	1,404	1,095	1,037	978	920	1,689
1982	2,458	3,227	3,202	3,108	3,156	2,848	2,541	2,233	2,782	3,331	3,880	6,456
1983	9,033	11,610	11,772	11,933	12,095	9,734	7,372	5,011	4,518	4,025	3,533	4,242
1984	4,952	5,662	5,248	4,835	4,421	3,972	3,523	3,074	3,549	4,023	4,497	11,589
1985	18,681	25,773	23,145	20,516	17,887	17,291	16,694	16,097	16,437	16,776	17,116	18,373
1986	19,631	20,889	18,655	16,420	14,186	13,753	13,320	12,887	13,525	14,164	14,803	16,702

[a]The estimates derived from equation (25) were originally expressed on a seasonal basis (e.g, southern spring = Jan. + Feb. + March) and have been put on monthly basis through linear interpolations between the central months of each season (i.e., February, May, July, November).

Anchoveta consumption of hake varied on a seasonal basis between 200,000 t (summer 1978) and 900 t (winter 1954) and on an annual basis between 370,000 t (1978) and 5,240 t (1954) (Fig. 10)

The variation in estimated anchoveta consumption depends on changes in (i) abundance of fish-feeding hake age groups, (ii) the north-south extension of hake distribution area and (iii) anchoveta availability for hake.

For age group abundance, the VPA-estimates of Espino and Wosnitza-Mendo (this vol.) has been used. These authors found an inverse relationship between anchoveta biomass and hake biomass and suggest that anchoveta controls hake population growth at the level of egg and larvae predation. This hypothesis is supported by time series analysis of hake larvae abundance (Sandoval et al., this vol.), and agrees with the findings of Muck et al. (1988) for sardine in that anchoveta controls population growth of other fish species by feeding on their eggs and larvae.

Hake distribution has been modeled as a function of SST, which reflects the seasonal and El Niño-related dynamics of the size of the oxygen minimum zone depths 100-200 m (Espino and Wosnitza-Mendo 1988). These dynamics are as follows: increasing sea surface temperature results in a southward hake population expansion, invading the main anchoveta distribution area (4-14°S.L.). Thus, anchoveta consumption of hake during summer (January-March) has been estimated 2-3 fold higher than during winter (July-September), when the overlap between predator and prey distribution areas is less pronounced.

These effects become more evident during El Niño events, when hake, usually distributed within 3-7°S, moves southward. The data of Fuentes et al. (in press) for Callao (12°S.L.) and Pisco (13.5°S.L.) show that when such conditions prevail, hake feed predominantly on anchoveta.

Anchoveta availability for hake is a positive function of anchoveta biomass and hake size. The model includes an anchoveta distribution component which results in an increasing availability of anchoveta to hake, in the area 4-7°S (= northern boundary of anchoveta distribution) with increasing anchoveta total biomass.

The modeling of SST, i.e., oxygen-related changes in north-south hake distribution was performed on the basis of a normal distribution whose parameters (mean, standard deviation) were empirically derived from survey data.

The model results in a latitudinal shift of the density maximum of hake distribution as a function of SST, accompanied by north-south expansion or contraction, respectively, of the (potential) hake distribution area. Thus hake is more concentrated during cold periods than during warm ones, which is bound to affect cannibalism and prerecruit survival, as suggested in Espino and Wosnitza-Mendo (this vol.).

With the estimation of anchoveta consumption by the Peruvian hake, the "cycle" of the most important anchoveta predators has been completed. When comparing mean anchoveta consumption by hake with the mean consumption by other anchoveta predators, fishery included, (Muck et al. 1988) for the period 1953-1987, hake occupies the penultimate position.

Similar to mackerel and horse mackerel, hake belongs to the group of opportunistic predators whose importance for anchoveta mortality varies with the dynamics of oceanographic conditions: changes in sea temperature (mackerel, horse mackerel) and oxygen conditions (hake) affect the distribution area of these species, resulting in a variable predation stress on anchoveta, which is higher in summer than during winter and very high during El Niño events.

Acknowledgements

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References

Dioses, T., 1985. Edad y crecimiento de la merluza peruana (*Merlucius gayi peruanus*). Anales I. Congreso Nacional de Biología Pesquera. July 1984, Trujillo, Perú:65-69.

Durbin, E.G., G. Durbin, R.W. Langton and R.E. Bowman, 1983. Stomach content of silver hake *Merluccius bilinearis*, and atlantic cod *Gadus morhua*, and estimation of their daily rations. U.S. Fish. Bull. 81:437-454.

Espino, M. and W. Urquizo. 1986. Effect of El Niño on the distribution and recruitment of the Peruvian hake (*Merluccius gayi peruanus*). Unpublished poster presented at the Chapman Conference on El Niño - an International Symposium, Guayaquil, Ecuador, 27-31 Oct. 1986. (p. 41 in Volume of Abstracts)

Espino, M. and C. Wosnitza-Mendo. 1988. Efecto de la concentración en la mortalidad natural y su aplicación en el análisis de cohortes, p.235-252. *In* T. Wyatt and M.G. Larrañeta (eds.) Long term changes in marine fish populations. A Symposium held in Vigo, Spain, 18-21 Nov. 1986, Vigo.

Fuentes, H., E. Antonietti and P. Muck. Alimentacion de la merluza *(Merluccius gayi peruanus)* de la zona de Paita. Bol. Comision Permanente del Pacifico Sur. (In press).

Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the peruvian anchoveta, 1953-1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and G. Sanchez. 1987. The importance of mackerel and horse mackerel predation for the peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P., M. Espino, H. Fuentes, C. Wosnitza-Mendo and M. Esquerre. 1988. Predación de la merluza peruana *(Merluccius gayi peruanus)* sobre la anchoveta *(Engraulis ringens)*, p. 249-253. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento Peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987a. VPA Estimates of monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., A. Ch. Vildoso, J. Mejía, M. Samame and M.L. Palomares. 1987b. Population dynamics and estimated anchoveta consumption of bonito (*Sarda chiliensis*) off Peru, 1953 to 1982, p. 240-267. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

The South Pacific Oceanic Horse Mackerel *(Trachurus picturatus murphyi)* Fishery

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PARRISH, R.H. 1989. The South Pacific oceanic horse mackerel *(Trachurus picturatus murphyi)* fishery, p. 321-331. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

The horse mackerel fishery of the South Pacific currently dominates the world's catch of horse mackerels. The rapid increases in catches of horse mackerel by South American purse seine fleets and the distant water USSR trawl fleet are discussed and the geographical expansion of the trawl fishery is shown utilizing ship surface weather observations.

Due to disagreement on the taxonomic identity of the species which supports the fishery, a review of the world's *Trachurus* was made. The results of this review show that neither of the eastern Pacific forms of *Trachurus* merits full species rank. It is concluded that both are subspecies of the oceanic horse mackerel *(Trachurus picturatus); T.p. symmetricus* in the northeastern Pacific and *T.p. murphyi* in the southeastern Pacific. It is further suggested that it is likely that the range of *T.p. murphyi* extends clear across the southern hemisphere west wind drift region (i.e., from the South Atlantic to Chile).

Resumen

Las pesquerías de jurel en el Pacífico Sur dominan actualmente las capturas mundiales de jureles. Se discute el rápido incremento en las capturas de jurel por las flotas cerqueras sudamericanas y la flota arrastrera soviética que opera en aguas distantes y se muestra la expansión geográfica de las pesquerías de arrastre mediante el empleo de observaciones del clima efectuadas por los barcos.

Se hace una revisión de los *Trachurus* del mundo, en vista de los desacuerdos en la identidad taxonómica de las especies que soportan las pesquerías. Los resultados de esta revisión muestran que ninguna de las formas de *Trachurus* del Pacifico Oriental amerita plenamente la jerarquía de especie. Se concluye que ambas son subespecies del jurel oceánico *(Trachurus picturatus); T.p. symmetricus* en el Pacífico Nororiental y *T.p. murphyi* en el Pacífico Suroriental. Se sugiere además que es probable que el rango de *T.p. murphyi* se extienda a través de la región con vientos del oeste del hemisferio sur (desde el Atlantico Sur a Chile).

Introduction

Horse mackerels, of the genus *Trachurus,* are a widespread group occurring in nearly all of the temperate and subtropical, neritic regions of the oceans and they have extensive, but poorly understood, oceanic distributions in several regions. They also occur in a number of tropical neritic regions. The taxonomy of the group is in considerable flux and their extensive distribution is undoubtedly, at least partially, the cause of the present taxonomic confusion: forms which are very similar in morphology and meristics, but widely separated geographically, are assumed, a priori, to be separate species by many workers.

Over the last two decades the horse mackerels have had one of the largest increases in the world's fish catch. Landings rose from 1.2 x 10^6 tonnes (t) in 1965 to 3.9 x 10^6 t in 1984. In 1965 catches of horse mackerel were principally from the northern hemisphere (0.80 x 10^6 t); however, the increase in catches has been entirely the result of developing fisheries in the

southern hemisphere (Fig. 1A). Although horse mackerel occur in much of the world ocean, the bulk of its catches, and supposedly biomass, is concentrated in the eastern boundary currents (Fig. 1B).

Regionally the catches of horse mackerels have exhibited tremendous changes over the last two decades (Table 1). In 1965 half of the world catch of *Trachurus* came from the northwestern Pacific (0.55 x 10^6 t) and the rest was primarily taken in the northeastern Atlantic (0.22 x 10^6 t) and southeastern Atlantic (0.31 x 10^6 t). By the early 1970s catches from the northwestern Pacific had declined greatly, whereas catches from the other two regions had significant increases. Catches reached a maximum of 0.91 x 10^6 t in the northeastern Atlantic in 1973 and a maximum of 0.97 x 10^6 t in the southeastern Atlantic in 1978. Most of these increases in catches were due to the development of distant-water trawl fisheries off North and South Africa by European nations.

Development of the South Pacific Fishery

The most significant change in the world's horse mackerel catches occurred as the result of the development of the southeastern Pacific fishery which rose from 0.015 x 10^6 t in 1965 to a maximum of 2.32 x 10^6 t in 1984 (Fig. 1C). The South Pacific fishery was developed in the early 1970s by Chilean purse seiners forced to alter their fishing strategies due to the collapse of the

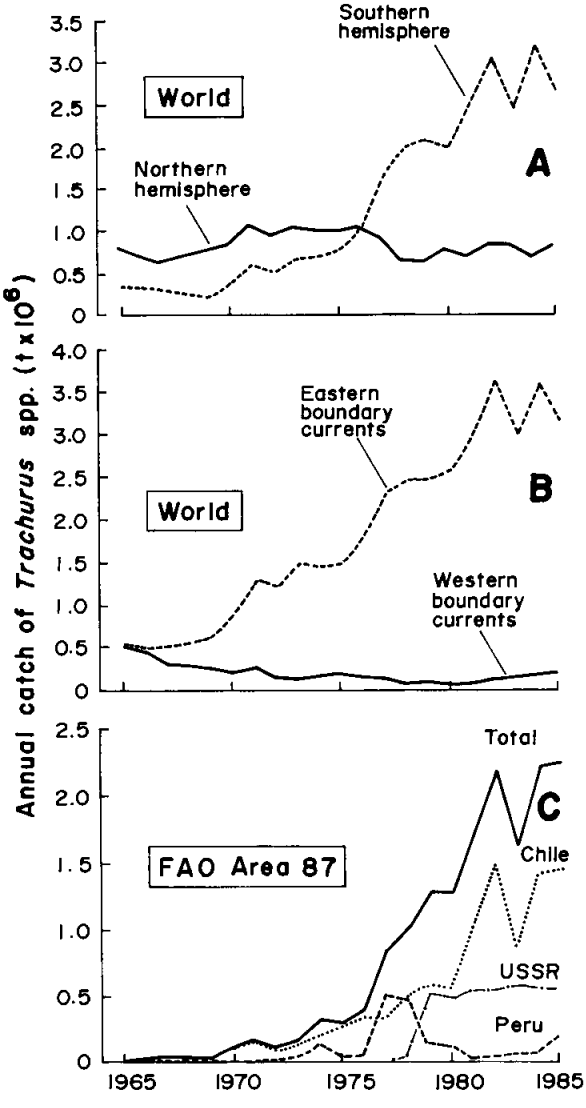

Fig. 1. Catches of *Trachurus* spp., 1965-1985. A. World catches, by hemisphere. B. Catches, by ecosystem type. C. Catches in FAO Area 87, by country.

Fig. 1. Capturas de Trachurus *spp., 1965-1985. A. Capturas mundiales, por hemisferios. B. Capturas, por tipos de ecosistemas. C. Capturas en el area 87 de FAO, por paises.*

Table 1. World catch of *Trachurus* by FAO statistical area (x 10^2 t).
Tabla 1. Captura mundial de Trachurus *por áreas estadísticas de FAO (x 10^2 t).*

OCEAN	Indian		N. Pacific		S. Pacific		N. Atlantic		S. Atlantic		Total
	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	
FAO AREA Year	51	57	61	67 + 77	81	87	31	27 + 37 + 34	41	47	
1965	0	0	5,534	303	0	153	0	2,175	2	3,121	11,288
1966	0	0	4,872	187	1	219	0	1,873	4	3,024	10,180
1967	0	0	3,342	174	5	295	0	2,779	37	2,492	9,124
1968	0	0	3,145	254	6	269	0	3,513	13	2,063	9,263
1969	0	0	2,858	236	3	227	0	4,25	3	1,838	9,688
1970	31	0	2,221	217	3	1,167	0	5,853	10	2,318	11,820
1971	4	0	2,834	272	138	1,676	0	7,626	4	3,992	16,546
1972	21	0	1,565	232	187	1,113	0	7,721	1	3,647	14,487
1973	16	0	1,308	94	157	1,644	0	9,067	2	4,818	17,106
1974	19	0	1,685	100	192	3,235	0	8,287	15	3,455	16,988
1975	45	0	1,932	204	138	2,991	0	7,855	5	4,534	17,704
1976	50	0	1,360	184	163	3,964	0	8,897	13	6,095	20,726
1977	349	0	948	501	175	8,480	0	7,792	17	7,511	25,773
1978	96	0	640	324	112	10,144	0	5,525	20	9,656	26,517
1979	79	0	932	166	75	12,873	0	5,112	6	7,672	26,915
1980	35	0	567	216	63	12,806	0	7,076	9	6,941	27,713
1981	24	0	716	159	116	17,403	0	6,054	14	7,725	32,211
1982	37	0	1,196	263	147	21,996	0	6,966	7	7,978	38,590
1983	64	0	1,461	187	207	16,682	0	6,739	4	7,464	32,808
1984	86	0	1,468	109	403	23,240	0	5,437	3	7,973	38,719
1985	83	0	1,738	97	413	21,488	0	6,487	4	4,472	34,782

anchoveta fishery in 1972-1973 (Table 2). Chilean landings of horse mackerel reached 0.5 x 10^6 t in 1978 and, except for the El Niño year of 1983, have exceeded 1.4 x 10^6 t since 1981. In the early 1970s Peru also began to develop a purse seine horse mackerel fishery; however, this fishery has not achieved the production of the Chilean fishery and with the exception of 1977-1978, when landings were near 0.5 x 10^6 t, landings have averaged less than 0.1 x 10^6 t.

Both the Chilean and Peruvian horse mackerel fisheries are neritic fisheries with catches almost exclusively coming from their respective 200 mile economic zones. The Chilean fishery started in northern Chile, in the Arica-Antofagasta region and expanded to central Chile in the late 1970s (Serra 1987). During the 1980s the Chilean landings have been about equally divided between the Arica-Antofagasta region (18-24°S) and the Talcahuano region (37°S); landings in the Coquimbo region of central Chile (30°S) have been an order of magnitude less than in the other two regions (Serra 1987). Fishing areas for the Peruvian catches are not well-documented in the available literature.

Table 2. Southeastern Pacific *Trachurus* catch by country (FAO Area 87; x 10^2 t).
Tabla 2. Captura de Trachurus *en el Pacífico Suroriental por países (Area 87 de FAO; x 10^2 t).*

	Chile	Peru	Ecuador	USSR	Other	Total
1965	127	26	0	0	0	153
1966	176	43	0	0	0	219
1967	264	31	0	0	0	295
1968	241	28	0	0	0	269
1969	185	42	0	0	0	227
1970	1,120	47	0	0	0	1,167
1971	1,584	92	0	0	0	1,676
1972	870	188	0	55	0	1,113
1973	1,216	428	0	0	0	1,644
1974	1,944	1,292	0	0	0	3,236
1975	2,612	379	0	0	0	2,991
1976	3,423	542	0	0	0	3,965
1977	3,408	5,049	0	0	22	8,479
1978	5,001	4,625	0	492	25	10,143
1979	5,975	1,516	0	5,322	60	12,873
1980	5,622	1,234	0	4,944	1,004	12,804
1981	10,609	379	0	5,546	868	17,402
1982	14,946	450	0	5,554	974	21,924
1983	8,652	679	249	5,910	792	16,282
1984	14,263	768	100	5,706	1,327	22,164
1985	14,569	1,843	6	5,639	398	22,455

In 1978, trawlers from the USSR began fishing for horse mackerel offshore of the 200 mile limits of Peru and Chile and during the period 1979-1985 they have annually taken between 0.49 and 0.59 x 10^6 t in the offshore area (Table 1). The development and distribution of this distant water trawl fishery is well documented in the positions of the trawlers as reported in international meteorological observations. At the beginning of the fishery (1979) the reported positions were spread out in a band along the coast, outside of the 200 mile zones (i.e., between 80°W and 90°W from 10°S to 45°S in Fig. 2A). By 1983 reports show the fishery was concentrated off southern Chile at about 80°W and 40°S (Fig. 2B); however, there were also a considerable number of reports along 85°W north of the area of concentration. There was an absence of reports within Chile's 200 mile zone; Chile also has 200 mile zones around San Felix Island and Juan Fernandez Archipelago. By 1985, in addition to a distribution of reports similar to 1983, the reports show that the fishery extended westward along the west wind drift between 39 and 45°S (Fig. 2C).

To evaluate the seasonality of the Soviet trawl fishery, the meterological reports were limited to Soviet vessels and to 1984-1987, the period when the fishery was operating in the offshore west wind drift region. During the austral spring (October-December) the meterological reports are furthest to the north with reports concentrated between 34-41°S and 78-92°W (Fig. 3A). Reports are noticeably absent in the 200 mile zones around San Felix Island (26°S, 80°W) and the Juan Fernandez Archipelago (33°S, 80°W) but there are reports in international waters between the two zones and between the San Felix Island 200 mile zone and the continental 200 mile zone. During the austral autumn (April-June) the reports are concentrated in two regions

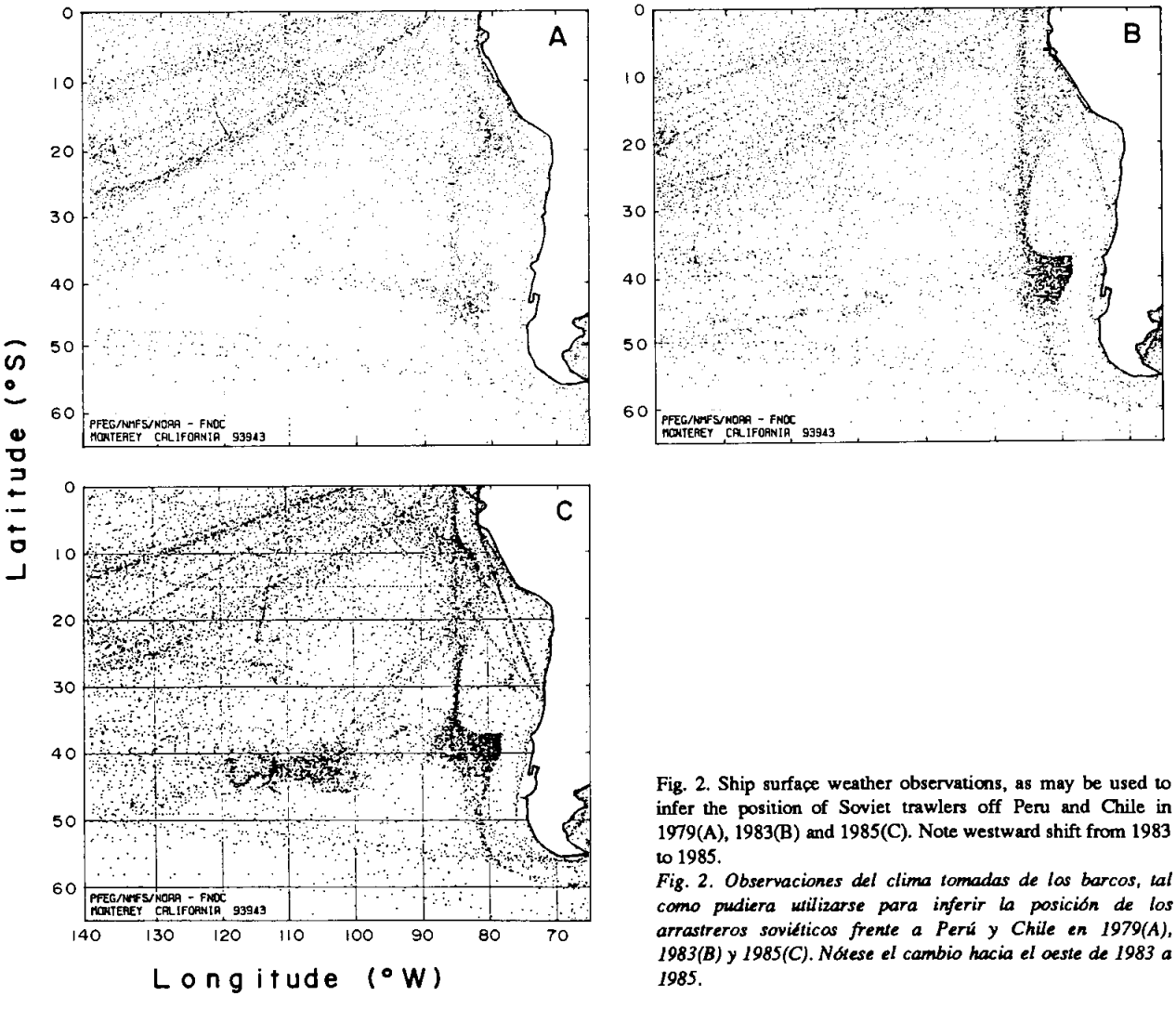

Fig. 2. Ship surface weather observations, as may be used to infer the position of Soviet trawlers off Peru and Chile in 1979(A), 1983(B) and 1985(C). Note westward shift from 1983 to 1985.

Fig. 2. Observaciones del clima tomadas de los barcos, tal como pudiera utilizarse para inferir la posición de los arrastreros soviéticos frente a Perú y Chile en 1979(A), 1983(B) y 1985(C). Nótese el cambio hacia el oeste de 1983 a 1985.

(Fig. 3B). The first is about five degrees south of the spring concentration (i.e., between 39-45°S and 79-90°W) and the second is much further offshore (39-45°S and 100-120°W). In both spring and autumn there are also considerable numbers of reports in the offshore region extending toward New Zealand.

The South Pacific distribution of the meterological reports from the Soviet trawl fleet suggests that, in the offshore region, horse mackerel are concentrated along the South Pacific subtropical convergence and that they seasonally move north and south with the convergence. It appears that the horse mackerel are able to complete their entire life cycle in the South Pacific subtropical convergence; independent of the neritic zone. Evseenko (1987) reported several larvae and a juvenile in the South Pacific convergence and Bailey (1989) shows that the horse mackerel spawns across the South Pacific from New Zealand to Chile. Bailey found juvenile horse mackerel along the subtropical convergence from 128°W to 166°W.

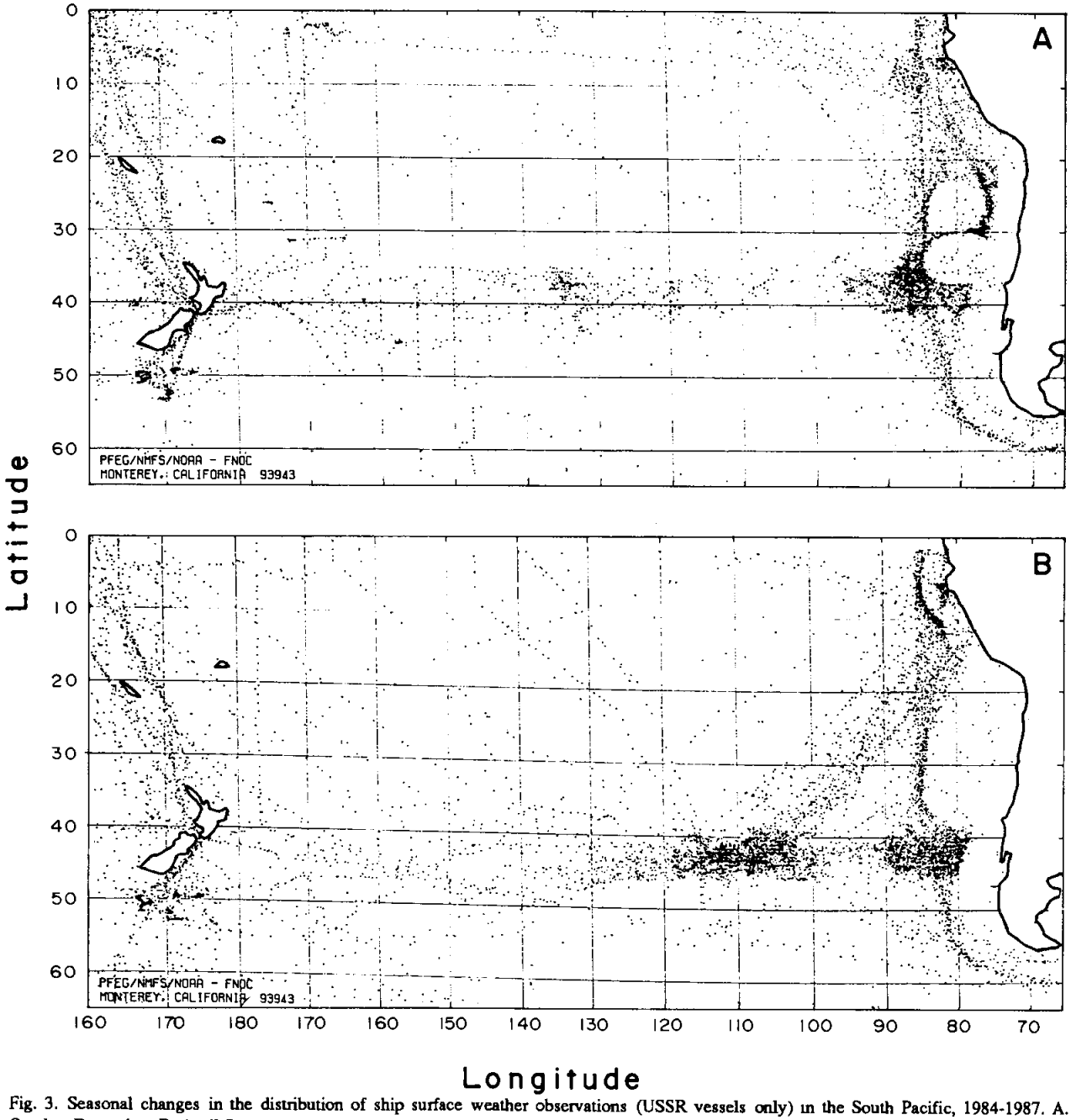

Fig. 3. Seasonal changes in the distribution of ship surface weather observations (USSR vessels only) in the South Pacific, 1984-1987. A. October-December. B. April-June.

Fig. 3. Cambios estacionales en la distribución de las observaciones del clima de los barcos (sólo embarcaciones soviéticas) en el Pacífico Sur, 1984-1987. A. Octubre-Diciembre. B. Abril-Junio.

Review of the Taxonomy of *Trachurus*

As shown above, the recent increase in the world's catch of *Trachurus* is primarily due to increases in the catch off Pacific South America. The FAO catch statistics consider the horse mackerel in this region to be *Trachurus murphyi,* but there is little agreement in the literature as to the correct species name. For example, in Peru the commonly used name is *T. symmetricus murphyi,* whereas in Chile the name *T. murphyi* is used (Santander and Flores 1983; Serra 1983). Therefore a review of the literature on the taxonomy of the horse mackerels was carried out to ascertain the status of the Pacific South American form.

The world's trachurids have been reviewed by Nichols (1920, 1940), Berry and Cohen (1974) and Shaboneyev (1980). Since Nichols (1920) the literature has contained 17 species and 2 subspecies (Table 3). The number and relative size of the scutes along the lateral line and the relative length of the dorsal accessory lateral line has been of primary importance in separating the various forms of *Trachurus* and all three reviews are heavily based on these characteristics. The taxonomy of the group is still in flux and it is not known if the forms in many regions are separate at the species, subspecies or even lower levels. The problem was perhaps best stated by Nichols (1940):

> "The systematic treatment of the forms of *Trachurus* is puzzling. They are sometimes so nearly identical from different oceans that authors synonymize them, but in no case where I have had material for comparison do they seem to me to be quite identical. They might all be races of a single widely distributed species except that two quite unlike forms are often recognized in the same waters."

Nichols (1940) recognized 12 species but he concluded by suggesting that the genus might be divided into 3 species, each having a number of geographically isolated races. Under this arrangement all of the species described to that time would have been races of *T. trachurus, T. picturatus* and *T. mediterraneus* (Table 4).

Table 3. Original descriptions of *Trachurus* used in recent literature.
Tabla 3. Descripciones originales de Trachurus *empleadas en la literatura reciente.*

Species	Author(s)	Synonyms
trachurus	Linnaeus 1758	
picturatus	Bowdich 1825	
semispinosus	Nillson 1832	= *trachurus*
declivis	Jenyns 1841	
novaezelandia	Richardson 1843	
japonicus	Temminck and Schlegel 1844	
symmetricus	Ayres 1855	
capensis	Castelnau 1861	
mediterraneus	Steindachner 1868	
murphyi	Nichols 1920	
muccullochi	Nichols 1920	= *novaezelandia*
lathami	Nichols 1920	
binghami	Nichols 1940	= *lathami*
trecae	Cadenat 1949	
indicus	Nekrasov 1966	
delagoa	Nekrasov 1970	
margaretae	Berry and Cohen 1974	= *delagoa*
Subspecies		
T. mediterraneus ponticus	Aleev 1956	
T. picturatus aleevi	Rytov and Razumovskaya 1984	

Berry and Cohen (1974) synonymized two of the species recognized by Nichols (1940), accepted two new species described by other authors and described a new species; thus recognizing 13 species. They did not group the species as did Nichols but described the relationships between similar forms in different regions. These descriptions result in groups of similar species which are very much like those of Nichols (Table 4). They also showed that there is only one species in the entire western Atlantic *(T. lathami)* and this has recently been verified by Saccardo (1987).

Table 4. Groupings of similar species by various authors.
Tabla 4. Agrupamiento de especies similares según diversos autores.

Nichols (1940)	Berry and Cohen (1974)	Shaboneyev (1980)	No. of [a] scutes	No. of [b] scutes	Scutes[c] depth
Trachurus Races	Similar Forms	*Trachurus* Group			
trachurus	*trachurus*	*t. trachurus*	74.3	72.9	26.4
capensis	*capensis*	*t. capensis*		73.8	
semispinosus		*japonicus*	71.5	71.5	25.6
muccullochi =		= *novaezelandia*	72.4	72.3	22.5
	margaretae[d] (= *delagoa*)	*delagoa*			
Mediterraneus Races	Similar Forms	*Mediterraneus* Group			
		m. ponticus			
mediterraneus	*mediterraneus*	*m. mediterraneus*	83.2	83.3	16.6
lathami	*lathami*	*lathami*	72.5	72.5	12.2
japonicus	*japonicus*		71.5	71.5	
	muccullochi				
	indicus	*indicus*	72.8	74.6	15.5
	trecae[d]	*trecae*	74.3	74.2	13.2
Picturatus Races	Similar Forms	*Picturatus* Group			
picturatus	*picturatus*	*picturatus*	98.3	99.4	13.5
symmetricus	*symmetricus*	*s. symmetricus*	99.0	100.1	17.3
murphyi	*murphyi*	*s. murphyi*	100.3	97.8	17.8
		Aberrant Form			
	declivis[d]	*declivis*	81.6	81.8	23.1

[a]Number of scutes as given in Shaboneyev (1980).
[b]Number of scutes as given by other authors.
[c] Depth of the largest scute in the posterior part of the lateral line as a percentage of head length as given in Shaboneyev (1980).
[d]Berry and Cohen (1974) made no comment on the relationships of these forms.

Shaboneyev (1980) accepted 11 species of *Trachurus*. He followed Nekrasov (1978) and Kompowski (1975) treating *capensis* as a subspecies of *T. trachurus* and he also followed Kotlyar (1976) and Shaboneyev and Kotlyar (1979) in considering *murphyi* to be a subspecies of *T. symmetricus*. Shaboneyev placed the 11 species into three groups of similar species and one aberrant form (Table 4).

The grouping of similar forms by Nichols (1940), Berry and Cohen (1974) and Shaboneyev (1980) are nearly identical and result in a separation of *Trachurus* into a temperate form (the *trachurus* type), a tropical form (the *mediterraneus* type) and an oceanic form (the *picturatus* type). The geographical distributions of Shaboneyev's *trachurus* group (Fig. 4A) and *mediterraneus* group (Fig. 4B) demonstrate the separation into a more temperate group *(trachurus)* and a more tropical group *(mediterraneus)*.

The number of scutes is considerably greater in the oceanic form than the other forms (Table 4) and all three reviews are in agreement in the species included in this group; however, there are minor differences in the inclusion of *japonicus* and *novaezelandia* within the other two groups. These are the two forms which Nichols (1940) was unsure of, stating that *muccullochi* (now *novaezelandia*) should perhaps be included in the *trachurus* group and that *japonicus* should perhaps be included in the *mediterraneus* group. Berry and Cohen (1974) stated that *muccullochi* may be a southern hemisphere cognate of *japonicus* and that *japonicus* was the most morphologically similar to *lathami* and they placed both *muccullochi* and *japonicus* in the *mediterraneus* group. Shaboneyev (1980) separates the various forms in his *trachurus* and *mediterraneus* groups primarily on the relative size of their scutes. In his *trachurus* group the depth of the largest scute in the posterior part of the lateral line averages from 12.2 to 16.6% of the head length; whereas in his *mediterraneus* group it averages from 22.5 to 26.4% (Table 4). He therefore placed both *novaezelandia* (= *muccullochi*) and *japonicus* in his *trachurus* group.

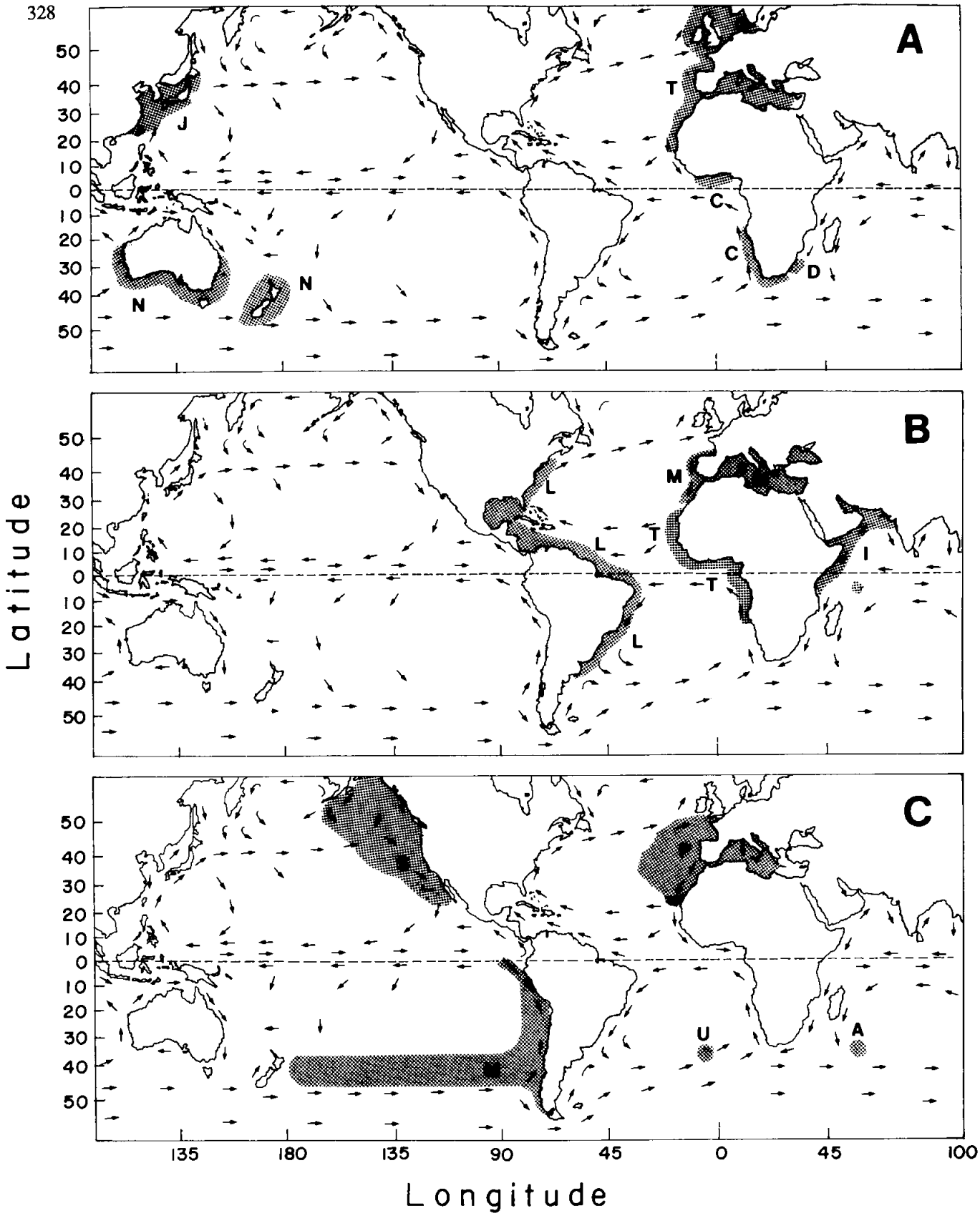

Fig. 4. Geographical distribution of trachurids: A. Shaboneyev's (1980) "*trachurus*" group: *trachurus* (T), *capensis* (C). *novaezelandia* (N), *japonicus* (J) and *delagoa* (D). B. Shaboneyev's (1980) "mediterranean" group: *mediterraneus* (M), *lathami* (L), *trecae* (T), and *indicus* (I). C. Oceanic horse mackerel: *picturatus* (P), *symmetricus* (S), *murphyi* (M), *aleevi* (A) and unnamed (U).

Fig. 4. Distribución mundial de trachuridos: A. Grupo "trachurus" *de Shaboneyev (1980):* trachurus *(T),* capensis *(C),* novaezelandia *(N),* japonicus *(J) y* delagoa *(D). B. Grupo "mediterraneo" de Shaboneyev (1980):* mediterraneus *(M),* lathami *(L),* trecae *(T), y indicus (I). C. Jureles oceánicos:* picturatus *(P),* symmetricus *(S),* murphyi *(M),* aleevi *(A) y sin nombre (U).*

Stephenson and Robertson (1977) showed that *T. muccullochi* was a junior synonym of *T. novaezelandia* and they found no grounds for distinction between *T. novaezelandia* and *T. japonicus*. They did not formally synonymize these forms apparently due to the fact that there is no gene flow across the present day Indo-Pacific gap in their distributions and they felt this necessitated retaining both species. Stephenson and Robertson (1977) also point out the close similarities between *japonicus, novaezelandia* and *lathami*.

There is a general consensus that the members of the *picturatus* or oceanic group are very closely related. Shaboneyev (1980) even states that the members of this group are morphologically so similar that it is difficult to identify them. This consensus rapidly disappears when it comes to deciding whether each is a distinct species or whether they differ at some lower level. Early workers (Jordan and Everman 1896; Meek and Hildebrand 1925) considered them a single species *(T. picturatus)*. Nichols (1940) tried to have it both ways by listing them as separate species but concluded by suggesting that *symmetricus, murphyi* and perhaps *declivis* might stand as races of *T. picturatus*.

Roedel and Fitch (1952) found minor differences between the relative size of scutes in *symmetricus* and *murphyi* but were unable to distinguish *symmetricus* from *picturatus*. Berry and Cohen (1974) gave all three the status of species but considered *murphyi* to be an ecotype of *picturatus* and considered *murphyi* and *symmetricus* to be an antitropical species pair. In contrast, Kotlyar's (1976) extensive morphological analysis of the Peruvian horse mackerel concluded that *murphyi* was not sufficiently different from *symmetricus* to merit species rank and he considered it to be a subspecies *(T.s. murphyi)*.

According to Shaboneyev and Kotlyar (1979), Aleyev (1957) considered the eastern Pacific forms to be a subspecies of *picturatus* and he also considered the northern and southern Atlantic forms of *picturatus* to be separate subspecies. In their morphological analysis of the eastern Pacific forms of *Trachurus* (i.e., *symmetricus* and *murphyi*) and the oceanic horse mackerel *(picturatus)*, Shaboneyev and Kotlyar (1979) state: "our data, based on a considerably greater amount of material, show overlap in all the characters investigated between the oceanic horse mackerel and the eastern Pacific forms of the genus *Trachurus*". However, they found differences in the number of gill rakers which they felt almost reached the subspecies level and differences in the length of the dorsal branch of the lateral line which reached the subspecies level. Although they admitted that they did not find sufficient morphological reasons for considering the eastern Pacific forms and *picturatus* as distinct species, they concluded by suggesting that the ecological differences between them was great enough to merit species rank for the Atlantic and Pacific forms. Their reasons for this conclusion were as follows:

- They considered that *picturatus* differed from the eastern Pacific forms in that it is a neritic-oceanic form widely distributed not only on the continental shelf but also far beyond its boundaries.
- This distribution demonstrated that *picturatus* may live in different water masses, for example, in the cold Canary Current, and in the subtropical waters south of the North Atlantic Current.
- "The most striking contrast with the eastern Pacific forms is provided by the possibility of the existence of the oceanic horse mackerel in the epicontinental Mediterranean, in water masses characterized by heightened salinity."

Recent work has added further complications to the *picturatus* group. Rytov and Razumovskaya (1984) have described a new subspecies of *picturatus (T.p. aleevi)* from the southern Indian Ocean and Evseenko (1987) and Bailey (1989) have shown that *murphyi* occurs in the west wind drift region (along about 40°S) from Chile to New Zealand. According to Rytov and Razumovskaya (1984), "the present grouping of the ocean scads into separate species on the basis of geographic isolation is artificial". They agreed with early authors who recognized only one species of oceanic horse mackerel *(T. picturatus)* which occurs in the eastern North and South Atlantic, the eastern North Pacific, the South Pacific and the southern Indian Ocean.

The distribution of three of the *picturatus* group are presently described; *picturatus* (Shaboneyev and Kotlyar 1979), *symmetricus* (Blunt 1969) and *murphyi* (Serra 1983; and Bailey, in press). Unfortunately the southern Indian Ocean distribution of *aleevi* is not given by Rytov and Razumovskaya (1984), who give only the location of the holotype. The distribution of

picturatus in the South Atlantic is also poorly documented in the literature and it is further confounded by the fact that *T. picturatus bingami* has been synonymized with *T. lathami* (Berry and Cohen 1974; Saccardo 1987). The only verified record found for *picturatus* from the South Atlantic was the holotype of *Decapterus longimanus,* from Tristan de Cunha examined by Berry and Cohen (1974). The distribution of the *T. picturatus* group as described in the above works is obviously underrepresented in the South Atlantic and Southern Indian Ocean (Fig. 4C). Its occurrence along the warm side of the west wind drift regions of the South Atlantic, South Indian and South Pacific suggests that *picturatus* may occur in a continuous band along the west wind drift region from the South Atlantic to Chile.

As shown above, Shaboneyev and Kotylar's (1979) ecological distinction between the Atlantic and Pacific forms of the *picturatus* group is unwarranted as the eastern Pacific forms should also be considered neritic-oceanic fishes in that they have even more extensive offshore distributions than *picturatus*. They occur from the cold waters of the Gulf of Alaska and Southern Chile to the subtropical waters of Southern Baja California and the Galapagos Islands. They also extend offshore from Chile to New Zealand. It is true that they are not known to occur in waters as saline as the Mediterranean. However, since such waters do not occur in the Pacific Ocean, this does not prove that the eastern Pacific forms are not capable of existing in such water. Therefore, Shaboneyev and Kotylar's (1979) arguments appear to be reduced to the fact that *picturatus* and *symmetricus* differ because they are isolated.

In summary, the differences between the various geographical forms of the oceanic horse mackerel are insufficent to warrant breaking the group into more than one species. The species *Trachurus picturatus* would appear to have at least three subspecies or races: *T.p. picturatus* in the northeastern Atlantic, *T.p. symmetricus* in the northeastern Pacific and *T.p. murphyi* in the southern ocean. The southern ocean form may be subdivided into three subspecies or races: *murphyi* in the Pacific, *aleevi* in the Indian and an unnamed form in the Atlantic. The recent large increase in the world's catches of horse mackerels therefore comes almost exclusively from exploitation of *Trachurus picturatus murphyi.*

Table. 5. Splitter and lumper classification of the genus *Trachurus*.
Tabla 5. Clasificación desdobladora y englobadora del género Trachurus.

Splitter species (13) and subspecies	Lumper species (7) and subspecies
trachurus	*trachurus*
capensis	*t. trachurus*
novaezelandia	*t. capensis*
japonicus	*novaezelandia*
delagoa	*n. novaezelandia*
mediterraneus	*n. japonicus*
m. mediterraneus	*n. delagoa*
m. ponticus	*mediterraneus*
lathami	*m. mediterraneus*
trecae	*m. ponticus*
indicus	*lathami*
picturatus	*trecae*
p. picturatus	*indicus*
p. aleevi	*picturatus*
symmetricus	*p. picturatus*
murphyi	*p. symmetricus*
declivis	*p. murphyi*
	p. aleevi
	p. unnamed
	declivis

After reviewing the available literature, in my opinion, a definitive analysis of the relationships between the *Trachurus* occurring in different geographical regions cannot be made without a properly designed biochemical genetics analysis. In the absence of such an analysis, the division of the genus into species is probably more a function of the philosophy of individual authors rather than the genetic relationships among the various populations. Therefore, I have included two classification schemes: one for splitters and one for lumpers (Table 5). I also note that considerable further lumping within the *trachurus* and the *mediterraneus* groups may be in order, perhaps even to the three species suggested by Nichols (1940).

References

Aleyev, Yu. G. 1957. *Trachurus* of the seas of the USSR. Tr. Sevastopol' skoy Biol. St. 9: 1-137.

Bailey, K. 1989. Description and surface distribution of juvenile Peruvian horse mackerel *Trachurus murphyi* Nichols from the Subtropical Convergence Zone of the Central South Pacific. U.S. Fish. Bull. 87(2): 273-278.

Berry, F.H. and A. Cohen. 1974. Synopsis of the species of *Trachurus* (Pisces, Carangidae). Q. J. Fla. Acad. Sci. 35(4): 177-211.

Blunt, J.E., Jr. 1969. The horse mackerel *(Trachurus symmetricus)* resource of the eastern North Pacific. Calif. Mar. Res. Comm., CalCOFI Rep. 13: 45-52.

Evseenko, S.A. 1987. Reproduction of Peruvian horse mackerel, *Trachurus symmetricus murphyi*, in the southern Pacific. J. Ichth. 27(3): 151-160.

Jordan, D.S. and B.W. Evermann. 1896. The fishes of North and Middle America. Bull. U.S. Nat. Mus., No. 47, pt. 1. p. 1240.

Kompowski, A. 1975. The intraspecific geographical variability of horse mackerel, *Trachurus trachurus* (L) in West African shelf waters. Acta Ichthyol. Piscat. 5(1): 13-29.

Kotlyar, A.N. 1976. A morphological description of the Peruvian horse mackerel. *Trachurus symmetricus murphyi*. J. Ichthyol. 16(1): 45-55.

Meek, S.F. and S.F. Hildebrand. 1925. The marine fishes of Panama. Chicago. 500 p.

Nekrasov, V.V. 1978. Systematic position of the horse mackerel of the genus *Trachurus* from the Western part of the Indian Ocean. J. Ichthyol. 18(1): 15-19.

Nichols, J.T. 1920. A key to the species of *Trachurus*. Amer. Mus. Nat. Hist. Bull. 42(13): 477-88.

Nichols, J.T. 1940. Notes on carangid fishes. V. Young *Trachurus* in the Gulf of Mexico. Amer. Mus. Nat. Hist., Amer. Mus. Novit. No. 1067. 4 p.

Roedel, P.M. and J.E. Fitch. 1952. The status of the carangid fishes *Trachurus* and *Decapterus* on the Pacific coast of Canada and the United States. Copeia 1: 4-6.

Rytov, A.N. and T.M. Razumovskaya. 1984. A new subspecies of ocean scad, *Trachurus picturatus aleevi*, from the southwestern Indian Ocean. J. Ichthyol. 24(2): 1-6.

Saccardo, S.A. 1987. Morfologia, distribuicao, e abundancia de *Trachurus lathami* Nichols, 1920 (Teleostei: Carangidae) na regiao sudeste-sul do Brazil. Bolm. Inst. Oceanogr. S. Paulo 35(1): 65-95.

Santander, H. and R. Flores. 1983. Los desoves y distribución larval de cuatro especies pelágicas y sus relaciones con las variaciones del ambiente marino frente al Perú. *In* Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. San José, Costa Rica. FAO Fisheries Rep. 293(2): 835-867.4.

Serra, J.R. 1983. Changes in the abundance of pelagic resources along the Chilean coast. *In* Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. San José, Costa Rica. FAO Fisheries Rep. No. 291(2): 255-284.

Serra, J.R. 1987. Impact of the 1982-83 ENSO on southeastern Pacific fisheries, with an emphasis on Chilean fisheries, p. 24-29. *In* M. Glantz, R. Katz and M. Krenz (eds.) Climate crisis: the societal impacts associated with the 1982-83 worldwide climate anomalies. Pub. NCAR, Boulder, Colorado.

Shaboneyev, I.Y. 1980. Systematics, morpho-ecological characteristics and origin of carangids of the genus *Trachurus*. J. Ichthyol. 20(6): 15-24.

Shaboneyev, I.Y. and A.N. Kotlyar. 1979. A comparative morphoecological analysis of the Eastern Pacific forms of *Trachurus symmetricus* and the Atlantic oceanic horse mackerel, *Trachurus picturatus picturatus*. J. Ichthyol. 19(2): 24-29.

Stephenson, A.B. and D.A. Robertson. 1977. The New Zealand species of *Trachurus* (Pisces: Carangidae). J. R. Soc. N. Z. 7(2): 243-53.

Reproductive Ecology of South American Fur Seals in Peru

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Abstract

The relationships between environmental fluctuations and the diet, pup production, mortality and weights of South American fur seals in Peru are examined. Data were collected between 1982 and 1988, covering two El Niño events and three cold years. Fur seal diet, as assessed from scat analyses, varied as a result of changes in availability of anchoveta (*Engraulis ringens*) at sea. When anchoveta were not available, fur seals took a wider range of prey. When anchoveta were abundant, fur seals ate little else. Annual pup production on the study beach ranged from 1,381 to 2,171. Pup mortality during the breeding season (October-December) ranged between 29 and 46%. Within any given year, mortality during the breeding season was correlated to adult female density, but there was no similar relationship between years. There was a significant correlation between pup weights and sea surface temperatures. Availability of prey, particularly anchoveta, appears to affect fur seals' foraging and reproductive performance.

Resumen

Las relaciones entre fluctuaciones ambientales y la dieta, la produccion total, mortalidad y pesos de crías de lobo fino de Sudamerica (*Arctocephalus australis*) son examinadas. Los datos fueron colectados entre 1982 y 1988 y cubren dos eventos El Niño y tres años frios. La dieta de los lobos, estimada a partir del análisis de heces, fue afectada por cambios en la disponibilidad de anchoveta (*Engraulis ringens*). En años cuando la anchoveta estuvo escasa, la dieta de los lobos fue mas variada. Cuando la anchoveta fue abundante, casi no comieron otra cosa. La producción anual de crías en la playa estudiada estuvo entre 1,381 y 2,171. La mortalidad de crías fue de 29-46%. Dentro de cada año, la mortalidad durante la temporada de reproducción estuvo relacionada con la densidad de hembras adultas. Se halló una relación significativa entre la temperatura superficial del mar y el peso de la crías. La disponibilidad de presa, en especial de anchoveta, parece afectar el suceso reproductivo y de alimentación de los lobos marinos en Perú.

Introduction

Like other members of the Family Otariidae (fur seals and sea lions), fur seals breed on land and forage at sea. They have long lactation periods (3-36 months), their pups grow slowly (0.05-0.10 kg/day) and females feed intermittently while suckling their young on land (Gentry et al. 1986). This reproductive strategy makes fur seals vulnerable to fluctuations in food availability at sea. Mothers replenish their fat reserves regularly in order to raise their young and thus depend on a constant food supply to breed successfully.

The South American fur seal (*Arctocephalus australis,* Zimmerman 1783) is found in the most diverse range of habitats of any fur seal. It occurs all around southern South America, from sub-tropical Peru, around Cape Horn and the Falkland Islands (Malvinas) and up to southern Brazil, covering a latitudinal range of about 35° (Majluf and Trillmich 1981). However, little is known about the ecology of South American fur seals and what limited information is available comes mainly from studies of the population in temperate Uruguay (Vaz-Ferreira 1956, 1971, 1982; Ximenez et al. 1984; Ponce de Leon 1984). The Peruvian population is of particular

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interest because it is the only one, along with that of the Galapagos fur seal *(A. galapagoensis),* which breeds on or close to the equator (Bonner 1981).

The presence of fur seals in Peru is linked to the flow of the cold Peruvian (Humboldt) current along the west coast of South America (Majluf and Trillmich 1981). This current dramatically affects the climate and productivity of coastal Peru by reducing air and sea surface temperature (SST) and giving rise to the richest upwelling system in the world (Idyll 1973; Cushing 1982; and see contributions in Pauly and Tsukayama 1987). This system sustains a large biomass of pelagic fish dominated by a single species, the Peruvian anchoveta *(Engraulis ringens),* which supports, in turn, large populations of seabirds and marine mammals (Idyll 1973; Tovar et al. 1987; Muck and Fuentes 1987).

By breeding in Peru, however, fur seals face unpredictable fluctuations in food supply. At variable intervals of between 2 to 7 years, the upwelling system is affected by major oceanic perturbations known as El Niño events (Cane 1983; Brainard and McLain 1987; Bohle-Carbonnel, this vol.). These affect the ecosystem by increasing SST and directly affecting the depth distribution and abundance of anchoveta, among other things. The effects of El Niño events on the Peruvian seabird populations and fisheries have been well documented (Cushing 1982; Arntz et al. 1985; Tovar et al. 1987; Muck and Pauly 1987; and other contributions in Pauly and Tsukayama 1987), but less is known about how fur seals in Peru are affected by these changes (Limberger et al. 1983; Majluf 1985; Trillmich et al. 1986).

This study examines how the Peruvian population of the South American fur seal has adapted to its environment by looking at its ecology and behavior, particularly how changes in food availability affect the fur seals' diet, pup production, mortality and weight. This could be done in the frame of a relatively short 6-year study because sea conditions varied widely during this period (1982-1988, see below). Only limited information was obtained during the severe 1982/1983 El Niño events; but where relevant, data from these years were included to show how conditions of extreme food shortage affected fur seals. One must bear in mind, however, that the 1982/1983 El Niño event was exceptionally strong, and that, its effects are likely to be considerably greater than those of previous events.

The study was carried out at Punta San Juan (PSJ, 15°22'S, 75°12'W, Fig. 1), which holds up to 50% of the fur seals in Peru (Majluf and Trillmich 1981). PSJ is the area of coldest waters, most intense upwelling (Zuta et al. 1978) and highest primary productivity (Cushing 1982) off the coast of Peru.

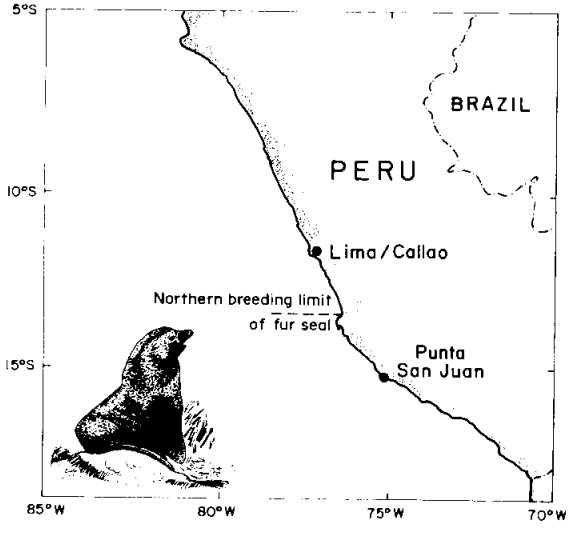

Fig. 1. Location of sampling area (Punta San Juan) and of northern limit of fur seal breeding off Western South America.

Fig. 1. Ubicación del área de estudio (Punta San Juan) y del límite norte del área reproductiva del lobo fino en la costa oeste de Sudamérica.

Methods

Data were collected between January 1983 and December 1988 as part of a long term study of the breeding ecology of fur seals. The methods used are described in detail in Majluf (1987) but a brief description is given here. Sea surface temperature (SST) data were kindly provided by Comdte. Hector Soldi (Department of Oceanography, Peruvian Navy).

Years mentioned in the text cover the breeding season when a given cohort was born and January, February and March of the subsequent year (e.g., 1985 includes data collected from October 1985 until March 1986). Survival data cover the period from birth to the following September. The 1982 data do not cover the breeding season; the 1983 data include January to August 1983 only.

From 1984 on, each year after the breeding season (late December) 200 pups were weighed and individually marked using plastic numbered tags (Allflex Medium) in both front flippers. Additionally, between 50-300 pups were weighed monthly between November and March.

Fur seal diet was studied from the analysis of hard parts (fish otoliths and squid beaks) found in fresh scats. Prey items were ranked by frequency of occurrence in the scats except for 1983 when the scats were not studied individually (they had been pooled before analysis). In 1983, the prey items were ranked by the proportion of the total number of otoliths belonging to particular prey species. Anchoveta *(Engraulis ringens)* length distributions from the fisheries were kindly provided by Ms. Isabel Tsukayama (IMARPE). Only data from 1983, 1984 and 1985 are presented here (see Tsukayama and Palomares 1987, for time series of length data covering the years 1953 to 1982 and Pauly and Palomares, this vol. for an update to 1987).

In January/February 1983, pup mortality under El Niño conditions was estimated from daily counts of dead pups on one beach at PSJ. Survival between February and March 1983 was estimated from resightings of pups tagged on another beach (n = 14), between 7-10 February, and resighted on the 7th March.

From 1984 onwards (but excluding 1986), the total number of pups born and mortality throughout the breeding season (mid-October to late December) were estimated from daily counts of freshly dead pups and of placentas observed early in the morning. The number of pups born each day was estimated as twice the placenta count (see Majluf 1987 for rationale). All animals ashore on the study beach (divided by age and sex classes) were censused daily at 6:00 throughout the breeding season. Outside the breeding season, apparent pup survival (i.e., including tag loss and dispersal, 1985-1987 only) was estimated from resightings of tagged pups (tag loss between years was assumed consant).

The statistical analyses were carried out using the SPSS-X statistical package on an IBM mainframe, and STATVIEW and STATWORKS on an Apple Macintosh Plus microcomputer.

Results

Environmental conditions during this study varied dramatically. The years covered include two El Niño events (1982 and 1986), two cold years (1984 and 1987) and a "normal" year (1985, Fig. 2). These variations appear to be related to changes in distribution and abundance of pelagic fish and of the seals' behavior and reproductive performance.

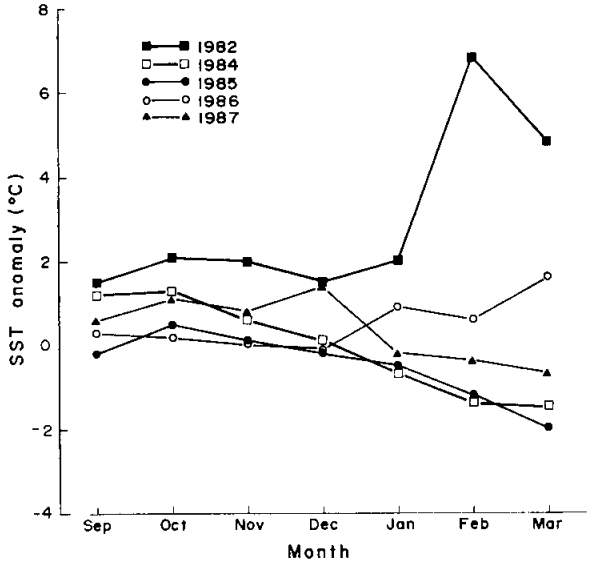

Fig. 2. Sea surface temperature anomalies near Punta San Juan, Peru in September to March 1982 and 1984-1987.

Fig. 2. Anomalias de la temperatura superficial del mar cerca a Punta San Juan, Perú, en Septiembre a Marzo 1982 y 1984-1987.

Diet

Between January 1983 and December 1985, 277 scat samples were collected, from which 1,938 otoliths and nine squid beaks were recovered. Twenty species of prey were identified but 86% of the otoliths belonged to only four species of fish: deep sea smelt *Leuroglossus urotramus* (Bathylagidae) (40%), anchoveta, *Engraulis ringens* (Engraulidae) (34%), sardines, *Sardinops sagax* (Clupeidae) (6%) and "species number 21" which is still unidentified (6%). Other prey species contributed less than 4% of the otoliths (Table 1).

The most important prey items were all less than 30 cm long, weighed less than 300 g and were either epi- or meso-pelagic species known to carry out vertical migrations at night (Fitch and Brownell 1971; Gjøsaeter and Kawaguchi 1980; Jordan 1971; Longhurst 1971). The few demersal species recorded also fell within similar length/weight ranges and are all known to leave the bottom after dark (Leible et al. 1981, Chirichigno et al. 1982).

Diet composition varied widely, but in most (8/12, Table 1) collection periods, anchoveta appeared as the most important item consumed (although *L. urotramus* made up to 40% of the otoliths collected, it was only found in three scats). The numbers and size ranges of otoliths of anchoveta varied between periods. The June and July 1983 samples only included one and four anchoveta otoliths respectively, and thus have not been included in the calculations presented below. When comparing the three years studied, the sizes of anchoveta taken by the seals were found to be significantly different in two of three cases (t-test: 1983 *vs* 1984: $t = -10.7$, $df = 66$, $P < 0.001$; 1984 *vs* 1985: $t = 18.5$, $df = 103$, $P < 0.001$; 1983 *vs* 1985: not significant). No differences in sizes were found within years. When the size distributions of anchoveta for each of these periods were compared with fishery catch data, the 1983 and 1985 samples closely matched the fishery catch composition for the same time periods while the 1984 sample was shifted to the left (Fig. 3). In 1983 and 1985, fur seals took mostly adult anchovetas (about 15 cm long), while in 1984, they took smaller fish.

Table 1. Prey species[a] ranked by frequency of occurrence. For each collection period, the occurrence of each species is indicated; the number 1 shows the most important species consumed during that period.[b]

Tabla 1. Tipos de presas consumidos por los lobos, ordenados según la frecuencia de ocurrencia. Para cada período de colección, la ocurrencia de cada especie es indicada; el número 1 muestra la especie mas importante que fue consumida durante éste período.

Prey species	1983						1984		1985				
	Jan./Feb.	Mar.	Apr.	June	Jul.	Aug.	Oct.	Dec.	Jan.	Sep.	Oct.	Dec.	Total
Engraulis ringens	1	1	1	x	x		1	1	x	1	1	1	11
Sardinops sagax	x	x	x	x	x	x	x	x	1	x	x		11
Leuroglossus urotramus							x	x	x	x	x		5
15-Bathylagidae							1	x		x	x	x	5
06-Myctophidae					x	x		x	x	x	x	x	7
21							x	x	x				3
Trachurus symmetricus				1	x	1	x					x	5
Squid										x	x		2
Merluccius gayi				x	x	x	x	x			x		6
16								x	x				2
Aphos porosus					x				x				2
Odonthestes regia	x		x				x	x					4
14							x				x		2
Cynoscion analis				x	x								2
Anchoa spp.					1				x				2
10-Serranidae		x			x	x							3
13							x						1
Mugil cephalus								x					1
24								x					1
09					x								1
Number of species/period	3	3	3	5	10	5	10	11	8	6	8	4	
Total number of otoliths	47	32	24	32	112	35	39	757	364	91	303	111	1947

[a]Species given as numbers have not been identified.

[b]Rank based on frequency of occurrence, except for 1983 when it is based on number of otoliths because the samples collected that year were not analyzed individually.

Diet diversity varied with the most important item taken. In the periods when adult anchoveta were the most important prey (January-March 1983 and September-October 1985, Table 1), the number of species in the diet was less ($\bar{x} = 4.5$, 0.8 species of prey/period, $n = 6$) than when smaller anchovetas or other species of prey were the most important prey items ($\bar{x} = 8.2$, 1.1 species of prey/period, $n = 6$). This difference was significant (Mann-Whitney $U = 4.5$, $P < 0.01$).

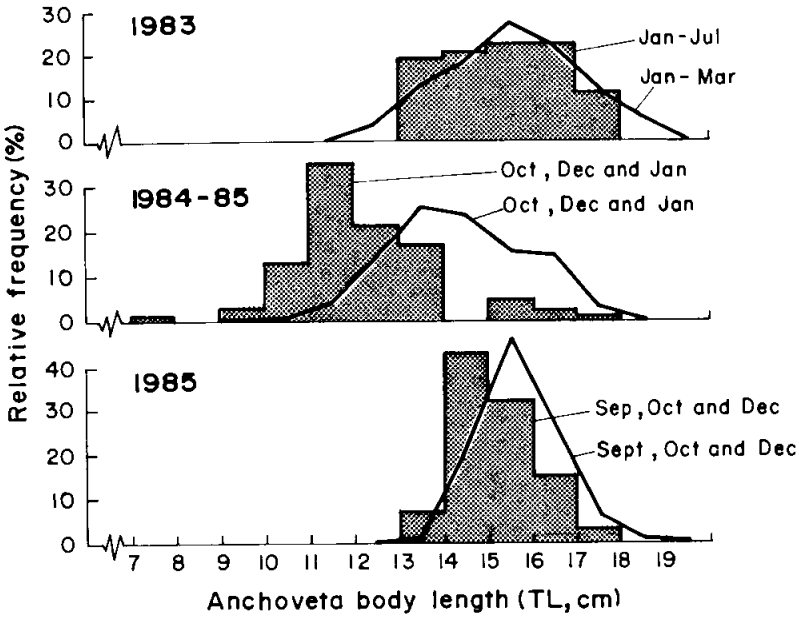

Fig. 3. Length-frequency distribution of anchoveta eaten by fur seal (shaded histograms) as reconstructed from otoliths recovered from scats compared with the fishery catch size distribution in a comparable period (solid line, unpublished IMARPE data). Note rough correspondence in 1983 and late 1985 and shift toward smaller sizes in 1984 and 1985.

Fig. 3. Distribución de frecuencias de longitud de las anchovetas comidas por los lobos finos (histogramas sombreados), obtenidos de los otolitos recuperados de las heces, comparadas con la distribución de frecuencia de longitud de la anchoveta capturada por la pesquería (líneas solidas, IMARPE datos inéditos). Notar correspondencia aproximada en 1983 y 1985 y el cambio hacia tamaños más pequeños en 1984 y 1985.

The periods when adult anchovetas were missing from the fur seals' scats were related to periods when they were not available to the fisheries. Adult anchovetas did not occur in the scats during the winter in 1983 (June-August), nor during the spring and summer of 1984/1985 (October-January), when the seals took only very small anchoveta. Environmental conditions in these two periods were very different but in both cases, it is possible to relate them to a low availability of adult anchoveta. During the El Niño event of 1982/83, in June 1983, the few anchoveta that had been present in January-February were either dead or had migrated south (Arntz 1986; Vilchez et al. 1988). Also during the winter, even in "normal" years, anchoveta become less available as they disperse when the warm water front moves away from the coast (Zuta and Urquizo 1978; Muck et al. this vol.) and the thermocline deepens (Mayers 1979; Cane 1983; Chavez 1987; Brainard and McLain 1987). With the information available, it is not possible to separate the El Niño effects from the normal winter dispersion. In 1984, no anchoveta were taken by the fisheries around PSJ (Pedro Llarena, pers. comm.) but the seals took small anchoveta, probably the first recruits following the 1982/83 El Niño event.

The periods when adult anchoveta did occur in the diet (January-April 1983 and September-December 1985) can be related to a relatively high availability of anchoveta in the area. In March, early on during the 1983 El Niño, a survey of the entire Peruvian coast carried out by IMARPE showed anchoveta schools only near PSJ, close to shore (IMARPE, unpubl. data). In 1985, surveys conducted by IMARPE reported the highest anchoveta biomass since the 1972/73 collapse (Vilchez et al. 1988). Preliminary analysis of the scats collected in 1987 suggest a similar abundance of anchoveta around PSJ (P. Vasquez, pers. comm.).

Pup Production and Mortality

The number of pups born per year on the study beach at PSJ ranged between 1,381 and 2,171 (Table 2). The differences between years could be related either to changes in the number of females coming to breed ashore or to variations in female fertility. There was no correlation between the peak number of females ashore during the breeding season and the number of births recorded. The highest number of females was observed in 1985 while pup production was highest in 1988.

There were no correlations between the number of pups born and mortality or peak number of females ashore during the breeding season (Table 2). The highest mortality was observed in 1987 when 46.5% of the pups (0-30 days old) died before the end of the breeding season. In general, mortality within the breeding period was high, never less than 29%. Outside of the breeding season, mortality was low, about 2% per month.

Most pups born during the breeding season, but before the 15th of October were stillborn or died within two days of birth. Mortality decreased from mid-October to mid-November, then picked up steadily again; peak mortality was reached in late November, when the highest numbers of females ashore were observed. For all four years, daily counts of females ashore were significantly correlated with the number of dead pups counted on the same day (Fig. 4). At peak female densities, mortality was highest.

Pup mortality outside the breeding season (January-March) was high only in 1982, during El Niño. Of about 70 pups on one beach, at least 29 (41%, not counting those washed out to sea) were seen dead on land between January and February. Afterwards, of 14 pups tagged in early February on another beach, only three (21%) were resighted by March. Only one of these three was resighted the following year.

Table 2. Comparison of environmental conditions/food availability, number of births, pup mortality, and number of females ashore during the breeding season on one beach at PSJ between 1982 and 1988.
Tabla 2. Comparación de condiciones ambientales/disponibilidad de alimento, número de nacimientos, mortalidad de crias, número de hembras en tierra y pesos de crias en una playa de PSJ entre 1982 y 1988.

Year	SST[a]/ Food availability	Births	Death/% Mortality	Females ashore[b]
1984	Cold/rich	1,381	538 / 38.9	433 ± 8
1985	Normal/medium	1,704	693 / 40.7	547 ± 6
1987	Cold/rich	1,700	790 / 46.5	514 ± 10
1988[c]	Cold/rich	2,171	645 / 29.7	533 ± 11

[a]If SST anomalies between January - March are positive, SST = Hot (> 2°C) or warm. If they are negative and greater than 1°C, SST = cold (Fig. 2). Cold = rich (high food), warm = poor (low food availability).
[b]Number of females ashore = mean (± s.e.) of daily counts of females ashore at 06:00 between 21-30 November at peak female densities.
[c]September to December 1988 only, weight data not analyzed yet.

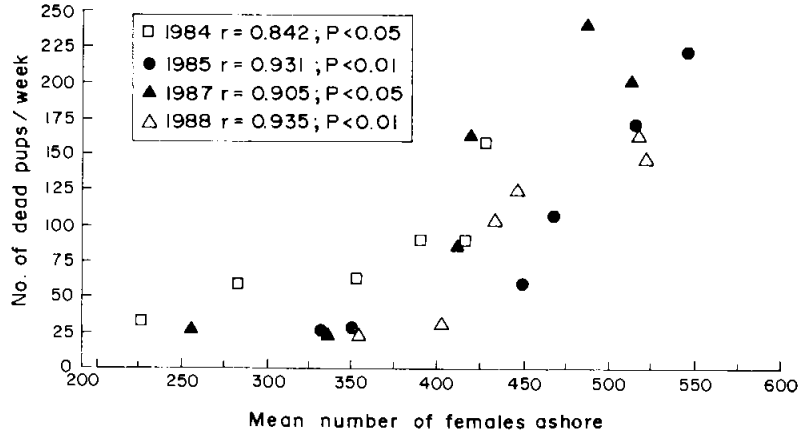

Fig. 4. Correlation between number of dead pups counted on one beach at Punta San Juan (total for a 7-day interval) during the breeding season (Oct.-Dec.) and the mean number of females ashore during the same interval (1984-1988).
Fig. 4. Correlación entre número de crias muertas contadas en una playa de Punta San Juan (total para un intervalo de 7 dias) durante la temporada de reproducción (Oct.-Dic.) y el número promedio de hembras en tierra para el mismo intervalo (1984-1988).

In subsequent years, even under varying environmental conditions (see above), pup survival rates outside the breeding season were much higher and did not vary much between years. Fig. 5 shows the survival rates of pups tagged in 1985, 1986 and 1987. Between 40-50% of the pups born survived to one year of age. The lower survival in 1987 was due to the high mortality during the breeding season.

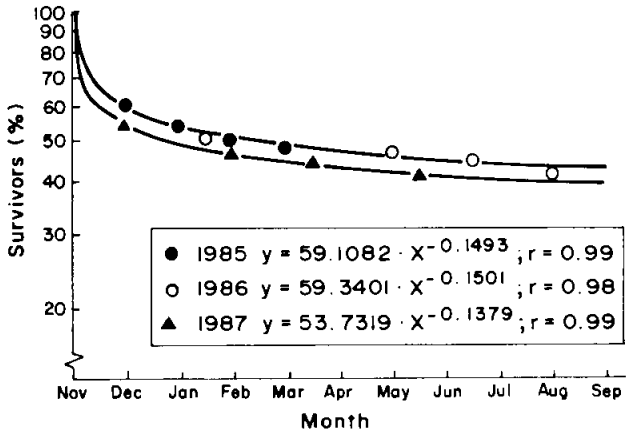

Fig. 5. Estimated survival of fur seal pups from November to September of the next year. (Note that upper curve represents both 1985 and 1986 cohorts; tag losses may suggest a lower survival than actually occur).
Fig. 5. Sobrevivencia estimada de crías de lobo fino entre Noviembre y Septiembre del año siguiente. (Notar que la curva superior representa la sobrevivencia de las cohortes de 1985 y 1986; la pérdida de marcas podria sugerir una menor sobrevivencia que la que occure realmente).

Pup Weight

Pups were born with a weight between five and seven kg and males were always heavier than females. Birth weights, however, varied between years (Table 3). The higher weights occurred in the cold years, in 1985 and 1987; the lowest in 1982 and 1986, during El Niño years. There was a significant negative correlation between SST and the weights of 90-day-old pups in February (the only month when weight was collected in all years, Fig. 6). In 1982, the very low weights resulted in higher mortality.

Table 3. Weight of 0-120 days old pups (1982-1987).
Tabla 3. Peso de crias de 0-120 dias de edad en PSJ (1982-1987).

Age (days)	Year	Females Mean	Females s.d.	Females n	Males Mean	Males s.d.	Males n
0	1984	5.19	0.99	58	5.86	0.77	48
	1985	5.70	0.87	49	6.20	1.05	51
	1986	5.18	0.82	26	5.84	0.98	24
	1987	5.54	0.89	57	6.34	0.96	62
30	1984	6.27	0.87	115	7.02	1.99	129
	1985	6.71	1.03	111	7.44	1.36	139
	1986	5.63	0.88	96	6.39	1.11	104
	1987	6.65	1.08	122	7.66	1.24	181
60	1985	7.84	1.34	141	8.69	1.48	186
	1987	8.27	1.33	95	10.05	1.60	122
90	1982	6.50	0.87	3	6.73	1.37	9
	1984	9.84	1.42	50	10.88	1.52	75
	1985	10.02	1.40	52	11.06	1.57	67
	1986	9.18	1.23	67	10.75	1.28	88
	1987	9.51	1.47	96	10.94	1.65	132
120	1985	12.09	1.61	59	13.64	1.39	68
	1986	9.87	1.70	43	11.83	1.65	49
	1987	11.03	1.56	74	12.99	1.37	96

Discussion

As was clearly observed, in spite of the short duration of this study, environmental conditions in the Peruvian upwelling system are highly variable. Changes in SST affect the availability of food resources to the fur seals and are reflected in changes of their diet, mortality and growth.

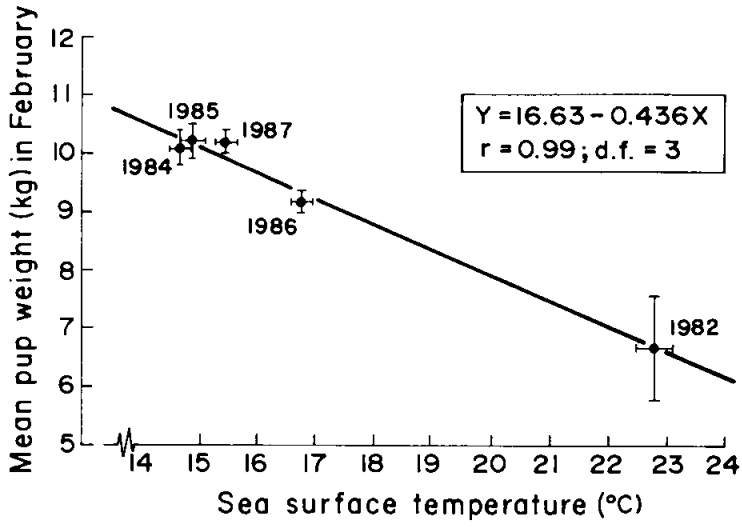

Fig. 6. Relationship between mean February fur seal pup weight and sea surface temperature near Punta San Juan, Peru.

Fig. 6. Relación entre el peso promedio de crias de lobos finos en Febrero y la temperatura superficial del mar cerca a Punta San Juan, Perú.

Diet

Studies of the northern fur seal (*Callorhinus ursinus*, Kajimura 1984) and of the California sea lion (*Zalophus californianus*, Antonelis et al. 1984; Bailey and Ainley 1982) for which concurrent data on food availability exist, have shown that the relative proportion of a specific prey item in the diet reflect availability and abundance of that item at sea. This apparently is also the case for the fur seals at PSJ. Although information on changes in availability of anchoveta for the area around PSJ is limited, the data here suggest that there is a relationship between the fur seals' diet, as described from faecal material, and prey abundance and availability. Also, it is apparent that South American fur seals at PSJ prey almost exclusively on small epi- or meso-pelagic fish, apparently with preference for adult anchoveta.

In eight of twelve sampling periods, anchoveta was the most important (i.e., most frequently occurring) prey. Diet diversity was apparently related to whether or not adult anchoveta were available at sea. In the periods when adult anchoveta were not the most frequently occurring item in the scats, a wider range of prey was taken and these coincide with the periods of reported anchoveta scarcity. In contrast, when adult anchoveta were abundantly available to the fisheries, fur seals took few other prey (84% of all otoliths recovered from the scats in 1985 were from adult anchoveta). Optimal foraging theory predicts, among other things, that predators should be more selective when food is abundant than when it is scarce (MacArthur and Pianka 1966; Krebs 1978). An increase in the diversity of species taken when the preferred prey item (hake) was not available has been shown to occur in the California sea lion (Bailey and Ainley 1982).

Thus, despite the dramatic decrease in biomass of anchoveta off the Peruvian coast since 1972 (Cushing 1982; Pauly et al. 1987), fur seals apparently still show a preference for anchoveta. Changes in the availability or abundance of this resource thus affect fur seals. When anchovetas are scarce, they have to take a wider range of prey.

Also, during El Niño events, even if adult anchoveta are available in sufficient density, fur seals will obtain less energy from the same number of fish because the condition of anchoveta is poor, resulting in a lower calorific content (Palomares et al. 1987).

Birth and Mortality Rates

The total number of births recorded varied between the four years studied. These differences could be due to changes in female fertility or in the number of females using the study beach to give birth each year. There was no correlation between births and number of females ashore,

therefore, changes in female fertility could have taken place between the years studied. With the information available, it is not possible to show this, but changes in female fertility as a result of variations in the environment or in the condition of the females have been shown in the Galapagos fur seal (Trillmich and Limberger 1985).

Pup mortality within the breeding season was high and varying in all years in a similar pattern. All pups born before mid-October were either stillborn or died within two days. Mortality peaked around late November, when female densities were highest.

High female densities and female thermoregulatory movements appear to be the main causes of the high pup mortality observed near the end of the breeding season. When the highest pup mortality was observed in late November, most females ashore had just given birth and were in their perinatal attendance period (approximately 8-10 days after giving birth, during which they remain fasting on land, suckling their pups) during which they are very aggressive towards any approaching seal. This aggression is exacerbated by the need to reach the water's edge for thermoregulation. This is so because their adaptations to avoid hypothermia while at sea adversely affect thermoregulation while they are on land. At high air temperatures, avoiding the sun and getting wet are among the most effective behavioural mechanisms to maintain thermal balance in otariids (Whittow et al. 1971; Limberger et al. 1986). At PSJ, there are only a few small caves and large boulders providing shade at the back of each beach. Therefore, the main means of thermoregulation for most animals is to wet their fur.

Females who give birth in areas with no access to water are forced to make daily excursions to and from the water's edge. These movements increase the probability of mortality of newborn pups, especially around the peak of pupping, when densities are highest. Females carrying pups in their mouths and trying to reach the water are attacked by other females while in transit. Often, the pup is dropped among other pups and confusion arises. It is very common to observe females fighting over pups, or "foreign" pups being thrown about by females who do not want them near. Later in the season, aggression appears to decrease as most of the females go to sea to forage and only a smaller portion of the female population remains on land (Majluf 1987).

High densities and crowding during the breeding season has been shown to be an important cause of mortality in other species of pinnipeds. Studies of Antarctic fur seals (*A. gazella,* Doidge et al. 1983), elephant seals (*Mirounga angustirostris,* Le Boeuf and Briggs 1977) and grey seals (*Halichoerus grypus,* Anderson et al. 1979) suggest that the proximate cause of mortality at high density sites or crowded situations is the higher probability of losing the pup and the "trauma-starvation" syndrome (injury, starvation and infections as a result of separation from the mother, Le Boeuf and Briggs 1977). The results from this study also suggest that mortality may be related to female movements at high densities causing the separation of mother and pup.

Mortality within the first month of life in all other species of fur seals does not exceed 20% (Majluf 1987). Thus, the 29-46% mortality reported here is exceptionally high. Within PSJ, almost 60% of the fur seals breed on the study beach. The amount of space available for females and their pups on this beach is limited by the need to have access to water for thermoregulation. Thus, in the hot hours of the day, females are concentrated in about one third of the beach area (approximately 0.5-1 female per m^2). Though densities in other fur seal rookeries may be similar or even higher (*Callorhinus* at St. George, M. Goebel, pers. comm.; *A. gazella* on Bird Is., J.P. Croxall, pers. comm.), the females there do not have to undertake daily thermoregulatory movements. Hence, the number of interactions with other aggressive females and therefore, mortality, are lower (Costa and Trillmich 1988).

If female density is related to pup mortality during the breeding season, there should be a correlation of peak number of females ashore with percentage mortality between years. Such correlation was not found. The highest mortality occurred in 1987 and the highest number of females ashore occurred in 1985. Thus, other factors may determine the differences in percentage mortality between years. The high mortality in 1987 could be related to the El Niño conditions in the previous year. Pup weights were lower; possibly these weaker pups were less able to survive the breeding season than in other years. Unfortunately, there is no data for the 1983 breeding season, following the intense 1982/83 El Niño event.

After the breeding season, mortality was much lower except for 1982 during El Niño, when pups died of starvation throughout the year (Majluf 1985). Subsequently, even under varying

environmental conditions (survival data were collected in 1985, 1986 and 1987, i.e., during "normal", warm (poor) and cold (rich) years, respectively), survival rates outside the breeding season did not differ between years. The higher mortality during the 1982 El Niño was mainly due to starvation caused by the long absence of mothers foraging at sea (Majluf 1985; Trillmich et al. 1986). In the case of milder El Niño events such as the one in 1986, pelagic fish tend to concentrate in areas where cold upwelled waters persist, particularly around PSJ (Villanueva et al. 1969; Vilchez et al. 1988). Thus, females at PSJ might be able to forage close to shore and return to their pups often enough to avoid their starvation. More information is needed to understand the factors determining survival outside the breeding season.

Pup Weights

Variations in SST were correlated to changes in pup weights. Pup weights and growth rates are indirectly affected by changes in prey availability at sea. If the mothers are not able to hunt efficiently, they either take longer to obtain enough food to cover their own and their pups' metabolic demands, or they return ashore with less or lower quality milk (Trillmich and Limberger 1985; Gentry et al. 1986). In either case, the pups' growth is slower and this is reflected in the recorded weights. In extreme cases, such as during the 1982/83 El Niño event, a decrease in food availability resulted in increased mortality. During events of lesser intensity, pup growth is impaired but survival in the first year of life seems not to be affected.

Conclusions

The results of this study indicate a relationship between fluctuations in prey availability at sea and the fur seals' behavior and reproductive performance. PSJ is an exceptional area because cold waters tend to persist in this area even under El Niño conditions. Thus, while even mild El Niño events may have a negative effect on the seals further north along the Peruvian coast (Muck and Fuentes 1987), at PSJ, the seals may benefit from such conditions. If fish are concentrated in the area, seals might find it easier to forage under mild El Niño conditions. If the event is as intense as the one in 1982/1983, however, even at PSJ, fur seals will be negatively affected.

Like many other marine vertebrates in the Peruvian upwelling system, fur seals have adapted to feeding mainly on anchoveta, a species once abundant in this system. A lower availability of this resource causes fur seals to take other less energetically profitable prey, and/or to spend more energy foraging and this decreases pup growth. Although the differences in growth did not appear to be reflected in survival in the first year (except in 1982), survival and/or reproductive success later in life might be affected. Smaller animals are less able to forage efficiently than larger ones (Kooyman et al. 1983; Gentry et al. 1986; Majluf 1987). Thus, a decrease in food availability is likely to have a greater effect on smaller individuals learning to forage independently after weaning (about 6 months to 3 years). Also, smaller animals may have lower reproductive success when adults. Smaller males are less able to compete for territories and therefore, have limited access to females (Majluf 1987). Small females have less fat resources than larger females and may be less able to sustain a pup in poor years. Thus, variations in anchoveta availability may affect the fur seals foraging and breeding performance. To test these various hypotheses, more information is needed on the changes (yearly, seasonal and daily) in anchoveta distribution and abundance around PSJ before definitive conclusions can be drawn.

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References

Anderson, S.S., J.R. Baker, J.H. Prine and A. Baird. 1979. Mortality in grey seal pups: incidence and causes. J. Zool. 189: 407-417.

Antonelis, G.A. Jr., C.H. Fiscus and R.L. DeLong. 1984. Spring and summer prey of California sea lions *Zalophus californianus* at San Miguel Island, California, 1978-79. Fish. Bull. 82(1): 67-76.

Arntz, W.E. 1986. The two faces of El Niño 1982-1983. Meeresforsch. 31: 1-46.

Arntz, W., A. Landa and J. Tarazona, Editors. 1985. "El Niño": su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 222 p.

Bailey, K.M. and D.G. Ainley. 1982. The dynamics of California sea lion predation on Pacific hake. Fish. Res. 1: 163-176.

Bonner, W.N. 1981. Southern fur seals - *Arctocephalus* sp., p. 161-208. *In* S.H. Ridgeway and R.J. Harrison (eds.) Handbook of marine mammals. Vol. 1. The walrus, sea lions, fur seals and sea otter.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984, p. 14-45. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Cane, M.A. 1983. Oceanographic events during El Niño. Science 222(4629): 1089-1195.

Chavez, F. 1987. The annual cycle of SST along the coast of Peru. Tropical Ocean-Atmosphere Newsletter 37: 4-6.

Chirichigno, N.W., W. Fischer and C.E. Nauen (eds.) 1982. INFOPESCA. Catalogo de especies marinas de interes economico actual o potencial para America Latina. Parte 2 - Pacífico centro y suroriental. Rome, FAO/PNUD, SIC/82/2. 588 p.

Costa, D.P. and F. Trillmich. 1988. Mass changes and metabolism during the perinatal fast: a comparison between Antarctic *(Arctocephalus gazella)* and Galápagos fur seals *(Arctocephalus galapagoensis)*. Physiol. Zool. 61(2): 160-169.

Cushing, D.H. 1982. Climate and Fisheries. Academic Press, London.

Doidge, D.W., J.P. Croxall and J.R. Baker. 1983. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. J. Zool. 202(3): 449-460.

Fitch, J.E. and R.L. Brownell, Jr. 1971. Food habits of the Franciscana *Pontoporia blainvillei* (Cetacea: Platanistidae) from South America. Bull. Mar. Sci. 21(2): 626-636.

Gentry, R.L., D.P. Costa, J.P. Croxall, J.H.M. David, G.L. Kooyman, P. Majluf, T.S. McCann and F. Trillmich. 1986. Synthesis and conclusions, p. 220-264. *In* R.L. Gentry and G.L. Kooyman (eds.) Fur seals: maternal strategies on land and a sea. Princeton University Press, New Jersey.

Gjøsaeter, J. and K. Kawaguchi. 1980. A review of the world resources of mesopelagic fish. FAO Fish. Tech. Pap. 193, Rome, 151 p.

Idyll, C.P. 1973. The anchovy crisis. Sci. Am. 228(6): 22-29.

Jordan, R. 1971. Distribution of anchoveta (*Engraulis ringens* J.) in relation to the environment. Inv. Pesq. (Barcelona) 35(1): 113-126.

Kajimura, H. 1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. NOAA Tech. Rep. NMFS SSRF-779. 49 p.

Kooyman, G.L., M.A. Castellini, R.W. Davis and R.A. Maue. 1983. Aerobic diving limits of immature Weddell seals. J. Comp. Physiol. 151: 171-174.

Krebs, J.R. 1978. Optimal foraging: decision rules for predators, p. 23-63. *In* J.R. Krebs and N.B. Davies (eds.) Behavioural ecology. An evolutionary approach. Blackwell Scientific Publications, Oxford.

Le Boeuf, B.J. and K.T. Briggs. 1977. The cost of living in a seal harem. Mammalia 51(2): 167-195.

Leible, M. E. Alveal and S. Maldonado. 1981. Catálogo de peces que habitan las aguas costeras de Concepción y Bahia San Vicente (informe de avance). Pont. Univ. Católica de Chile. Sede Regional Talcahuano, Depto. de Biología y Tecnología del Mar.

Limberger, D. F. Trillmich, H. Bieback and R.D. Stevenson. 1986. Temperature regulation and microhabitat choice by free-ranging Galapagos fur seal pups (*Arctocephalus galapagoensis*). Oecologia (Berlin) 69: 53-59.

Longhurst, A.R. 1971. The clupeoid resources of tropical seas. Oceanogr. Mar. Biol. Ann. Rev. 9: 349-385.

MacArthur R.H. and E.R. Pianka. 1966. On the optimal use of patchy environment. Amer. Nat. 100: 603-609.

Majluf, P. 1985. Comportamiento del lobo fino de Sudamérica (*Arctocephalus australis*) en Punta San Juan, Perú, durante "El Niño" 1982-83, p. 187-193. *In* Arntz W., A. Landa and J. Tarazona (eds.) "El Niño": su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario.

Majluf, P. 1987. Reproductive ecology of female South American fur seals at Punta San Juan, Peru. University of Cambridge, UK. Ph.D. thesis.

Majluf, P. and F. Trillmich. 1981. Distribution and abundance of sea lions *(Otaria byronia)* and fur seals *(Arctocephalus australis)* in Peru. Z.f. Säugetierkd. 46: 384-393.

Mayers, G. 1979. Annual variation in the slope of the 14° isotherm along the equator in the Pacific Ocean. J. Phys. Oceanogr. 9: 885-891.

Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Palomares, M.L., P. Muck, J. Mendo, Chumán de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1982, p. 117-141. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987. VPA estimates of monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Ponce de Leon, A. 1984. Lactancia y composición cuantitativa de la leche del lobo fino sudamericano *Arctocephalus australis* (Zimmermann 1783). Anales ILPE. Montevideo, Uruguay: 43-58.

Tovar, H., V. Guillen and M.E. Nakama. 1987. Monthly population size of three guano birds species off Peru, 1953 to 1982, p. 208-218. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Trillmich, F., G.L. Kooyman, P. Majluf and M. Sanchez-Griñan. 1986. Attendance and diving behaviour of South American fur seals during El Niño in 1983, p. 153-167. *In* R.L. Gentry and G.L. Kooyman (eds.) Fur seals: Maternal strategies on land and at sea. Princeton University Press, New Jersey.

Trillmich F. and D. Limberger. 1985. Drastic effects of El Niño on Galapagos pinnipeds. Oecologia (Berlin) 67: 19-22.

Tsukayama, I. and M.L. Palomares. 1987. Monthly catch and catch composition of Peruvian anchoveta (*Engraulis ringens*) (Northern-Central stock 4-14°S), 1953 to 1982, p. 89-108. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Vaz-Ferreira, R. 1956. Ecología terrestre de *Arctocephalus australis* (Zimmermann) ("lobo fino") en las islas Uruguayas. Montevideo, Servicio Oceanografico y de Pesca, Trabajos Sobre Islas de Lobos y Lobos Marinos 2: 3-22.

Vaz-Ferreira, R. 1971. Repertorio vocal aéreo y sus funciones sociales en *Arctocephalus australis* (Zimmermann) y *Otaria byronia* (Blainville). Bol. Zoc. Zool. Uruguay 1: 62-65.

Vaz-Ferreira, R. 1982. *Arctocephalus australis* Zimmermann, South American fur seal, p. 497-508. *In* Mammals in the seas. FAO Fish. Series 4(5).

Vílchez, R., P. Muck and A. Gonzales. 1988. Variaciones en la biomasa y en la distribución de los principales recursos pelágicos del Perú entre 1983 y 1987, p. 255-264. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento Peruano. Bol. Inst. Mar. Perú-Callao. Volumen Extraordinario.

Villanueva, R., R. Jordán and A. Burd. 1969. Informe sobre el estudio de comportamiento de cardúmenes de anchoveta. Inf. Esp. Inst. Mar Perú-Callao No. IM-45. 18 p.

Whittow, G.C., D.T. Matsuura and Y.C. Lyn. 1972. Temperature regulation in the California sea lion, *Zalophus californianus*. Physiol. Zool. 45:68-77.

Ximenez, I., A. Ponce de Leon, L.M. Batalles, M. Lima and A. Malek. 1984. Grado de asociación entre la longitud, peso total y peso de algunos órganos de *Arctocephalus australis*. Anales ILPE. Montevideo, Uruguay: 59-72.

Zuta, S. and W. Urquizo. 1972. Temperatura promedio de la superficie del mar frente a la costa peruana, período 1928-1969. Bol. Inst. Mar. Perú-Callao 2(8): 459-520.

Zuta, S., T. Rivera and A. Bustamante. 1978. Hydrological aspects of the main upwelling areas off Peru, p. 235-257. *In* R. Boje and M. Tomczak (eds.) Upwelling ecosystems. Springer-Verlag, Berlin.

The Marine Mammals of Peru: A Review

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Abstract

This paper reviews the status, distribution and ecology of marine mammals in Peruvian waters. Although very little is known about most species of marine mammals in Peru, all the common species are or have been directly exploited. Seal and large whale populations were severely depleted but are now legally protected. The effect of exploitation on the legally unprotected small cetaceans remains unknown. Marine mammals are top predators in the marine ecosystem and feed primarily on small pelagic fish or squid. Most Peruvian small cetaceans and pinnipeds feed primarily on anchoveta *(Engraulis ringens)* which was depleted by a combination of overfishing and a strong El Niño event. The lower prey availability may prevent marine mammal species from recovering to their former population levels. For adequate management of these marine mammal populations, more information is needed. Tourism (whale and seal watching) is suggested as an alternative nonconsumptive use of these animals.

Resumen

Este artículo hace una revisión del status, distribución y ecología de los mamíferos marinos en aguas peruanas. Aunque se sabe muy poco sobre la mayoría de especies de mamíferos marinos en el Perú, todas las especies comunes son o han sido explotadas comercialmente. Los lobos marinos y los grandes cetáceos fueron casi exterminados pero en la actualidad se hallan protegidos legalmente. Aun se desconoce el efectos de la caza sobre las poblaciones de pequeños cetáceos quienes no cuentan con ninguna protección legal. Los mamíferos marinos son los predadores tope del ecosistema y se alimentan primordialmente de pequeños peces pelágicos y de calamares. En el Perú, la mayoria de pequeños cetáceos y pinnípedos se alimentan principalmente de anchoveta (*Engraulis ringens*), cuya población fue casi extinguida por la sobrepesca combinada con los efectos de "El Niño". La menor disponibilidad de anchoveta en la actualidad puede limitar la recuperación de las poblaciones de mamíferos marinos a sus niveles previos. Para el manejo adecuado de estas poblaciones, es necesaria mayor información. Se sugiere al turismo (tours para observar ballenas y lobos marinos) como una alternativa no-destructiva para el uso de los mamíferos marinos.

Introduction

As a consequence of human activities throughout the world (both direct exploitation and disturbances), some marine mammal species (whales, dolphins, seals, otters and sirenians) have become extinct, and many populations are seriously depleted. Hence, there is a need to determine the status of the remaining marine mammal populations, to measure the extent of current exploitation and if necessary, implement measures to ensure the preservation of those species most endangered.

Little is known about most marine mammals in Peru. This is despite the fact that high concentrations of whales, seals and dolphins are still found in this area and that most of these species have been exploited for at least the last 50 years. Whaling occurred in Peruvian waters from the 17th century (Clarke 1962) to 1986 and from early in this century, sea lions were

hunted in high numbers for their skins and oil (Gamarra Dulanto 1943; Gonzales Zúñiga 1944; Piazza 1969). They are still hunted illegally by fishermen claiming they get caught in and damage their gear. The Peruvian fisheries for small cetaceans seem to have developed only in the last 15 years partly as a result of the collapse of the anchoveta *(Engraulis ringens)* fishery in the early 1970s and has increased dramatically in recent years due to the deterioration of the economic situation in Peru (Read et al. 1988). However, despite this continuous exploitation of marine mammals in Peru, not even a complete list of the species found in these waters is available and for most, their distribution and abundance remain unknown.

Since 1983, detailed studies of the small cetaceans and seals in the Peruvian upwelling ecosystem have been carried out (i.e., Majluf 1985, 1987, this vol.; McKinnon 1988; Read et al. 1988; Reyes et al. 1988; Van Waerebeek and Reyes 1986, 1988a, 1988b; Van Waerebeek et al. 1987, 1988) and we are starting to learn how the most common species are adapted to this highly variable system. Also, through these studies, several new records of species of marine mammals previously unknown to occur in these waters have been obtained. Here, we will review the available information on the marine mammals in Peru; riverine species (manatees, river dolphins and river otters) are not included. For the most common species, names (spanish common name in italics within brackets), the size, status, distribution, breeding and feeding ecology, and interactions with fisheries will be described. All species known (Table 1), including those which are known only from a few stranded animals, will be listed (for full details, see Van Waerebeek et al. 1988). Fig. 1 provides a map with all locations mentioned in the text. With this review, we hope to provide a better basis for future management plans and to improve the existing protection of these animals.

Table 1. Species of marine mammals recorded from Peru (species with an * are illustrated in Fig. 2).
*Tabla 1. Especies de mamíferos marino reportados del Perú (especies señaladas con * estan illustradas en la Fig. 2).*

Order **PINNIPEDIA**
- Family ***Otariidae***
  - **Arctocephalus australis* (Zimmermann 1783)
  - **A. philippii* (Peters 1866)
  - **Otaria byronia* (Blainville 1820)

Order **CETACEA**
- Sub-order **Mysticeti**
  - Family ***Balaenopteridae***
    - **Balaenoptera musculus* (Linnaeus 1758)
    - **B. physalus* (Linnaeus 1758)
    - **B. borealis* Lesson 1828
    - *B. edeni* Anderson 1878
    - **Megaptera novaeangliae* (Borowski 1781)
- Sub-order **Odontoceti**
  - Family ***Physeteridae***
    - **Physeter macrocephalus* Linnaeus 1758
    - **Kogia breviceps* (de Blainville 1838)
    - *K. simus* (Owen 1866)
  - Family ***Ziphiidae***
    - *Ziphius cavirostris* Cuvier 1823
    - *Mesoplodon grayi* von Haast 1876
    - *Mesoplodon* sp. (undescribed)
  - Family ***Phocoenidae***
    - *Phocoena spinipinnis* Burmeister 1865
  - Family ***Delphinidae***
    - *Lagenorhynchus obscurus* (Gray 1828)
    - **Tursiops truncatus* (Montagu 1821)
    - **Grampus griseus* (Cuvier 1812)
    - **Delphinus delphis* Linnaeus 1758
    - *Stenella attenuata* (Gray 1846)
    - *S. coeruleoalba* (Meyen 1833)
    - *S. longirostris* (Gray 1828)
    - *Peponocephala electra* (Gray 1846)
    - *Feresa attenuata* Gray 1874
    - *Globicephala melaena* (Traill 1809)
    - **G. macrorhynchus* Gray 1846
    - **Pseudorca crassidens* (Owen 1846)
    - **Orcinus orca* (Linnaeus 1758)

Order **CARNIVORA**
- Family ***Mustelidae***
  - **Lutra felina* (Molina 1782)

Annotated Species List

Pinnipeds

Arctocephalus australis
South American fur seal *(Lobo fino)*

Size: Adult female fur seals in Peru are about 1.4 m long and may reach 90 kg (mean weight = 60 kg, Majluf 1987). No weights for males have been recorded for Peru. In Uruguay, they are

around 1.8 m long and weigh up to 200 kg (Vaz-Ferreira 1982). Newborns weigh between 3.5 and 7.5 kg (Majluf 1987).

Status and distribution: South American fur seals occur all around the southern coasts of South America, from Rio de Janeiro in Brazil to Paracas in Peru (Majluf and Trillmich 1981). There is only limited information on the size of the fur seal population in Peru. At present, the population is recovering from near extinction at the beginning of this century (Murphy 1925). By 1943, only a few small groups of fur seals were found in isolated areas in southern Peru (Gamarra Dulanto 1943; Gonzales Zuñiga 1944). Piazza (1969) reports having found only 40 fur seals in Paracas (13°55'S) during an extensive seal survey in southern Peru in the early 1950s. Other counts performed in 1961, 1963 and 1964 showed that Paracas was still the most important fur seal colony but a few other small colonies were found south of there. Grimwood (1969) reported Paracas as the only breeding colony with about 2,000 animals but estimated a total fur seal population of 4,000-5,000 (Laws 1973). The latest census of 1984 gives a total of around 15,000 fur seals in Peru (Tovar and Fuentes 1984). This is likely to be a minimal estimate because the censuses carried out by the Peruvian government agencies did not consider seasonal and diurnal variations in numbers of seals ashore.

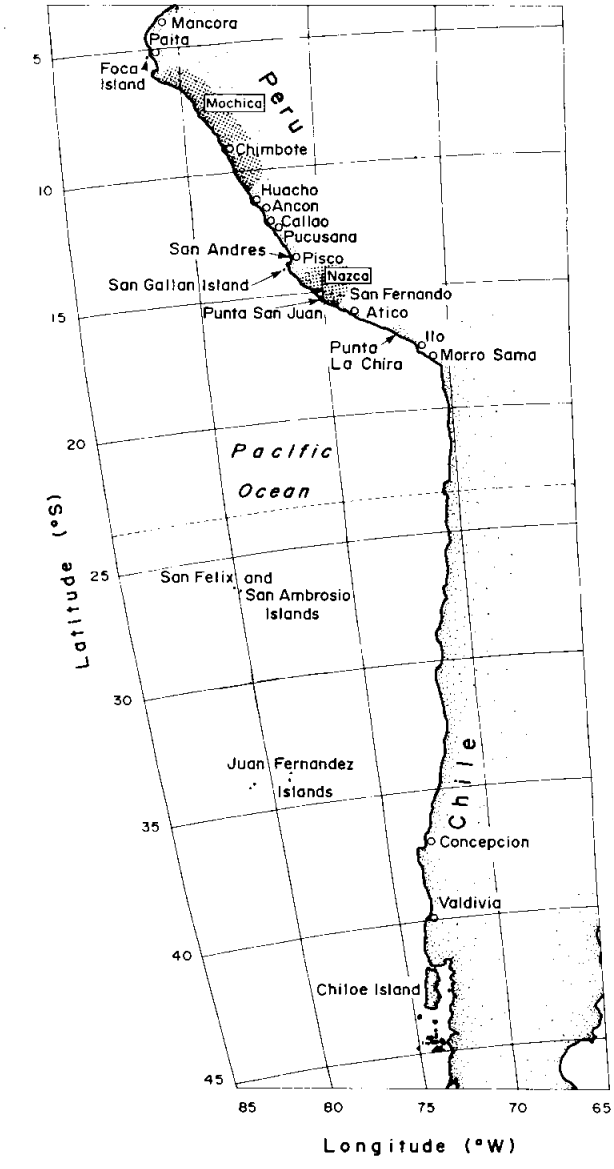

Fig. 1. Partial map of the western coast of South America, showing all locations mentioned in the text of this contribution, as well as the areas previously inhabited by the Mochicas and the Nazcas (shaded).

Fig. 1. Mapa de parte de la costa oeste de Sud América mostrando todas las localidades mencionadas en el texto de esta contribucion, asi como las áreas ocupadas previamente por las culturas Mochica y Nazca (sombreabo).

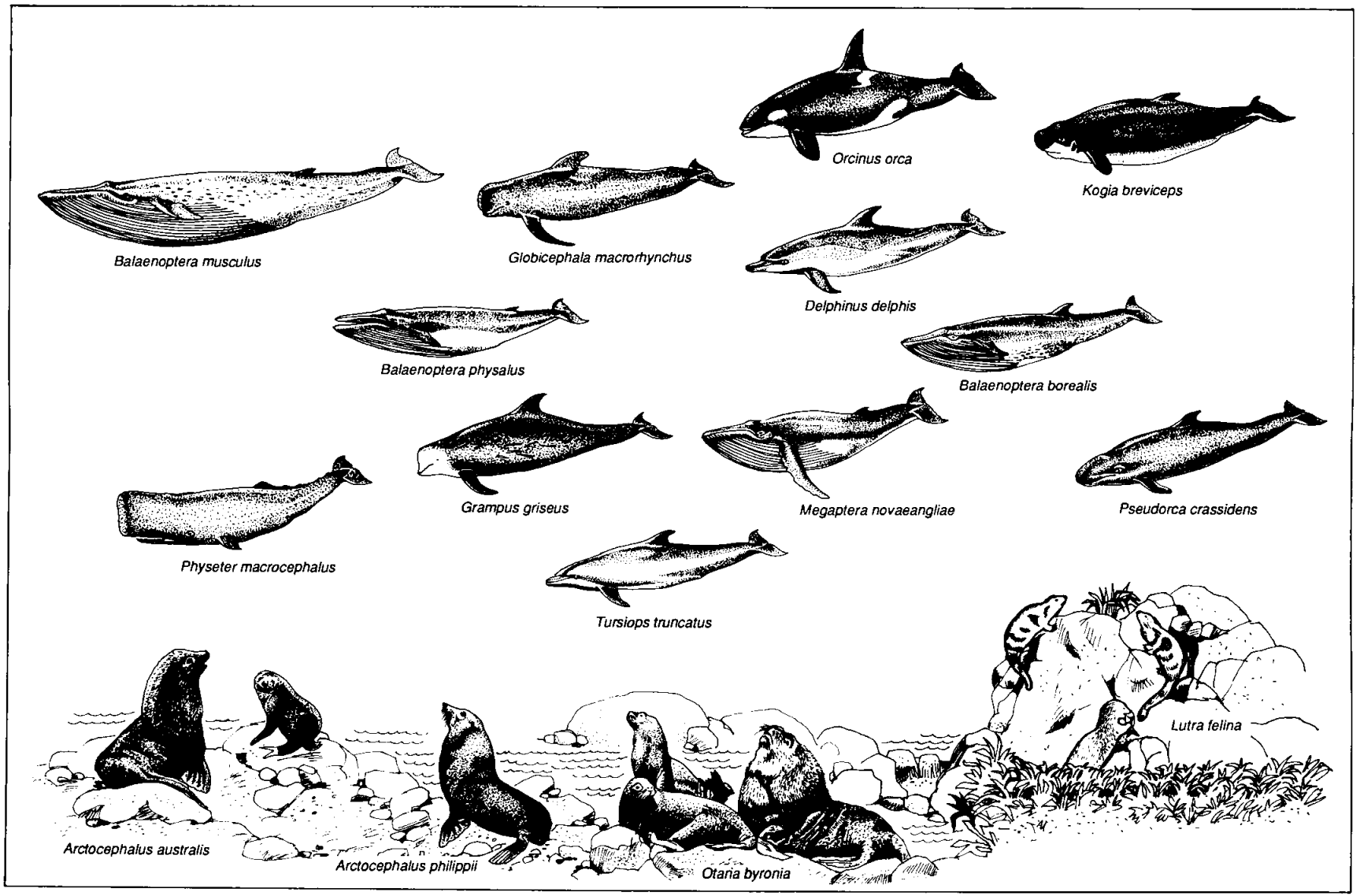

Fig. 2. Some of the species of marine mammals occurring off Peru. Adapted from drawings by Phil Schuyler (in Daugherty 1979), various photographs and drawings in King (1983) and Fig. 1 in Castilla (1982).

Fig. 2. Algunas de las especies de mamífero marino que se encuentra en aguas peruanas. Adaptado de los dibujos por Phil Schuyler (en Daugherty 1979), de varias fotografías y de dibujos en King (1983) y de la Fig. 1 en Castilla (1982).

Until 1979, over 90% of the fur seals in Peru were concentrated in three large colonies: Paracas (13°54'S), San Fernando (15°09'S) and Punta San Juan (15°22'S) (Majluf and Trillmich 1981). During the 1982-1983 El Niño, large numbers of fur seals migrated to colonies further south in Peru (Majluf 1985) or to northern Chile (Guerra and Torres 1987). The 1984 census shows that some previously smaller colonies in the south increased their numbers. South American fur seals are listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES).

Breeding: fur seals are highly seasonal, polygynous breeders. In Peru, they reproduce between October and December with 90% of all births occurring during a period of about 40 days with a peak around 18-20 November. Females give birth to a single pup almost every year, but due to high mortality, only one out of every 3-4 pups survive to one year of age (see Majluf, this vol.). Pregnancy lasts 12 months and lactation may last up to 4 years. As a result of this extended lactation, females are often observed suckling more than one young simultaneously. Females mate for the first time when they are three years old (Majluf, unpub. data). Males may not reproduce until they are 6-8 years old.

Diet: The main food item for fur seals in Peru is adult anchoveta. They take other small pelagic schooling fish, but do so only when adult anchoveta availability is low (see Muck and Fuentes 1987; Majluf, this vol.). Young fur seals eat small benthic fish while they are learning to forage.

Fur seals feed almost exclusively at night following the vertical migrations of anchoveta (see Mathisen, this vol.). Variations in their prey distribution (increased depth or dispersion) cause female fur seals to lose weight because they have a lower foraging efficiency. This is reflected in an increase in pup mortality due to starvation (Majluf 1987; Muck and Fuentes 1987).

Interactions with fisheries: Fishermen in Peru always complain that seals take commercially valuable fish. However, even though adult fur seals do eat anchoveta, the biomass they take is negligible compared to that taken by the fisheries (see Muck and Fuentes 1987, and other contributions in Pauly and Tsukayama 1987a). Adults rarely eat the demersal fish which are most valued by the small-scale fishermen; young fur seals (1-3 years old) may be the only ones eating small benthic fish (P. Majluf, pers. obs.). As a result, they are commonly caught in demersal gill nets during their foraging attempts. Poaching of fur seals for their valuable skins is common everywhere in Peru.

Arctocephalus philippii
Juan Fernandez fur seal *(Lobo fino de Juan Fernandez)*

Size: Juan Fernandez fur seals are slightly larger than South American fur seals. Standard length of adult males is 2.1 m (Torres 1987) and for females, 1.4 m (J. Francis, unpub. data). No weights are available for adult males; for females, average weight is 46 kg (J. Francis, unpub. data). Newborn pups measure about 65-70 cm and weigh 6-7 kg (Torres 1987).

Status and distribution: Juan Fernandez fur seals have never been reported on land outside the Juan Fernandez archipelago (33°80'S) and the San Felix and San Ambrosio Islands (26°80'S) off Chile (Torres 1987; Guerra and Torres 1987), where no more than 10,000 animals exist (Torres 1987). Juan Fernandez fur seals are listed in Appendix II of CITES.

From 1983, 10-15 adult or juvenile males (1-3 at any given time) have been observed hauling out in the South American fur seal rookeries at Punta San Juan every year mainly during the autumn and winter (Majluf, unpub. data). Mr. M. Rojo, a guard working at Punta San Juan between 1973 and 1984, reports having seen small mixed groups of Juan Fernandez fur seals at Punta San Juan (Marcial Rojo, pers. comm.). No females have been observed after 1983.

Because fur seals are all very similar, it is possible that more Juan Fernandez fur seals occur in Peru but remain undetected because observers do not notice the difference between them and the more common South American fur seal.

Breeding: Juan Fernandez fur seals exhibit similar breeding behavior to that of South American fur seals except for the lactation period, which rarely exceeds one year (D. Torres, pers. comm.). Juan Fernandez fur seals do not breed in Peru.

Feeding ecology: There is no information on the diet of Juan Fernandez fur seals in Peru. In Chile, they feed mainly on squid (Torres 1987).

*Otaria byronia**
South American sea lion *(Lobo chusco)*

Size: South American sea lions are the largest otariids in Peru. Males may reach up to 400 kg and females 120 kg (Hamilton 1934). Newborns weigh 10-15 kg.

Status and distribution: Sea lions have, in South America, a distribution similar to that of fur seals. Their northern breeding limit in Peru is at Isla Foca in Piura (5°13'S). They show a continuous and uniform distribution along the Peruvian coast (Majluf and Trillmich 1981).

The most recent estimate for the sea lion population in Peru is for 1984 when 33,000 individuals were counted (Tovar and Fuentes 1984). Since 1984, the population may have increased because of the exceptionally good environmental conditions in 1985 and 1987. Fishermen report dramatic increases in the rookeries south of 16°S.

Breeding: South American sea lions are polygynous, seasonal breeders. Females produce a single pup annually and may nurse it for one year and sometimes for a second year. The main breeding period for sea lions in Peru is between January and February but they have been observed pupping and mating throughout the rest of the year. In July, there is a secondary breeding period during which medium-sized males hold territories for 2-4 days and mate with very young, most probably virgin females (Majluf, unpub. data). No pupping is observed during this time.

Feeding ecology: Sea lions in Peru eat mostly small pelagic fish but are more opportunistic feeders than fur seals. They have been recorded taking anchoveta, horse mackerel *(Trachurus murphyi)* and sardines *(Sardinops sagax)*. A detailed study of their diet is presently being carried out by Ing. Pedro Vasquez (Forestry Dept., Universidad Nacional Agraria, Lima) and should be completed in late 1989.

Interactions with fisheries: Sea lions are commonly observed taking fish from small-scale fishing gear and for this reason, they are regularly killed by fishermen when encountered at sea. There is no estimate of the damage by sea lion to the fisheries nor of the impact that the killing of sea lions by fishermen might have on the sea lion populations.

Cetaceans

Mysticeti: the baleen whales

Balaenoptera musculus
Blue whale *(Ballena azul)*

Size: The blue whales are the largest of all living mammals. They may reach up to 30 m in length and over 160 t (Leatherwood and Reeves 1983). Females are slightly larger than males. Newborns measure about 7 m long. Blue whales caught off Peru range between 12 and 24 m for males and 12 and 26 m for females (Ramírez 1983).

Status and distribution: Blue whales occur in all oceans, along ice fronts and the edge of continental shelves. They are also found in deep oceanic waters and shallow coastal regions. In the southern hemisphere, they spend the summer south of 40°S and migrate northwards in the winter (Leatherwood and Reeves 1983; Mizroch et al. 1984). In Peru, blue whales can be sighted throughout the year but most often in the summer (Ramírez 1983). They are observed regularly north of Chimbote (09°04'S) up to 200 miles offshore, where most whaling operations were carried out. There is no information on the distribution and abundance of this species south of these areas.

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*Appears in many publications as *O. flavescens*. Oliva (1988) recently confirmed the taxonomic validity of *O. byronia*.

There are no recent estimates for the Peruvian blue whale population. A total of 644 and 622 blue whales were sighted in 1981 and 1982, respectively. Only 97 were sighted during the 1982-1983 El Niño (Ramírez and Urquizo 1985). The population is likely to consist of at least a few hundred individuals (Northridge 1984). Since 1965, blue whales have been protected by international agreement throughout most of the world; however, off Peru they were hunted until 1966.

Breeding: Blue whales show no well-defined social structure and most usually are observed singly, in pairs or in small groups. Mating occurs in the winter over a five-month long period. A single calf is produced every 2-3 years after a gestation period of about 12 months. Sexual maturity is reached by both sexes at about 5-15 years of age (Leatherwood and Reeves 1983; Mizroch et al. 1984).

Feeding ecology: Blue whales feed almost exclusively on euphausiids (krill), small crustaceans which tend to school close to the surface. A blue whale may consume up to 8 t of krill in one day. Most feeding occurs during summer; during winter, they fast, i.e., live off their fat reserves (Leatherwood and Reeves 1983).

Balaenoptera physalus
Fin whale *(Ballena de aleta)*

Size: The second largest whales. Adult fin whales may grow to about 27 m long in the southern hemisphere and, as all other rorquals, females are slightly larger than males. Calves are born measuring 6 to 6.5 m (Leatherwood and Reeves 1983). Until 1967, the mean length of animals caught off Peru was 13.6 m and afterwards 18.2 m. the longest was a female caught in 1971 measuring 23.4 m (Ramírez 1988a).

Status and distribution: Fin whales are also found in all oceans but are less common in tropical waters. They remain between 47 and 60°S during the summer and migrate northwards during the austral winter, going as far as Peru on the west coast of South America. Fin whale migration routes are not well known because they tend to travel in the open ocean instead of along coastlines (Leatherwood and Reeves 1983; Mizroch et al. 1984). Off northern Peru, they were sighted during whaling operations from September to April and less frequently throughout the rest of the year (Ramírez 1988a).

There are no estimates of abundance of fin whales in Peruvian waters. The stock for Peru and Chile has been estimated to be of no more than a few thousand animals (Northridge 1984). The catch of fin whales in the southern hemisphere was prohibited by the International Whaling Commission (IWC) in 1976 but catches off Peru continued through 1977.

Breeding: Fin whales are normally found singly or in small groups. They appear to have a biennial reproductive cycle. Mating takes place over a five-month period during the winter. Every 2-3 years, females produce a single large, precocial calf after a 12-month long pregnancy. Both sexes become sexually mature at 5-15 years of age (Leatherwood and Reeves 1983; Mizroch et al. 1984).

Feeding ecology: The main prey item of fin whales is krill. They feed only during the summer and fast during the winter. In the northern hemisphere, they may also feed on small pelagic schooling fishes (Leatherwood and Reeves 1983). A few fin whales have been observed eating krill off Paita but this is very rare. Most animals caught off Peru had empty stomachs (P. Ramirez, pers. comm.).

Balaenoptera edeni
Bryde's whale *(Ballena de Bryde)*

Size: Maximum body length for Bryde's whales is 14 m. Females are larger than males. Two distinct forms have been described for Peru: a coastal or "southern" form and an offshore or "northern" form (Valdivia et al. 1981; Ramirez and Urquizo 1985). Bryde's whales belonging to the coastal form are slightly smaller than those belonging to the oceanic form (mean length = 12.6 and 13.5 m, respectively; Valdivia et al. 1981).

Status and distribution: Concentrations of Bryde's whales are found in coastal areas of high productivity off Peru, Brazil, Venezuela, the Gulf of California, Japan and South Africa. Tropical populations may be sedentary but migration may occur in temperate populations (Leatherwood and Reeves 1983).

In Peru, the oceanic form is commonly found near Paita (05°05'S) in the spring and summer, close to the coast between December and March (Valdivia et al. 1981). The coastal form is found further south, near Chimbote (09°04'S), more often during the fall and winter but may also be seen during the rest of the year (Ramírez and Urquizo 1985). The latest estimates for the Peruvian stock of Bryde's whales range between 8,500 and 11,300 but these estimates have been criticized as too high (Northridge 1984). Bryde's whales were hunted off Peru until March 1985, when all Peruvian whaling activities finally stopped.

Breeding: Bryde's whales are usually observed singly or in small groups. They may also have a biennial breeding cycle. Mating and calving occur all through the year. Females produce a single calf every two years, after a gestation of about 12 months. Females attain sexual maturity at about 12.5 m and males at about 12.2 m (Leatherwood and Reeves 1983).

Feeding ecology: Bryde's whales appear to prefer small schooling fish throughout their range. In Peru, the coastal form feeds predominantly on sardines and other pelagic fish. The oceanic form feeds mainly on *Vinciguerria lucetia* and sardines. During the 1982-1983 El Niño, the coastal form also fed on horse mackerel and the oceanic form took euphasiids as well as *Vinciguerria* (Ramirez 1986). Feeding on anchoveta *(Engraulis ringens)* appears to be extremely rare, i.e., one case in three decades of sampling (P. Ramírez, pers. comm. to Pauly and Tsukayama 1987b).

Balaenoptera borealis
Sei whale (*Ballena sei)*

Size: Males reach 17 m in length and females 21 m. Newborns are 4.5-4.8 m long (Leatherwood and Reeves 1983). Mean length for sei whales off Peru is 12.8 m (Ramírez 1988c).

Status and distribution: The distribution and movements of sei whales are very poorly known. This is partly because they are very difficult to distinguish from Bryde's whales in the field.

Like other baleen whales, they migrate to and from Antarctic waters, feeding at higher latitudes in the summer. They seem to prefer temperate and oceanic waters (Leatherwood and Reeves 1983). Off Peru, sei whales were caught in the northern whaling grounds. There is no information on their status in southern Peru. Sei whales are observed only between July and December (Ramírez 1988c).

There are no reliable estimates for the sei whale population off Peru but there might be a few thousand (Northridge 1984).

Breeding: Sei whales usually occur in groups of 2-5 individuals but may concentrate in larger groups in the feeding grounds. The gestation period lasts about 12 months, the females attain sexual maturity at ten years of age (at six in heavily exploited areas) and may reproduce every 2-3 years (Leatherwood and Reeves 1983).

Feeding ecology: The diet of sei whales consists mainly of krill and small schooling fish. Feeding in this species also occurs almost exclusively in the summer in the Antarctic, but off Peru, they have occasionally been observed eating krill (P. Ramírez, pers. comm.).

Megaptera novaeangliae
Humpback whale (*Ballena jorobada)*

Size: Female humpback whales are slightly larger than males. Adult females may reach up to 16 m and males up to 15 m long (Leatherwood and Reeves 1983). Off Peru, however, a male measuring 17.5 m has been reported (Ramírez 1988b). Mean length for female humpbacks off Peru is 12.4 m and for males, 12.0 m (Ramírez 1988b). Newborns are 4-4.5 m long (Leatherwood and Reeves 1983).

Status and distribution: Humpback whales may be found in all oceans. They undergo extensive annual migrations along well-defined routes. In the southern hemisphere, most humpbacks spend the summer in Antarctic waters and migrate northward towards the equator in the winter (Leatherwood and Reeves 1983; Johnson and Wolman 1984). In Peru, they are observed in the whaling grounds between May and December but more frequently between September and November (Ramírez 1988b). There are no population estimates for humpbacks off Peru, but they probably do not exceed a few hundred (Northridge 1984).

Humpback whale stocks in the southern hemisphere have been protected since 1964; however, Peru continued hunting this species until 1966.

Breeding: Humpbacks are usually found alone or in groups of 2-3 individuals but may form larger groups (up to 15) in breeding or feeding areas. Females reproduce every two or more years but are able to do so annually. The gestation period lasts 12 months (Leatherwood and Reeves 1983; Johnson and Wolman 1984).

Feeding ecology: Humpback whales feed in summer on krill and schooling fish and fast in winter, as do most other baleen whales. There is no information on their feeding habits off Peru.

Interactions with fisheries: Off Peru, humpbacks tend to occur close to shore in the spring (Ramírez 1988b), making themselves vulnerable to entanglement in fishing gears. There is a single record of entanglement of a humpback whale at Punta San Juan in October 1988. The whale was released alive and the fishermen were partially compensated for the damage to their nets[a].

Odontoceti: the toothed whales, dolphins and porpoises

Physeter macrocephalus
Sperm whale *(Cachalote)*

Size: Sperm whales are highly sexually dimorphic with males being much larger than females. Adult males may attain 18 m in length although at present, due to intense exploitation of large males, few exceed 15 m. Females rarely reach 12 m in length. Newborns weigh one tonne and are 3.5-4.5 m long (Leatherwood and Reeves 1983; Gosho et al. 1984).

Status and distribution: This species is found in all oceans between 60°N and 70°S in very deep waters and only rarely in waters less than 180 m deep. Off Peru, the highest concentrations are found around Pisco and Paita, the grounds of past whaling days. The highest concentrations off Pisco occur in the winter and for Paita, in the spring and summer. These differences suggest a seasonal migration between these two areas (Saetersdal et al. 1963). There is no information on their distribution south of Pisco but they are regularly sighted north of Punta San Juan and in Ilo in the spring.

There are no reliable estimates for the sperm whale population off Peru but it may be in the tens of thousands (Northridge 1984).

Breeding: Sperm whales have a polygynous breeding system. Although often seen singly or in small groups, they may form large groups of up to several hundreds. The largest groups are observed during the breeding season. Groups can be mixed (breeding schools) or consist of only young males (bachelors' schools). Large adult males are usually solitary but join the breeding schools during the breeding season (Leatherwood and Reeves 1983; Gosho et al. 1984).

Mature females in the southern hemisphere ovulate between October and February and produce a calf every 3-6 years, after a 15-month long gestation. Lactation lasts 1-2 years. Females attain sexual maturity at about 9 years when they are about 9 m long and males at about 20 years and 12 m long (Leatherwood and Reeves 1983; Gosho et al. 1984).

Some aspects of the reproductive behavior of sperm whales off Peru have been described by Ramirez (1988d).

Feeding ecology: Sperm whales feed primarily on squid but may also eat octopus and fish. The main prey species for sperm whales in Peru is the jumbo flying squid *(Dosidiscus gigas)* which occurs in very high densities in Peruvian waters. According to Clarke et al. (1968), the high abundance of sperm whales in Peru may be related to the high concentrations of squid in the Peruvian upwelling system.

[a]By the senior author (Editors' note)

Phocoena spinipinnis
Burmeister's porpoise *(Marsopa espinosa)*

Size: Maximum length is about 1.8 m (Reyes et al. 1988). Males and females appear to be similar in size.

Status and distribution: Temperate and coastal waters of South America. On the Pacific coast, Burmeister's porpoise occurs from Paita, Peru, south to Valdivia, Chile. On the Atlantic coast, it ranges from Punta del Diablo (Uruguay) to Golfo San Jose (Argentina). The distribution of this porpoise in southern South America is poorly known (Brownell and Praderi 1984).

Brownell and Praderi (1982) suggest the existence of two separate stocks, the Atlantic and the Pacific stocks, with probably the Pacific stock being the larger of the two. They describe this species as the most abundant small cetacean in coastal waters around southern South America and that about 2,000 are caught by fishermen off Peru every year. There are no estimates of abundance for this species in Peru.

Breeding: Burmeister's porpoise usually occurs in groups of up to six or eight animals. There is no information available on the breeding ecology of this species (Leatherwood and Reeves 1983).

Feeding ecology: This is an inshore species which preys on a variety of pelagic and demersal fishes, especially anchoveta, drum *(Sciaena deliciosa)* and hake *(Merluccius gayi)* as well as squids such as Patagonian squid *(Loligo gahi)* (McKinnon 1988).

Interactions with fisheries: Burmeister's porpoises are captured incidentally in the gill net fishery along its range (Brownell and Praderi 1984). The demersal gill-net fishery for sharks accounts for a relatively high number of these porpoises taken in Peruvian waters (Read et al. 1988).

Lagenorhynchus obscurus
Dusky dolphin *(Delfin oscuro)*

Size: Maximum length is 2.1 m, weight = 136 kg. Males are slightly larger than females (Leatherwood and Reeves 1983).

Status and distribution: Circumpolar distribution in warm temperate and cold temperate waters of the southern hemisphere (Leatherwood and Reeves 1983). Along the Peruvian coast, it has been recorded between Huacho (Brownell 1974) and Atico (Bini 1951). No population size estimates exist for this species.

Breeding: In the S. Atlantic herds of 5 to 30 are common, but groups may reach several hundred. Group size seems to vary seasonally (Würsig and Würsig 1980). Data from New Zealand show a gestation of 9-11 months with calves born in mid-winter. Lactation lasts for 18 months. Off Argentina, young are born in the summer (Leatherwood and Reeves 1983).

Feeding ecology: Dusky dolphins are known to feed on fishes, primarily anchovies, and squids (Leatherwood and Reeves 1983). In Peruvian waters, anchoveta is the main food, while horse mackerel, hake and Patagonian squid are eaten in smaller proportions (McKinnon 1988).

Interactions with fisheries: In Peru, dusky dolphins are taken both incidentally and directly by fishermen. The bulk of these catches occurs in the small-scale fishery off Central Peru, where gill nets, harpoons and purse seines are used. About 1,500 of these dolphins were taken in two Peruvian ports in 1985 (Read et al. 1988).

Delphinus delphis
Common dolphin *(Delfin comun)*

Size: Maximum length = 2.5 m, with males slightly larger than females. Weight = not more than 75 kg. Newborns are about 80 cm long (Leatherwood and Reeves 1983).

Status and distribution: Cosmopolitan, absent only from high latitudes. In the South Pacific, there are records from the equator to 40°S off Chile, on the Pacific coast of South America. There are no population estimates for this species.

Breeding: Herds of over a thousand are not uncommon but groups numbering many hundreds are the rule. Gestation lasts 10-12 months. Calving interval is about 1.3 years. In the north Pacific, calving appears to peak in spring and fall. Sexual maturity is reached at 3 to 4 years (Leatherwood and Reeves 1983; Minasian et al. 1984). There is no information on breeding in Peru.

Feeding ecology: Common dolphins are primarily pelagic, commonly found above depths of 200 m, but inshore forms occur in some areas. There appears to be a daily cycle of activity related to the movements of the organisms associated with the deep scattering layer. Common dolphins prey on small pelagic fishes such as anchovies, lanternfish, sardine and herring, as well as squid. There is no available information on the feeding habits of these dolphins off Peru.

Interactions with fisheries: Common dolphins are taken in the small-scale fishery along the Peruvian coast either with nets or harpoons. Some catches also occur in the industrial purse seine fishery, especially off the central Peruvian coast (Read et al. 1988;Van Waerebeek and Reyes 1988).

Tursiops truncatus
Bottlenose dolphin *(Delfin pico de botella)*

Size: Maximum recorded length is 3.9 m; weight, 275 kg. Males are larger than females. Length at birth is about 0.9-1.2 m (Leatherwood and Reeves 1983; Reyes at al. 1988).

Status and distribution: This species is cosmopolitan in all temperate, subtropical and tropical waters, and is present all along the coast of Peru. An inshore form and an offshore form have been described for this species in Peruvian waters (Van Waerebeek et al., in press). The offshore form inhabits the tropical waters outside the coastal upwelling zone and is known to range as far south as 13°S (Walker 1981; Donovan 1984). The inshore form is restricted to the shallow waters along the coast and has been reported from Mancora in northern Peru (Grimwood 1969) to Concepcion, Chile (37°S) (Oliver 1946). There are no estimates for the size of the Peruvian population of bottlenose dolphins.

Breeding: Inshore bottlenose dolphins swim in groups of ten or less. Group size in the offshore form is about 25 but herds of several hundred may occur (Leatherwood and Reeves 1983). Sexual maturity is reached at 10-12 years in males and 5-12 years in females. Gestation lasts 12-18 months. The life span is believed to be about 35 years (Leatherwood and Reeves 1983; Minasian et al. 1984).

Feeding ecology: The inshore form preys on a variety of fish including mullets and sciaenids, while offshore dolphins have been reported to feed mainly on oceanic squid (Walker 1981). In Peruvian waters, bottlenose dolphins identified as belonging to the inshore form eat anchoveta, drums, mullets, hake and Patagonian squid. Several types of squid beaks, some of them from jumbo flying squids, are common in the stomachs of offshore bottlenose dolphins, along with some fish species (Van Waerebeek et al., in press).

Interactions with fisheries: Incidental and direct catches occur throughout the species' range (Leatherwood and Reeves 1983). A small number is taken each year in the small-scale fishery off Peru, although greater numbers are captured by the industrial fleet in some of the larger Peruvian ports (Read et al. 1988; Van Waerebeek et al., in press). Offshore dolphins are captured mainly during the summer months when the width of the coastal upwelling zone is reduced and the fishermen are able to reach tropical offshore waters(Van Waerebeek et al., in press).

Globicephala macrorhynchus
Short-finned pilot whale *(Ballena piloto de aleta corta)*

Size: Males reach 5.4 m and 3,000 kg; females are 4 m long with an estimated weight of 1,200 kg. Length at birth is about 1.4 m (Leatherwood and Reeves 1983; Minasian et al. 1984).

Status and distribution: Tropical and warm temperate waters of the Pacific, Atlantic and Indian oceans. This species was only recently identified in Peruvian waters (Van Waerebeek and Reyes 1986) and thus, there is only limited information on its distribution and no population estimates are available. The population of the eastern tropical Pacific has been estimated as 60,000 (Leatherwood and Reeves 1983).

Breeding: Group size ranges from a few to several hundred. Males become sexually mature when they are 4.2-4.8 m in length; females mature at 3-3.3 m. The breeding season appears to be extended, while the gestation period is about 11-13 months. Calving interval is approximately 3 years (Leatherwood and Reeves 1983; Minasian et al. 1984). Lactation lasts a minimum of 2 years, although it may continue for considerably longer periods (Kasuya and Marsh 1984).

Feeding ecology: Short-finned pilot whales are found mainly in offshore waters, but they seem to migrate to inshore waters following the squid which are their main food (Leatherwood and Reeves 1983).

Interactions with fisheries: Gill net and commercial purse seine fisheries off Peru take a few short-finned pilot whales every year (Van Waerebeek and Reyes 1986; Read et al. 1988).

Orcinus orca
Killer whale, Orca *(Orca)*

Size: Males may reach up to 9.5 m and around 8,000 kg; females rarely exceed 7 m in length and 4,000 kg in weight. Length at birth is about 2.1-2.4 m (Leatherwood and Reeves 1983).

Status and distribution: Cosmopolitan. In Peru they have been reported around Chancay (11°22'S, Bini 1951) and around northern Peru by Dahlheim et al. (1982). In southern Peru in recent years they have been sighted close to the coast mainly in winter (July-September) around Punta San Juan (P. Llerena, pers. comm. and P. Majluf, pers. obs.), Paracas and Ilo (J.C. Riveros, pers. comm.). There are no estimates of abundance for this species in Peru.

Breeding: Moderately gregarious, polygynous. They form stable groups (pods) varying in size reaching up to 30 individuals and containing adults of both sexes as well as calves and juveniles. Sometimes pods form short-term aggregations of a hundred or more individuals (Leatherwood and Reeves 1983). In Peru they have been sighted in pairs and small groups (3-4 animals). There are no data on the composition of these groups.

Little is known of the breeding biology of this species. Females may give birth every two years or more. Gestation lasts for at least a year and perhaps several months longer. Calves are born around August to March and may remain dependent on their mothers for at least a year (Leatherwood and Reeves 1983; Bigg et al. 1987). A single birth was reported off Punta San Juan in 1988, but this has not been confirmed (P. Llerena, pers. comm.).

Feeding ecology: According to Leatherwood and Reeves (1983), "There seems to be no palatable marine organism of any size that is safe from attack". They have been observed feeding on virtually all species of oceanic cetaceans (including their own kind), pinnipeds, penguins, many kinds of seabirds, sea turtles and fish. In Peru they have been observed feeding on both fur seals and sea lions off Punta San Juan. On a single day they were estimated to eat at least 50 young (0-2 year old) sea lions. Adults were also taken occasionally. Hunting occurred singly or in pairs (R. Harcourt, pers. comm. and P. Majluf, pers. obs.).

Interactions with fisheries: There is a single report of an orca having been caught by fishermen off Pucusana (Cesar Cárcamo, pers. comm.). Around Punta San Juan, fishermen observe orcas regularly but do not report interactions.

Otters

Lutra felina
Marine otter *(Chungungo, gato marino)*

Size: Maximum length, 1.0 m (Cabello 1983). Average weight, 4.0 kg (IUCN 1982). Males and females appear to be similar in size.

Status and distribution: Marine otters are found along the coasts of Peru and Chile from 9 to 56°S (Brack 1978; Cabello 1983). They are mainly found in rocky shores but there are reports of occurrences in rivers and streams not altered by fisheries for crayfish (Hvidberg-Hansen 1970).

The status of marine otter in Chile was discussed by Castilla (1981, 1982). There are, on the other hand, no reliable population estimates for the species in Peru. In some relatively

undisturbed areas such as Isla San Gallan (13°49'S), Punta La Chira (16°31'S) and Morro Sama (18°00'S), there is approximately one otter per 100 m of shoreline (J.C. Riveros, unpub. data). This estimate is similar to that of Cabello (1983) for Chiloe Island (42°10'S) in Chile. Fishermen report a decrease in the otter population in recent years.

Marine otters are listed in Appendix I of CITES and are included as vulnerable in the IUCN Red List of Threatened Animals (1986). In Peru, legal protection is limited to a short season when hunting is prohibited between 15 December and the end of January. This regulation appears unknown to fishermen along the Peruvian coast.

Breeding: Marine otters occur singly or in family groups. The young are born in burrows onshore during the austral spring (Sielfeld 1983). Gestation lasts 60-65 days and there are 1-2 young per litter (Estes 1986).

Feeding ecology: There are no detailed studies of the diet of this species in Peru. Preliminary analysis of scats by Riveros and Hays (unpubl. data) suggested that they mainly feed on reef-dwelling fish, small crabs and *Tegula* snails, while fishermen report them feeding on freshwater prawns *(Cryphiops caementarius)* (Hvidberg-Hensen 1970). A comprehensive study by Castilla and Bahamondes (1979) showed a Chilean population to feed on marine invertebrates, especially *Concholepas concholepas* and *Fissurella* spp.

Interactions with fisheries: In Peru, marine otters are killed occasionally by fishermen for their fur and meat and sold as stuffed animals (Hvidberg-Hensen 1970). There appears to be no conflict with the fisheries. Shellfish fishermen are seen commonly working next to otters (J.C. Riveros, pers. comm.). However, in Pucusana (12°30'S) and Punta San Juan, there are reports of otters becoming entangled and drowned in gill nets (J.C. Reyes, pers. obs., and P. Llerena, pers. comm.).

History of Exploitation

The Seals

The use of seals in Peru dates as far back as preceramic times (>5,000 BC). Large numbers of fur seal and sea lion remains have been found in archaeological diggings along the entire coast of Peru (Bonavia 1982). Seals were taken together with guano birds *(Phalacrocorax bougainvillii, Sula variegata and Pelecanus thagus)* and various species of pelagic fish. Wing and Reitz (1982) have calculated, using estimates of the biomass of different species consumed by humans, that the two seal species constituted the major component of the diet of coastal Peruvians in preceramic times (Wing and Reitz 1982).

In pre-Hispanic times, seals appear to have been hunted on a regular basis for their meat, oil and skins. Inflated skins may have also been used as floats (Cobo 1956). The Mochicas left numerous representations of seals and the seal hunt in their ceramics (Bonavia 1982). López de Gomara (1941) and Gutiérrez de Santa Clara (1905) both describe seals being baked and eaten and their oil being used for different purposes up to the 16th century. By the first half of the 18th century, seals were only taken for their oil (Cobo 1956).

Large-scale commercial exploitation of seals may not have started until the 18th century when sperm whalers, in search of new whaling grounds, killed millions of fur seals (*Arctocephalus* spp.) and depleted most southern hemisphere fur seal populations (Bonner 1981). Unfortunately, there are no records of the numbers of seals taken off Peru before 1925. From then on, there are yearly export figures given in "tonnes of skin[b]" for the period 1925-1946. Presumably, more than one company was involved in the seal hunt and the export figures include only those skins *legally* exported. To interpret these figures, we can use the following example: between December 1941 and March 1942, a single company collected 36,650 skins (32,400 pups, 3,700 adult females and 550 adult males) (Piazza 1969), while 10,400 "tonnes of skin" were reported (for all companies). If we assume that these skins were mainly those of sea lion[c] pups with live weights of 30-40 kg at the most and that hence, the skins may not weigh more than 2-3 kg a piece, then in 1942 alone, several thousand pups were killed to make up 10,400 "tonnes of skin" and several million more were killed to complete the 806,252 "tonnes of skin" exported between 1925 and 1946.

[b]No indication of species is given nor is it clear whether "skin" included blubber as well. Here, we assume "1 tonne of skin" = 1,000 kg of skin without blubber.

Under this intense exploitation, the seal population was so rapidly depleted that it had to be granted partial protection in 1946. That year, the Peruvian government limited the seal hunt to the period between 1 January and 15 March and prohibited the killing of young pups. In 1950, protection was extended to adult female sea lions and to all fur seals. In 1958, all seal hunting was banned (Tovar and Fuentes 1984). By June 1967, however, "experimental" exploitation of seals was again allowed even though the populations had not recovered. No records of the hunt after 1946 are available.

Between 1971 and 1975, under the auspices of the military government, Empresa Peruana de Servicios Pesqueros (EPSEP) took 12,699 sea lions and 4,188 fur seals (Table 2), a high proportion of the total population in each year (over 20% in 1974). This excessive catch must certainly have had a negative effect on the population. In 1975, only sea lions were taken. In 1976, all hunting of seals was again prohibited (Tovar and Fuentes 1984).

Since then, seals in Peru have been legally protected but due to a complete lack of coastguards, poaching at sea and in isolated rookeries has taken place on a regular basis. Fishermen shoot or harpoon seals which approach their boats, claim damage to their fishing gear and demand permission again to hunt seals legally. So far, these claims and demands have been ignored by the Peruvian government.

Table 2. Catch and total population of seals in Peru, 1971-1975.
Tabla 2. Captura y población total de lobos marinos en Perú, 1971-1975.

	O. byronia		*A. australis*	
Year	Catch[a]	Total population[b]	Catch[a]	Total population[b]
1971	0	22,810	557	7,252
1972	2,134	n.a.	246	n.a.
1973	2,280	n.a.	1,680	n.a.
1974	4,733	20,042	1,705	10,168
1975	3,552	19,809	0	10,168

[a] from Tovar and Fuentes (1984)
[b] from Majluf and Trillmich (1981)
n.a. - not available

The Large Whales

Large cetaceans apparently were not hunted in Peru until the 18th century when North American sperm whalers traveling to and from the Antarctic discovered the rich whaling grounds off central and northern Peru. Previously, only the remains of stranded whales were used opportunistically. In preceramic times, ribs and other large bones were used as building material instead of wood which is a scarce resource in coastal Peru (Bonavia 1982). Large vertebrae were also used as bases for grinding stones (D. Bonavia, pers. comm.).

Cobo (1956), a priest describing Peru in the early 17th century, also mentioned that whales were not hunted by the coastal people and that only stranded animals were used for various purposes. However, both Vasquez de Espinoza (1948) and Lopez de Gomara (1941) describe Indians in northern Peru and in the Atacama desert in Chile hunting whales using copper harpoons. In general, there is very little information on the early exploitation of large whales in Peru in the 16th-19th centuries. As mentioned above, whale hunting in Peruvian waters was started by North American whalers on their way to and from the Antarctic. These were soon followed by British and Norwegian whalers attracted by the abundance of sperm whales in these waters (Hertz and Kapel 1986). These early whalers used sail vessels and could only catch sperm whales and the slow swimming humpback whales. Townsend (1935) describes sperm whales being hunted at all seasons of the year off Peru, Ecuador and Chile between 1761 and 1920. Humpbacks only rarely were caught off Peru and Chile but were caught in great numbers in Ecuadorian waters.

[c]The fur seal population in Peru was at very low levels throughout the first half of the 20th century (see above).

Modern whaling, using steam vessels and harpoon guns, did not start in Peru until 1925-1926 (Clarke 1962). This allowed whalers to hunt the faster swimming species (blue, fin, sei and Bryde's whales) but sperm whales were still their main target.

The catch numbers and composition early in this century is poorly documented. Detailed numbers and species composition of the catch are only available from 1936 (Table 3). Whaling off Peruvian waters in the first half of the 20th century was mainly offshore and carried out intermittently. The main expeditions took place in 1936-1938, 1941-1943, 1947-1948, 1951 and 1954. Shore-based whaling in Peru did not start until 1951 (Clarke 1962). Baleen whales were caught intermittently between 1936-1937, 1947-1956, and from 1959 onwards. Between 1953

Table 3. Species composition of the whale catch off Peru between 1936 and 1985.
Tabla 3. Composición por especies de la caza de ballenas frente a Perú entre 1936 y 1985.

Year[a]	Blue[b]	Fin[c]	Humpback[d]	Sei + Bryde's[e]		Sperm
1936*	135	139	4	10		2,021
1937*	67	97	9	3		3,776
1938*						602
1941*						1,914
1942*						3,346
1943*						3,299
1947*		1	2			2,887
1948*	1	2		1		2,497
1951**	4	21	23	1		6,365
1952	7	14	20	17		37
1953	10	28	6	36		1,260
1954**	292	196	89	14		5,584
1955	8	7	2	1		1,869
1956		1	7			2,019
1957						2,381
1958						2,554
1959				1		3,406
1960						3,423
1961	2	2	37			3,438
1962			1			3,300
1963			36			3,269
1964	1	6	118	1		1,973
1965	80	148	54	2		938
1966	106	347				872
1967		116		26		503
1968		187		664		1,597
1969		74		784		1,452
1970		85		414		1,432
1971		37		415		1,321
1972		9		337		1,554
1973		11		Sei 332	Br.	1,497
1974		5		67 170	283	1,286
1975		5		128	417	793
1976		8		12	398	1,500
1977		2		5	387	799
1978				3	297	770
1979					300	742
1980					211	450
1981					162	225
1982					320	
1983					149	
1984					181	
1985					158	

a* = pelagic catch; ** = pelagic + coastal catch (based on Clarke (1980)), complemented by (b) to (e).
[b]Blue whales 1961-1966: Ramirez (1983)
[c]Fin whales 1961-1967: Ramirez (1988a)
[d]Humpback whales 1961-1965: Ramirez (1988b)
[e]1936-1973: Sei + Bryde's combined; Bryde's, sei and sperm whales 1973-1985: Ramirez (unpubl. data).

and 1966, there were attempts to introduce whale meat for human consumption (Ramírez 1988a, 1988b) and the last blue and humpback whales were caught for this purpose. Hunting of blue and humpback whales was banned by the IWC in 1966. Fin whales were also protected by the IWC in 1966 but were hunted in Peru until 1977.

The catches of sperm whales off Peru were very large and during the early years of this century, contributed up to 20-60% of the worldwide catch (Fig. 3). Due to their greater size and their spermaceti, the larger males were preferred and thus, only few females were caught before 1951. This preference was reflected soon in a decrease in availability of large males which caused whalers to catch a greater proportion of females after 1951 (Saetersdal et al. 1963).

Between 1954 and 1961, there was a noticeable decrease in catch per unit effort (Saetersdal et al. 1963) but catches did not decline until 1965. From then and until 1982, when hunting of the species was banned by the IWC, catches did not exceed 2,000 animals per year (Ramírez 1989).

Bryde's whales were the last species to be hunted in Peruvian waters. When most other countries in the world had agreed to stop whaling, Peru, Japan, the USSR, Norway and Iceland continued. The company running the whaling operations in Peru was Japanese-owned and most of the whale meat was exported to Japan. However, due to international pressure and after it was shown that there was no market for whale meat in Peru, all whaling operations were finally stopped in Peru in 1985.

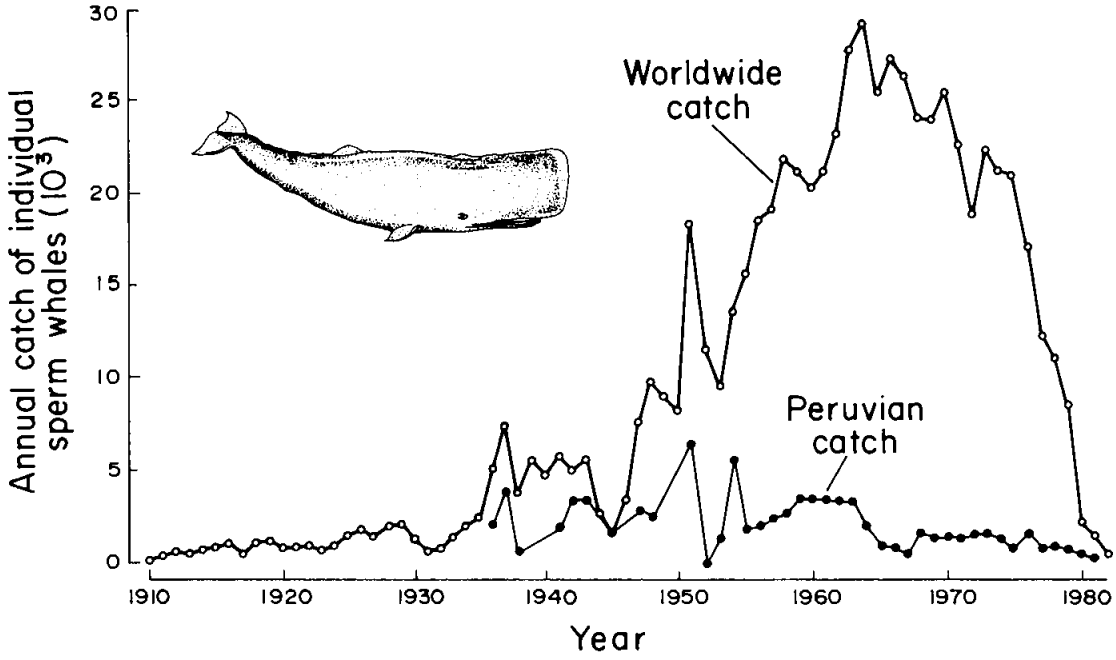

Fig. 3. Catches of sperm whale, 1910-1982, in the world and in Peru (from Gosho et al. 1984 and Table 2).
Fig. 3. Capturas de cachalote, 1910-1982, en el Perú y el mundo (tomado de Gosho et al. 1984 y de la Tabla 2).

The Dolphins and Porpoises

Little is known of the use of dolphins by ancient Peruvians. Dolphin remains have not been found in preceramic sites (D. Bonavia, pers. comm.). The Nazcas left multiple representations of orcas on ceramics (Proulx 1983), but no bones of this species have been found in diggings (D. Bonavia, pers. comm.). There is no information on the history of exploitation of small cetaceans in Peru prior to 1962. In this year, Clarke (1962) reported that Burmeister's porpoises were sold every day in the port of Chimbote. Grimwood (1969) reports that dolphins and porpoises were frequently caught by small boat fishermen in ports such as San Andres and others. He wrote "... the price they fetch, however, is so low compared to that obtained for fish that it is doubtful if they are fished for deliberately." Subsequently, Clarke et al. (1978) report observing porpoises in the markets of Chimbote, Ancon, Callao, Pucusana, San Andres and Ilo in 1971-1972.

The first estimate of the magnitude of the catch of small cetaceans in Peru were from Mitchell (1975) who based his estimates on information provided by the Instituto del Mar del Peru (IMARPE) and on unpublished data from K.S. Norris. According to his report, about 1,000 tonnes of porpoises were sold in fish markets every year, mainly Burmeister's porpoises, and a small number of dusky dolphins. At least 2,000 small cetaceans were reportedly taken incidentally in gill nets set for sciaenids (Brownell and Praderi 1982).

Recent studies have revealed that several species of small cetaceans currently are taken along the Peruvian coast, with higher numbers being taken off the central coast (Read et al. 1988). The development of this fishery seems to have originated after the collapse of the anchoveta fishery in the early 1970s. The most exploited species is the dusky dolphin, for which

a directed gill-net fishery exists, but bottlenose dolphins are also taken regularly. Small cetaceans are caught incidentally in gill nets set for sharks, and directly with gill nets and hand-thrown harpoons. Catches also occur in the industrial purse-seine operations for pelagic fishes. Approximately 10,000 animals were caught in 1985 by the fisheries, the meat being used for human consumption (Read et al. 1988). A dramatic increase in the small cetacean fisheries in recent years has been shown by Van Waerebeek and Reyes (1988) and has been linked to a worsening of the economic situation in Peru. At present, there is no legal protection for small cetaceans in Peru.

Discussion

The studies carried out in recent years have led to a better understanding of the seal and small cetacean populations in Peru. However, what we know about them is still very limited and not sufficient to design a conservation strategy for any of these species. Some of these are known from only a few specimens stranded on beaches and for most, we have only details of their anatomy and/or ecology. For the large cetaceans, the information available covers only the main whaling areas in northern Peru, while nothing is known about their distribution and abundance in the south of the country. Because commercial fisheries in Peru are aimed mainly at small pelagic fish, the major prey of most marine mammals, conflict is always likely. Also, marine mammals are highly valued for their skins, oil, and meat and thus, with the present economic crisis in Peru, the impoverished fishermen are even more likely to hunt these animals, legally or not, to supplement their incomes.

Management of the fisheries for marine mammals has always been deficient. Quotas for the exploitation of whales were based on dubious estimates of abundance in Peruvian waters. Seals were hunted intensively without their numbers being known and based on estimates of breeding success from related species now known to have much higher pup production. Small cetaceans are still hunted in very high numbers without any population estimates. Both seals and small cetaceans are particularly vulnerable during their reproductive periods, when they are close to the land. Many species of dolphins and small whales are only available to the fisheries during the summer, when the Humboldt current is narrower and fishermen can reach oceanic waters close to the coast (Read et al. 1988). Fortunately, at present, the exploitation of large whales has been banned internationally and it is no longer carried out in Peru. However, some large cetaceans, for example humpback whales, also approach the coast in the spring and are likely to get entangled in gill nets.

Human activities also have an indirect effect on marine mammal populations in Peru. Overexploitation of pelagic species of fish reduced the food base of marine mammals. Once very abundant in Peruvian waters, the anchoveta population collapsed in the early 1970s and has not recovered since (see contributions in Pauly and Tsukayama 1987a and other contributions in this vol.). This resource used to sustain large populations of marine mammals off Peru. Recovery of these marine mammal populations to their former levels is therefore unlikely, since the biomass of anchoveta necessary to maintain large numbers of sea mammals is no longer available.

Marine mammal populations in Peru are not only affected by human activities. Being the top predators in the marine ecosystem, natural changes in prey availability also affect their breeding success and survival. During El Niño events, anchoveta migrate to deeper waters or disperse (Arntz 1986) and so fur seal females have to spend more energy for foraging (see Majluf, this vol.). Particularly, they must dive to great depths more frequently than in "normal" years and the prey they obtain is of lower energy content. As a result, they are not able to cover the energy demands of lactation and their pups starve or have reduced growth. Adults may also be affected if the intensity of the event is high (Majluf 1987). Similar effects of El Niño events have been described for sea lions (Limberger et al. 1983). Small cetaceans can be assumed to be affected in an analogous fashion. Bryde's whales feeding off Peruvian waters were found to have empty stomachs more often during El Niño events than in years without such events (Ramírez and Urquizo 1985). There is no information on the effect of decreased foraging success on whale reproductive output, but it is likely to be negative. Thus, even though living in the rich Peruvian upwelling system allows marine mammals access to abundant food resources, they also have to endure unpredictable variations in their food supply, which makes them, in poor years, even

more vulnerable to human predation. Although we now have a better understanding of some of the natural factors affecting the marine mammals in Peru and of their interaction with fisheries, we still need detailed information on their life history, distribution and survival before we can design adequate conservation/management policies.

Also, Peruvian marine mammals have been exploited only as fisheries resource. Alternative uses, such as for tourism (seal and whale-watching) have not been considered. The tourist potential of ares such as the Paracas National Reserve and Punta San Juan, where large numbers of fur seals and sea lions are readily accessible and where dolphins, whales and otters are regularly observed, should be assessed. In other South American countries, for example Argentina, Chile and Mexico, there are numerous areas where whale and/or seal watching has replaced direct harvesting and are currently generating substantial revenues (Barstow 1986).

There is a history of overexploitation of all fisheries resources in Peruvian waters and marine mammals are no exception. Nonconsumptive utilization of marine mammals as a tourist attraction not only is an effective means of conservation of these animals through direct protection and increased public awareness of these animals, but also has the potential to continue to generate revenue in the long term. There is already a large tourist industry in Peru, and therefore, it should be relatively straightforward to add whale- and seal-watching trips to tours of this country. However, tourism has the potential to cause harm to marine mammals, e.g., through disturbance at mating sites (Barstow 1986) and it is important that care be taken in designing and implementing any tourist scheme. Considering the depressed economic climate in Peru, and the relatively poor return from the marine mammal fishery, nonconsumptive use is a potentially attractive option which should not be ignored.

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References

Amtz, W.E. 1986. The two faces of El Niño 1982-83. Meeresforsch. 31: 1-46.

Barstow, R. 1986. Non-consumptive utilization of whales. Ambio 15(3): 155-163.

Bigg, M.A., G.E. Ellis, J.K.B. Ford and K.C. Balcomb. 1987. Killer whales. A study of their identification, genealogy and natural history in British Columbia and Washington State. Phantom Press and Publishers Inc., Nanaimo, BC, Canada. 79 p.

Bini, G. 1951. Osservazioni su alcuni mammiferi marini sulle coste del Chile e del Peru. Boll. Pesca, Pisc. Idrob. (Roma) 27(6): 5-19.

Bonavia, D. 1982. Los Gavilanes: precerámico peruano. Mar desierto y oasis en la historia del hombre. Ed. Ausonia, Lima. 512 p.

Bonner, W.N. 1981. Southern fur seals - *Arctocephalus* sp., p. 161-208. *In* S.H. Ridgeway and R.J. Harrison (eds.) Handbook of marine mammals. Vol. 1. The walrus, sea lions, fur seals and sea otter. Academic Press, New York.

Brack, A. 1978. Situación actual de la lutrias (*Lutrinae*, Mustelidae) en el Perú. IUCN Publications New Series. Otters. Proc. First Working Meet. Otter Spec. Group. Paramaribo, Suriname, 1977: 108-118.

Brownell, R.L. Jr. 1974. Small odontocetes of the Antarctic. *In* G. Llano (ed.) Antarctic mammals. Amer. Geogr. Soc. Map. Folio Ser. 18: 13-197.

Brownell, R.L. Jr. and R. Praderi. 1982. Status of Burmeister's porpoise, *Phocoena spinipinnis*, in southern South American waters. *In* Mammals in the seas: small cetaceans, seals, sirenians and otters. FAO Fish. Ser. 5(4): 91-96.

Brownell, R.L., Jr. and R. Praderi. 1984. *Phocoena spinipinnis*. Mammalian Species No. 217: 1-4.
Cabello, J. 1983. La nutria de mar en la Isla de Chiloe. CONAF. Bol. Tec. No. 6. 37 p.
Castilla, J.C. 1981. La Lutra de mare chilena: especies en extinction. Creces 2(1): 31-34.
Castilla, J.C. 1982. Nuevas observaciones sobre conducta, ecología y densidad de *Lutra felina* (Molina 1782) (Carnivora: Mustelidae) en Chile Museo Nacional de Historia Naturales Publ. Ocas. 38: 197-208.
Castilla, J.C. and I. Bahamondes. 1979. Observaciones conductuales y ecológicas sobre *Lutra felina* (Molina 1782) (Carnivora: Mustelidae) en las zonas Central y Centro-Norte de Chile. Arch. Biol. Med. Exper. 12: 119-132.
Clarke, R. 1962. Whale observation and whale marking off the coast of Chile in 1958 and from Ecuador towards and beyond the Galapagos Islands in 1959. Norsk. Hvalf. Tid. 51(7): 265-287.
Clarke, R. 1980. Catches of sperm whales and whalebone whales in the Southeast Pacific between 1980 and 1975. Rep. Int. Whal. Commn. 30: 285-288.
Clarke, R., A. Aguayo and O. Paliza. 1968. Sperm whales of the Southeast Pacific. Part I: Introduction. Part II: Size range, external characters and teeth. Hvalradets Skrifter 51: 1-80.
Clarke, R., A. Aguayo and S. Basulto del Campo. 1978. Whale observation and whale marking off the coast of Chile in 1964. Sci. Rep. Whales Res. Inst. 30: 117-177.
Cobo, P.B. 1956. Historia del nuevo mundo. Biblioteca de autores Españoles desde la formacíon del lenguaje hasta nuestro dias. Obras del P. Bernabé Cobo. Madrid. Tomo 81. 47 p.
Dahlheim, M.E., S. Leatherwood and W.F. Perrin. 1982. Distribution of killer whales in the warm temperate and tropical eastern Pacific. Rep. Int. Whal. Commn. 32: 647-653.
Daugherty, A.E. 1979. Marine mammals of California, Univ. Calif. Sea Grant Mar. Adv. Progr. and Calif. Dept. Fish Game. 61 p.
Donovan, G.P. 1984. Small cetaceans seen during the IWC/IDCR research cruise in the eastern tropical Pacific, and in particular off Peru. Rep. Int. Whal. Commn. 34: 561-567.
Estes, J.A. 1986. Marine otters and their environment. Ambio XV(3): 181-183.
Gamarra Dulanto, L. 1943. Los lobos marinos. Bol. Cia. Admin. Guano 19(4): 121-131.
Gosho, M.E., D.W. Rice and J.M. Breiwick. 1984. The sperm whale, *Physeter macrocephalus*. Mar. Fish. Rev. 46(4): 54-64.
Gonzales Zúñiga, A. 1944. Lobos marinos, fuente de Riqueza. Bol. Cia. Admin. Guano, Peru. 20(5): 119-135.
Grimwood, I.R. 1969. Notes on the distribution and status of some Peruvian mammals. 1968 N.Y. Zool. Soc. Spec. Publ. 21: 1-86.
Guerra, C. and D. Torres. 1987. Presence of the South American fur seal, *Arctocephalus australis*, in northern Chile. *In* J.P. Croxall and R.L. Gentry (eds.) Status, biology and ecology of fur seals. NOAA Tech. Rep. NMFS 51: 169-175.
Gutierrez de Santa Clara P. 1905. Historias de las guerras civiles del Perú (1544-1548) y de otros sucesos de las Indias.. Libreria General de Victoriano Suarez. Madrid. Tomo 3.
Hamilton, J.E. 1934. The southern sea lion, *Otaria byronia* (De Blainville). Discovery Reports 8: 269-318.
Hertz O. and F.O. Kapel. 1986. Commercial and subsistence hunting of marine mammals. Ambio 15(3): 144-151.
Hvidberg-Hansen, H. 1970. A survey of the coast otter (*Lutra felina*) Molina in the Peruvian rivers of Camana and Ocoña. FAO-UNDP/SP No. 116.
IUCN. 1982. The IUCN mammal red data book - Part 1. IUCN, Gland and Cambridge.
IUCN. 1986. Red list of threatened animals. IUCN, Gland and Cambridge.
Johnson, J.H. and A.A. Wolman. 1984. The humpback whale, *Megaptera novaeangliae*. Mar. Fish. Rev. 46(4): 30-37.
Kasuya, T. and H. Marsh. 1984. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. Rep. Int. Whal. Commn. (Special Issue 6): 259-310.
King, J.E. 1983. Seals of the world. British Museum (Natural History) and Oxford University Press, London and Oxford.
Laws, R.M. 1973. The current status of seals in the southern hemisphere. *In* Seals: Proceedings of a Working Meeting of Seal Specialists on Threatened and Depleted Seals of the World. IUCN Publ. New Series Suppl. Pap. No. 39: 144-161.
Leatherwood, S. and R.R. Reeves. 1983. The Sierra Club Handbook of whales and dolphins. Sierra Club Books, San Francisco. 302 p.
Limberger, D., F. Trillmich, G.L. Kooyman and P. Majluf. 1983. Reproductive failure of fur seals in Galapagos and Perú in 1982-1983. Trop. Ocean. Atmosp. Newsl. 21: 16-17.
Lopez de Gomara, F. 1941. Historia general de las Indias. Espasa-Calpe, Madrid.
Majluf, P. 1985. Comportamiento del lobo fino de Sudamérica (*Arctocephalus australis*) en Punta San Juan, Perú, durante "El Niño" 1982-83, p. 187-193. *In* W. Arntz, A. Landa and J. Tarazona (eds.) "El Niño": su impacto en la fauna mariña. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario.
Majluf, P. 1987. Reproductive ecology of female South American fur seals at Punta San Juan, Peru. University of Cambridge, UK. 254 p. Ph.D. Dissertation.
Majluf, P. and F. Trillmich. 1981. Distribution and abundance of sea lions (*Otaria byronia*) and fur seals (*Arctocephalus australis*) in Peru. Z.f. Säugetierkunde 46(6): 384-393.
McKinnon, J.S. 1988. Feeding habits of three small odontocetes from the coastal waters of Peru. University of Guelph, Ontario. 94 p. M.Sc. thesis.
Minasian, S.M., K.C. Balcomb III and L. Foster. 1984. The world's whales. Smithsonian Books, Washington DC. 224 p.
Mitchell, E.D. 1975. Porpoise, dolphin and small whale fisheries of the world. IUCN Monograph No. 3: 1-129.
Mizroch, S.A., D.W. Rice and J.M. Breiwick. 1984. The fin whale, *Balaenoptera physalus*. Mar. Fish. Rev. 46(4): 20-24.
Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.
Murphy, R.C. 1925. Bird islands of Peru. G.P. Putnam's Sons, New York and London.
Northridge, S.P. 1984. World review of interactions between marine mammals and fisheries. FAO Fish. Pap. 251. 190 p.
Oliva, D. 1988. *Otaria byronia* (de Blainville 1820), the valid scientific name for the southern sea lion (Carnivora: Otariidae). J. Nat. Hist. 22: 767-772.

Oliver, C. 1946. Catálogo de los mamíferos de los Provincia de Concepción. Orden Cétacea. Bol. Soc. Biol. (Concepción) 21: 79-83.

Pauly, D. and I. Tsukayama, editors. 1987a. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama. 1987b. On the implementation of management-oriented fishery research: the case of the Peruvian anchoveta, p. 1-13. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusamennarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Piazza, A. 1969. Los lobos marinos en el Perú. Pesca y Caza (Perú) 9: 1-29.

Proulx, D. 1983. The Nazca style, p. 86-105. *In* Art of the Andes. The Arthur M. Sackler collection. The Arthur M. Sackler Foundation and the Ames Foundation for the Arts and Humanities, Washington.

Ramírez, P. 1983. Capturas y observaciones de la ballena azul *Balaenoptera musculus* L. en Paita - Perú 1961-66 y 1975-1982. IMARPE. Rev. Com. Perm. Pac. Sur 13: 97-102.

Ramírez, P. 1986. Distribución y alimentación de la ballena Bryde durante el fenomeno "El Niño" 1982-83. Bol. Erfen 17: 20-27.

Ramírez, P. 1988a. Capturas de la "ballena de aleta" en Paita, Perú (*Balaenoptera physalus* L.). Boletin de Lima (58): 93-96.

Ramírez, P. 1988b. La ballena jorobada *Megaptera novaeangliae* en la costa norte del Perú: Períodos 1961-1965 y 1975-1985. Boletin de Lima (56): 91-96.

Ramírez, P. 1988c. Captura de la Ballena Sei (*B. borealis*) frente a Paita, Perú, p. 341-343. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinamica del ecosistema de afloramiento Peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario

Ramírez, P. 1988d. Comportamiento reproductivo del "cachalote" (*Physeter catodon* L.). Boletin de Lima (59): 29-32.

Ramírez, P. 1989. Captura de cachalotes en Paita: 1976-1981. Boletín de Lima (63): 81-88.

Ramírez, P. and W. Urquizo. 1985. Los cetaceos mayores y el fenomeno "El Niño" 1982-83, p. 201-206. *In* W. Arntz, A. Landa and J. Tarazona (eds.) "El Niño": su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario.

Read, A.J., K. Van Waerebeek, J.C. Reyes, J.S. McKinnon and L.C. Lehman. 1988. The exploitation of small cetaceans in coastal Perú. Biological Conservation 46: 53-70.

Reyes, J.C., A.J. Read and K. Van Waerebeek. 1988. Clave para la identificación de los pequeños cetaceos más comunes en la costa peruana. Boletin de Lima (57): 93-95.

Saetersdal, G., J. Mejía and P. Ramírez. 1963. La caza de cachalotes en el Perú. Estadisticas de captura para los años 1947-1961 y un intento de analizar las condiciones de la población en el periódo 1954-1961. Bol. Inst. Mar Peru-Callao 1(3): 45-84.

Sielfeld, W.K. 1983. Mamíferos marinos de Chile. Ediciones de la Universidad de Chile, Santiago. 199 p.

Torres, D. 1987. Juan Fernández fur seal, *Arctocephalus philippii*. *In* J.P. Croxall and R.L. Gentry (eds.) Status, biology and ecology of fur seals. NOAA Tech. Rep. NMFS 51: 37-41.

Tovar, H. and H. Fuentes. 1984. Magnitud poblacional de lobos marinos en el litoral peruano en Marzo de 1984. Informe Inst. Mar Perú-Callao No. 88. 32 p.

Townsend, C.H. 1935. The distribution of certain whales as shown by the logbook records of American whaleships. Zoologica 18: 1-50.

Valdivia, J., F. Franco and P. Ramírez. 1981. the exploitation of Bryde's whales in the Peruvian sea. Rep. Int. Whal. Commn. 31: 441-448.

Van Waerebeek K. and J.C. Reyes. 1986. The first records of the short-finned pilot whale *Globicephala macrorhynchus* for Peruvian waters. Abstract, 14th Symp. Europ. Assoc. Aquat. Mam., Barcelona, 16-19 March 1986.

Van Waerebeek, K. and J.C. Reyes. 1988a. La captura de pequeños cetáceos en la costa central de Perú: un ejemplo. Abstract. III Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de America del Sur. Montevideo, 25-30 Julio 1988.

Van Waerebeek, K. and J.C. Reyes. 1988b. First record of the Pygmy killer whale, *Feresa attenuata* Gray, 1875 from Peru, with a summary of distribution in the eastern Pacific. Z. Säugetierkunde 53, p. 253-255.

Van Waerebeek, K., J.C. Reyes and B.A. Luscombe. 1987. A second record of the Pygmy sperm whale *Kogia breviceps* (de Blainville, 1838) (Cetacea, Physeteridae) from the Peruvian coast. Z. Säugetierkunde 52, p. 192-194.

Van Waerebeek, K., J.C. Reyes and B.A. Luscombe. 1988. Revisión de la distribución de pequeños cetáceos frente al Perú, 345-351. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de Afloramiento Peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario.

Van Waerebeek, K., J.C. Reyes, A.J. Read and J.S. McKinnon. Preliminary observations of bottlenose dolphins from the Pacific coast of South America. *In* S. Leatherwood and R.R. Reeves (eds.) The Bottlenose Dolphin, *Tursiops* spp. Academic Press, Florida. (In press)

Vasquez de Espinosa, A. 1942. Compendium and description of the West Indies. Smithsonian Miscellaneous Collection. Washington, DC.

Vaz-Ferrerira, R. 1982. *Arctocephalus australis* Zimmermann, South American fur seals. *In* Mammals in the seas. FAO Fish. Rep. Ser. 4(5): 497-508.

Walker, W.A. 1981. Geographical variation in morphology and biology of bottlenose dolphins *(Tursiops)* in the eastern North Pacific. NOAA, NMFS. SWFC Admin. Rep. LJ-81-03C. La Jolla, California. 54 p.

Wing, E.S. and J.E. Reitz. 1982. Pisces, Reptilia, Aves, Mammalia. *In* D. Bonavia (ed.) Los Gavilanes: preceramico peruano. Mar desierto y oasis en la historia del hombre. Ed. Ausonia, Lima. 512 p.

Würsig, K. and M. Würsig. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. Fish. Bull. 77(4): 871-890.

Reanalysis of Recruitment Estimates of the Peruvian Anchoveta in Relationship to Other Population Parameters and the Surrounding Environment

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Abstract

New recruitment estimates of the Peruvian anchoveta are analysed with respect to other population parameters and the surrounding ocean environment. The inshore and offshore environmental variables differ in their dynamics, and the inshore series vary north to south. For the inshore locations, it is not possible to resolve if a wind-related effect is due to transport or turbulence. The new recruitment estimates differ significantly from the old estimates, partly due to mackerel consumption acting as a surrogate for SST. Models using the monthly data were not possible due to correlations in the populations that could be spurious. On a yearly basis, a nonlinear additive model using parent biomass and transport at Trujillo explained 75% of the variance in the recruitment estimates.

Resumen

Nuevos estimados de reclutamiento de la anchoveta peruana se analizan en relación con otros parámetros poblacionales y el ambiente en que habita. Las variables ambientales costeras y distantes de la costa difieren en su dinámica, y las series costeras varian de norte a sur. Para las localidades costeras, no es posible establecer si un efecto relacionado con el viento es ocasionado por el transporte o la turbulencia. Los nuevos estimados de reclutamiento difieren significativamente de los estimados antiguos, debido parcialmente al consumo del jurel que actúa como un indicador de la temperatura. No ha sido posible aplicar modelos que utilizan datos mensuales debido a que las correlaciones en la población pudieran ser espurias. Un modelo aditivo no lineal usando la biomasa parental y el transporte de Trujillo, sobre una base anual, explica el 75% de la variancia de los estimados del reclutamiento.

Introduction

One of the main goals of the contributions in Pauly and Tsukayama (1987) was to estimate the demographic parameters of the Peruvian anchoveta, taking into account all sources of mortality. Thus, estimates of anchoveta consumption by birds (Muck and Pauly 1987), marine mammals (Muck and Fuentes 1987) and bonito (Pauly et al. 1987) were included in the estimation algorithms. Muck and Sanchez (1987), however, presented evidence that mackerel and horse mackerel are major predators of the anchoveta, with consumptions levels approaching that of the fishery at its highest levels. As the mackerel consumption was not included in the original estimates, new population estimates have been calculated (Pauly and Palomares, this vol.).

These new population estimates, as well as the corrected alongshore stress series in Bakun and Mendelssohn (this vol.), are the impetus for redoing the analysis in Mendelssohn and Mendo (1987, hereafter referred to as M&M). Besides examining some models for using population and

environmental parameters to forecast the new estimates of anchoveta recruitment, this reanalysis affords me the opportunity to delve in more detail into some issues glossed over in M&M, as well as to tie together some loose ends. In particular, the interrelationships among some environmental variables mentioned in M&M are discussed here in more detail.

M&M used a form of non-parametric regression that estimated transformations for both the dependent and the independent variables. The algorithm did not produce tables analogous to the ANOVA tables in linear regression. Non-parametric regressions are also used in this paper, but in a form more analogous to standard regression analysis, even allowing "error bars" on the estimated transformations. This should make the resulting models more easily interpreted. Cury and Roy (1989) estimate optimal environmental windows for a number of eastern boundary current regions, including the Peruvian anchoveta. I reestimate these windows for the new data. Finally, Bohle-Carbonell (this vol.) examines fractal dimensions for some of the time series in Pauly and Tsukayama (1987). I estimate a related parameter, fractional differencing, for a larger number of the environmental series, and show how these estimates relate to the models of this paper.

Many of these issues were examined in my original efforts with Jaime Mendo, but were only alluded to in M&M. My knowledge of the Peruvian ecosystem derives from my working with J. Mendo, and while we did not work on this reanalysis together, I would like to acknowledge my debt to him and indicate that this paper would not have been possible otherwise.

Data and Methods

For the population data, I use the estimates of recruitment, parent and female biomass, and egg production in Pauly and Palomares (this vol.) and Pauly and Soriano (this vol.). For the environmental series, I use the corrected alongshore stress given in Bakun and Mendelssohn (this vol.), the turbulence series ("wind speed cubed") in Bakun (1987), the Southern Oscillation Index (SOI) in Brainard and McLain (1987), and the estimates of upwelling and turbulence for Trujillo and Callao in Mendo et al. (1987). For convenience, I will refer to the Bakun estimates of transport and turbulence as the "oceanic" estimates, while the estimates of Mendo et al. (1987) will be referred to by location.

Spectral estimates were calculated for the mean corrected series by first tapering the series using a split-cosine bell taper (Bloomfield 1976)

$$u_t = \begin{cases} .5\left(1-\cos\left(\pi(t-.5)/m\right)\right), & t=0, \ldots, m-1 \\ 1, & t=m, \ldots, n-m-1 \\ .5\left(1-\cos\left(\pi(n-t+.5)/m\right)\right), & t=n-m, \ldots, n-1, \end{cases} \qquad \ldots 1)$$

where m is chosen so that 2m/n is the desired proportion of the data to be tapered. I have used a 20% taper. Tapering data reduces leakage between frequencies, but tends to make spectral peaks flatter and broader. The discrete Fourier transform of each tapered series was calculated as

$$d_x(\lambda_j) = \frac{1}{T}\sum_{t=0}^{T-1} e^{-i\lambda_j t} x(t) \qquad \ldots 2)$$

where $\lambda_j = (2\pi j)/T$ is the j th Fourier frequency. The raw (cross)-periodogram is then calculated as

$$p_{xy}(\lambda_j) = d_x(\lambda_j) d^*_y(\lambda_j) \qquad \ldots 3)$$

where the notation d^* denotes conjugate (transpose). Spectral density matrices were then calculated as the overlapping moving average of the raw periodograms,

$$f_{xy}(\lambda_j) = \sum_{l=-m}^{m} p_{xy}(\lambda_{j+l}). \qquad \text{... 4)}$$

I have used a value of $m = 5$, giving 22 degrees of freedom.

Most analyses of time series data assume stationarity, or that stationarity can be achieved after applying a relatively short-term filter to the data. This assumption may not be valid for natural processes. Hurst (1951) studied the flows of rivers. Let $x_1, x_2, \ldots, x_T$ be the historical sequence of flows. Then the cumulative flows up to time t are

$$Su_t = \sum_{j=1}^{t} x_j, \quad t = 1, 2, \ldots, T. \qquad \text{... 5)}$$

Related to reservoir construction is the sequential range

$$R = \max Su_t - \min Su_t \qquad \text{... 6)}$$

Hurst (1951) looked at the normalized sequential range (or "rescaled adjusted range") where Su_t has the mean flow removed and the result is divided by the standard deviation of the flows. If the flows are independent over long time scales, then one would expect that $R/S \sim (T/2)^{.5}$. However, Hurst (1951) found that for a wide range of river flows $R/S \sim (T/2)^H$ for H in the range (.6,.8). This can be explained in terms of fractional Gaussian noise (fGn) (Mandelbrot and Van Ness 1968, Mandelbrot 1971). Let $B(s)$ be Brownian motion, a stochastic process such that $B(s+u)-B(s)$ are $N(0,1)$ and independent. Then fractional Brownian motion takes the form

$$B_H(t) = \int_{-\infty}^{t} (t-a)^{H-.5}\, dB(s), \quad -\infty < t < \infty \qquad \text{... 7)}$$

or

$$B_H(t) - B_H(0) = \int_{-\infty}^{t} (t-s)^{H-.5}\, dB(s) - \int_{-\infty}^{0} (-s)^{H-.5}\, dB(s). \qquad \text{... 8)}$$

Discretizing the equation yields

$$b_t(H) = B_H(t) - B_H(t-1). \qquad \text{... 9)}$$

Fractional Gaussian noise can be described by its autocorrelation function

$$C(s) = \frac{1}{2}(|s-1|^{2H} - 2|s|^{2H} + |s+1|^{2H}). \qquad \text{... 10)}$$

Fractional Gaussian noise also exhibits the self-similarity property, that is

$$x(t\lambda) \sim (\lambda)^a x(t). \qquad \text{... 11)}$$

A concept related to *fGn* is "fractional differencing" (Granger and Joyeux 1980, Hosking 1981) described as

$$(1-B)^d x(t) = e(t) \qquad \text{... 12)}$$

where d is possibly nonintegral, B is the backshift operator, and the $e(t)$ are independently distributed as $N(0, \sigma^2)$. Note that this is not a nonintegral lag operator, but rather an infinitely lagged polynomial in B whose weights die out at a rate given in the autoregressive representation (14). The spectral density of this model is

$$f(\lambda) = \frac{\sigma^2}{2\pi} (2(1-\cos(\lambda))^{-d}, \quad \lambda \neq 0. \qquad \text{... 13)}$$

Granger and Joyeux (1980) derive the following autoregressive representation of a fractionally differenced process

$$\sum a_j x(t-j) = e(t); \qquad a_j = \frac{\Gamma(j-d)}{\Gamma(1-d)\Gamma(j+1)} \quad j > 1. \qquad \text{... 14)}$$

Porter-Hudak (1982) and Geweke and Porter-Hudak (1983) show that the power spectrums of the error terms from an *fGn* process and a fractionally differenced process only differ by a short-term memory component. Thus both models are estimating essentially the same long-term memory component. I find fractional differencing more intuitive, as it is a long-term extension of the usual ideas of differencing and filtering to obtain stationarity. (The first few terms of the expansion of the differencing polynomial are

$$1 - dB - \frac{1}{2}d(1-d)B^2 - \frac{1}{6}d(1-d)(2-d)B^3 \qquad \text{... 15)}$$

The parallels with the usual differencing schemes used to achieve stationarity are immediate.)

Porter-Hudak (1982) and Kashyap and Eom (1988) give methods for estimating the fractional differencing parameter *d*, based on regressions between the log of the theoretical spectrum and the log of the observed periodogram. The property of concern here is that a process has long-term memory if *d* is in the range *(0,.5);* the process has short-term memory if $d < 0$; and the process has infinite variance if $d > .5$ (Granger and Joyeux 1980, Hosking 1981). Both long-term and short-term memory time series models assume that the basic input process is a random variable. The main difference is that in long-memory models any impulse to the system takes a long time to die out. Another way to view this is that the system is sensitive to initial conditions. A small difference in two identical systems at a given time period will be evident for many time periods to come. Depending on the dynamics involved, the difference between the two systems caused by this impulse may grow, rather than disappear through time. The models in M&M as well as the ones in this paper, assume a relationship between anchoveta recruitment and other variables. If this relationship is on the proper scale and is stationary, then long-term memory in any of the predictor variables will not affect the system. However, the length of time ahead that a forecast can be made can be affected by long-term memory, as longer forecast horizons could imply forecasting one of the predictor variables. As errors can propogate in long-memory systems, long-term predictions become unreliable. An alternative is to find another, less direct predictor variable, that is related to anchoveta recruitment at a longer lag. (See also Bohle-Carbonell, this vol., who estimates the fractal dimension of several of the series in Pauly and Tsukayama 1987).

Trends in time-series are estimated using two different algorithms. The first is the "locally-weighted sums of squares" or LOWESS algorithm of Cleveland (1979), and the other is the decomposition algorithm of Kitagawa and Gersch (1984). LOWESS fits to each point a weighted linear regression using some fixed percentage of points surrounding the given point. The regression is then made robust by weighting against outliers. I use a proportion of $F = .05$, which corresponds to two years of data in calculating the smooths in this paper.

Kitagawa and Gersch (1984) assume that an observed time series can be decomposed as

$$y(t) = T(t) + S(t) + A(t) + e(t) \qquad \text{... 16)}$$

where *T(t)* is a trend component at time *t*, *s(t)* is a seasonal component at time t, *A(t)* is a stationary random component (i.e., and AR component) at time *t*, and *e(t)* is an error term. They assume a smoothness prior for the trend and seasonal components, which means that at some level of differencing the component is equivalent to a zero mean normal variate with unknown variance. The degree of differencing and the amount of variance in the random variate causes a tradeoff between the smoothness of the component and the reduction in variance due to that component. This is the same as fitting the discrete equivalent of a smoothing spline for that component (Kohn and Ansley 1988). Kitagawa and Gersch (1984) show that this can be formulated as a state-space model and estimated using a combination of Kalman filtering and maximum likelihood estimation.

The usual regression model has a response random variable Y and p predictor random variables $X_1, X_2, \ldots, X_p$. A set of n independent realizations of these random variables is observed, denoted by $(y_1, x_{11}, \ldots, x_{1p}), \ldots, (y_n, x_{n1}, \ldots, x_{np})$ and it is desired to estimate the conditional expectation $E(Y \mid X_1, X_2, \ldots, X_p)$. Linear regression assumes that the conditional expectation is linear, that is

$$E(Y \mid X_1, X_2, \ldots, X_p) = \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \qquad \ldots 17)$$

and given a sample, estimates of the β_i are usually found by least squares. A natural generalization is to consider additive nonlinear models (Hastie and Tibshirani 1986) of the form

$$E(Y \mid X_1, X_2, \ldots, X_p) = \sum_{j=1}^{p} s_j(X_j) \qquad \ldots 18)$$

where the nonlinear functions s_j are to be estimated. This is accomplished by estimating the s_j as an "average" of some part of the data surrounding a point, in this case a scatterplot smoother fit using the backfitting algorithm of Breiman and Friedman (1985). In particular, I use the running lines smoother in Hastie and Tibshirani (1986).

When the functions s_j in generalized additive models are estimated using a fixed span smoother, then it is possible to estimate the degrees of freedom used in forming the estimate of s_j, as well as an analysis of deviance table that is directly analogous to the standard analysis of variance table in regression analysis (Hastie and Tibshirani 1986; see Hastie 1987 for a good description of deviance and how it relates to sums of squares). This allows for a comparison of models using measures such as AIC (Akaike 1977), BIC (Schwarz 1978) or cross-validation. A smaller span produces a closer fit to the observed data (smaller variance), but with a greater bias and larger number of degrees of freedom, equivalent to fitting more parameters in a normal regression model. A larger span is smoother, with smaller bias, but greater variance. The choice of the span is thus a tradeoff between variance and bias, as in most situations where extra parameters can be added to the model. Hastie and Tibshirani (1985) show how to construct 95% confidence intervals for the estimated functions s_j.

Environmental Variables

There are a large number of environmental variables that could be used to model the anchoveta, but brute force searching through all of them can lead to spurious results. The environmental variables available for this study in all likelihood are surrogates for the actual physical processes that affect the anchoveta. It is likely, then, that the dynamics of the variables will be the important element in modeling. While each of these large number of series could be argued to be a surrogate variable, it is possible to separate variables that reflect more direct influences on the fish from those with indirect influences. For this reason, the SOI is not used in any of the direct analyses. The SOI reflects processes distant from the environment of the Peruvian anchoveta. The changes reflected in SOI would have to be reflected in changes in the more local environment to have any effect on the anchoveta. If, however, a local variable is a good predictor of anchoveta recruitment, and there is a strong relationship between the SOI and this local variable, then there exists the possibility for a more extended (longer lead time) forecast.

For completeness, I show the major environmental series with trends estimated using LOWESS. SST (Fig. 1), shows a sharp drop through 1954-1956, and then a peak during the El Niño period of 1957-58. SST remained fairly steady through mid-1971, and then peaked in the 1972 El Niño. The 1983 El Niño produced a strong peak in the series. A slight upward trend in SST is noticeable from 1971 onward.

Oceanic transport (Fig. 2) has been fairly steady, with noticeable increases during the El Niño periods of 1957-58, 1972 and 1983. The 1960s appeared to have been a decade of decreased variance in the transport, and the mean level during the 70s and 80s appears to be somewhat higher.

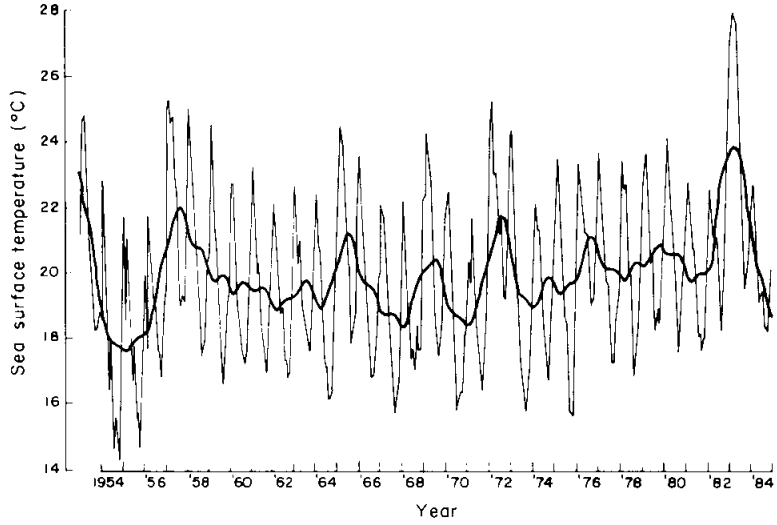

Fig. 1. SST off Peru with estimated local trend line.
Fig. 1. TSM frente a Perú con línea de la tendencia local estimada.

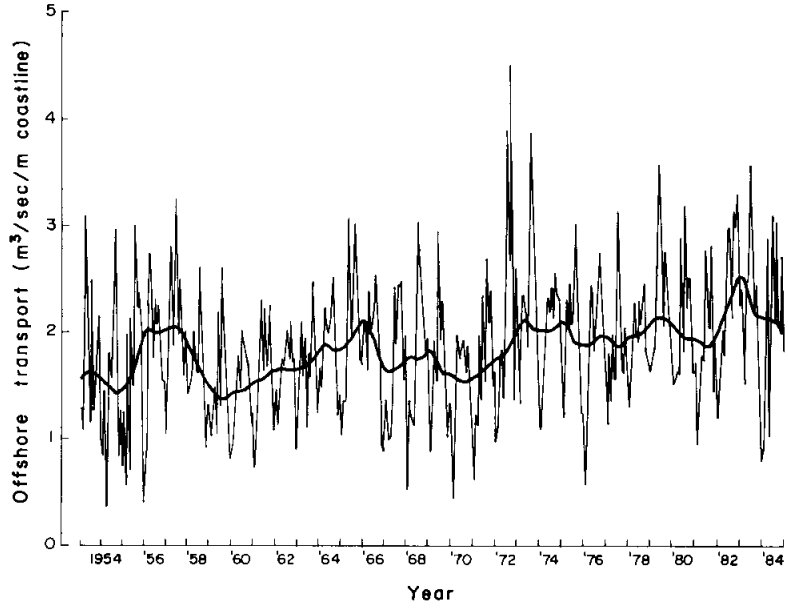

Fig. 2. Oceanic transport off Peru with estimated local trend line.
Fig. 2. Transporte oceánico frente a Perú con línea de la tendencia local estimada.

Transport at Trujillo (Fig. 3) shows the strongest trends among the data series. Transport increased through the El Niño of 1958, and then decreased and stayed relatively constant through the early 1960s. Starting around 1968, transport at Trujillo increased, staying at a higher level through 1972. Transport then dropped sharply till 1974, rose again till 1976, and then declined very sharply until 1982. Coincindent with the El Niño of 1983, transport at Trujillo increased to a more normal level. Transport at Callao (Fig. 3) displays similar behavior, except that the drop in 1974 is not as precipitous, and the sharp decline from 1976-1983 is not noticeable.

None of the subsurface series in Brainard and McLain (1987) are used in this paper, even though Bohle-Carbonell (this vol.) suggests that the subsurface has the strongest relationship with the earlier recruitment estimates. I note that, as mentioned in the article, only 20% of the subsurface data are from actual observations; the rest are from an interpolation scheme of unknown statistical properties. It would be difficult to ascertain to what degree any fit using these data was due to the actual physical process or due to the interpolator.

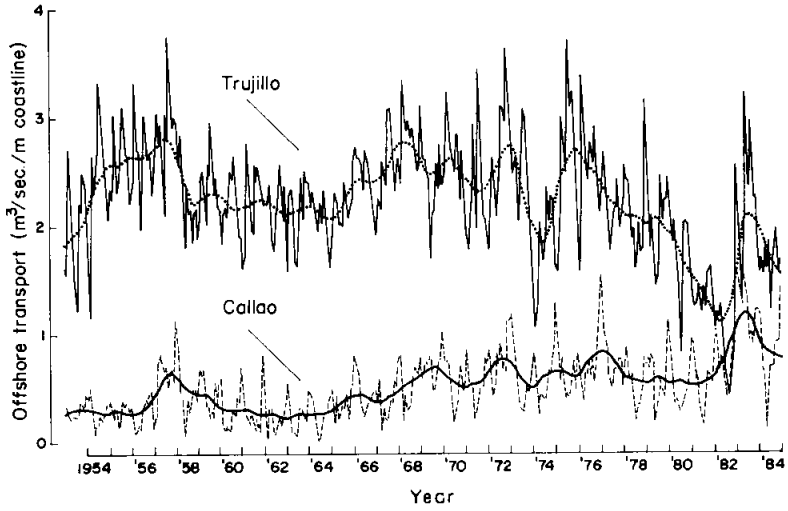

Fig. 3. Transport at Trujillo and Callao, with estimated local trend lines.
Fig. 3. Transporte en Trujillo y Callao, con lineas de las tendencias locales estimadas.

SST also is not used as a predictor. There are good *a priori* reasons for believing that SST would influence anchoveta recruitment. Unfortunately, several of the estimates of anchoveta consumption by other species (Muck and Pauly 1987; Pauly et al. 1987; Muck and Sanchez 1987) make explicit use of SST to modify the amount consumed. In the model of Muck and Sanchez (1987) for mackerel and horse mackerel, the offshore biomass of these fish are assumed at equilibrium sizes, but the relative number of mackerel close to shore varies with SST. Estimated consumption by these species are thus proxy variables for SST. Using SST in any further analysis leads to an obvious, direct bias. SST is also correlated with many of the other environmental variables, which may lead to indirect biases which cannot be totally avoided.

If the environmental variables are viewed as surrogates for a physical process in the ocean, one method for selecting which environmental variables to use in modeling is to see what unique information (in the statistical sense) each of the series contains. If each of the series contains essentially the same information, then there is little matter which is used. If the variables differ greatly in the information contained, then variables should be selected a priori based on knowledge of the fish and of the oceanographic processes likely to affect them.

Bakun and Parrish (1982) and Parrish et al. (1984) give cogent arguments as to why wind-induced transport should be an important factor in recruitment. Lasker (1978) has argued that turbulence affects early survival of larvae by affecting the concentration of available food. Based on these arguments, the transport and turbulence indexes discussed above are natural starting points for the analysis. The SOI will also be examined in relationship to these variables to see if it is reflected in any of these series.

Bakun's estimate of transport and wind is based on averaging a broad area off the coast of Peru, and is dominated by offshore observations. The series of Mendo et al. (1987) are from airports by the coast in Trujillo and Callao, and these authors present anecdotal evidence that these series accurately reflect the nearshore surface winds over the water. If these series differ in their information, then a basis for choosing a series is which area (nearshore or offshore, north or south) most likely influences the areas where the anchoveta are spawning.

The oceanic transport has the expected red noise spectrum at low frequencies, with a strong peak at a yearly frequency and small peaks at the harmonics of the yearly frequency (Fig. 4). Transport at Trujillo and Callao have a weak seasonal signal, and are dominated by the red noise spectrum (Fig. 4). The coherences between the oceanic transport and the transport at Trujillo and Callao are relatively low except at a few frequencies (Fig. 4) and the series are significantly out of phase. This implies that the inshore measures of wind and the oceanic measures contain quite different information about the environment.

Similarly, transport at Trujillo has significantly different dynamics than transport at Callao (Fig. 5). The spectrum of Trujillo transport has a more dominant red noise component, while the

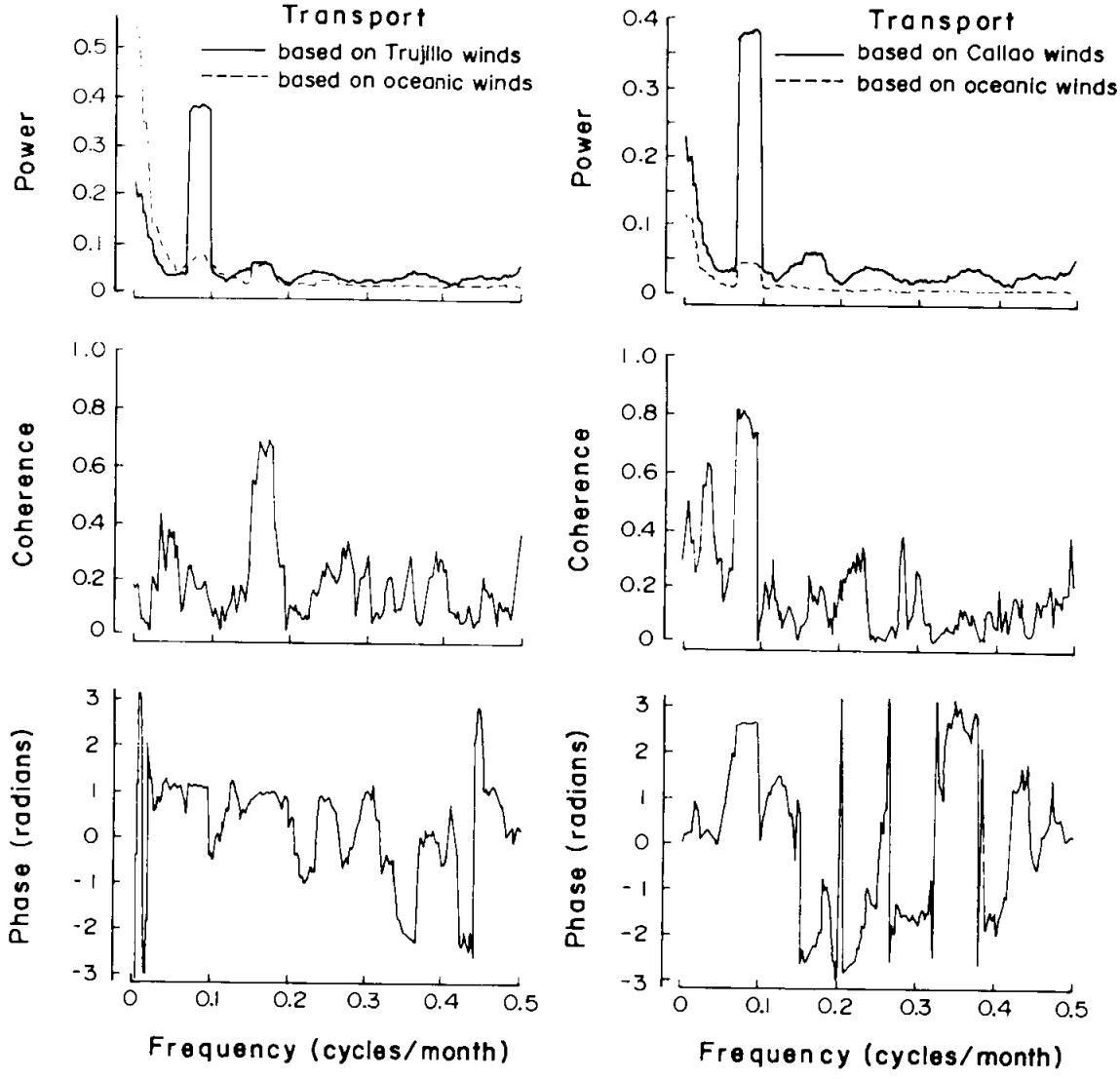

Fig. 4. Spectral analysis of transport off Peru (oceanic winds), Trujillo and Callao (local winds) transport.
Fig. 4. Análisis espectral del transporte frente a Perú (vientos oceánicos), transporte de Trujillo y Callao (vientos locales).

Callao transport has a relatively stronger seasonal cycle. The coherences are not particulary large, and the two series are significantly out of phase. A similar result is valid for the turbulence index at Trujillo and Callao (not shown). Thus, none of the three transport series closely reflects what is occurring in the other two series.

The SOI and oceanic transport have similar spectra, particularly at the yearly frequency and at a peak that would correspond roughly to the occurrence of El Niño (Fig. 5). The two series are highly coherent at these frequencies, and almost 180° out of phase. The same is not true of the SOI and Trujillo transport (Fig. 6), where the main coherence is at the half-yearly frequency. The SOI appears to be a significant advance indicator of what will happen offshore at the longer frequencies, but not of the more inshore behavior.

Long-term memory, if it exists in the ocean, has implications for forecasting too far ahead any process that depends on variables that exhibit this property. The more oceanic series, such as SOI and transport and turbulence calculated over the broad area, exhibit a similar, weak degree of long-term memory (Table 1). The more inshore measures exhibit a stronger long-term memory, approaching infinite variance. As I will be arguing that the more inshore environmental series are the most appropriate, the models involved will be using variables of limited predictability.

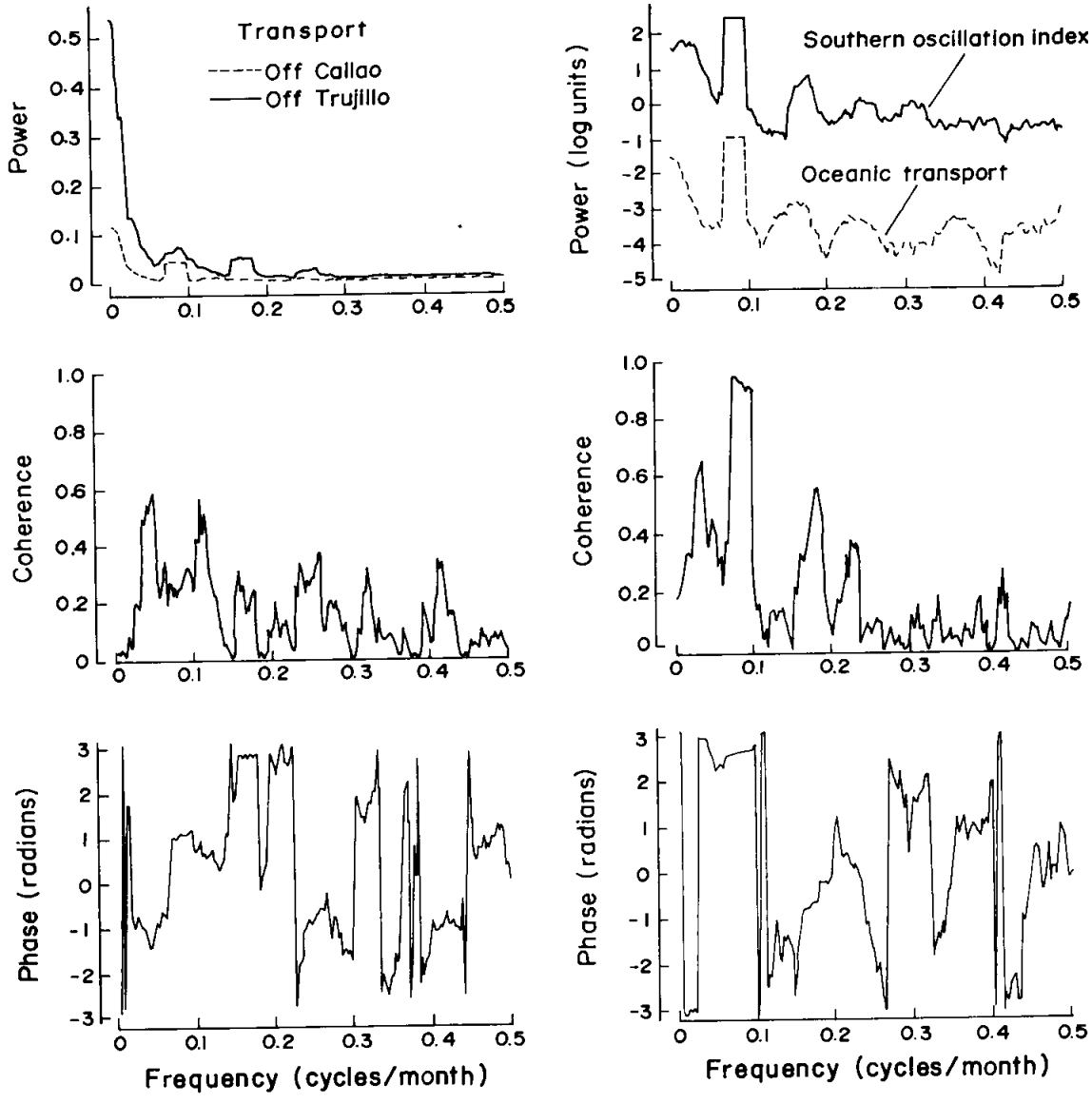

Fig. 5. Spectral analysis of local transport at Trujillo and Callao, of transport off Peru and of SOI.
Fig. 5. Análisis espectral del transporte local en Trujillo y Callao, del transporte frente a Perú y del Indice de Oscilación Sur (SOI).

Turbulence and transport, though both wind-induced, measure very different processes in terms of the anchoveta. If the wind does affect anchoveta recruitment, resolving if it is mainly through transport (most likely transporting larvae offshore) or mainly through turbulence (by affecting food availabilty to larvae) is an important issue. At Trujillo, transport and turbulence are highly coherent except at very high frequencies, and in phase at all frequencies (Fig. 6). As mentioned in M&M, the wind at Trujillo is predominantly from one direction, so that transport is close to wind speed squared, while turbulence is wind speed cubed. The difference in behavior at higher frequencies appears to be one of scale, where turbulence is more variable since it is the cube of the observed speed. As I will be using mostly non-linear techniques to model the data, this difference becomes negligible. (For example, on a log scale, the two series will differ by a multiplicative constant, which can be factored into the parameter on the series. This would not be the case if the wind varied greatly in its direction, so that the alonghore stress differed greatly from the wind speed squared). A similar result was found for Callao. Thus, though biologically there are significant differences between transport and turbulence, statistically for the inshore wind series, it will not be possible to discriminate if an effect is due to transport or turbulence.

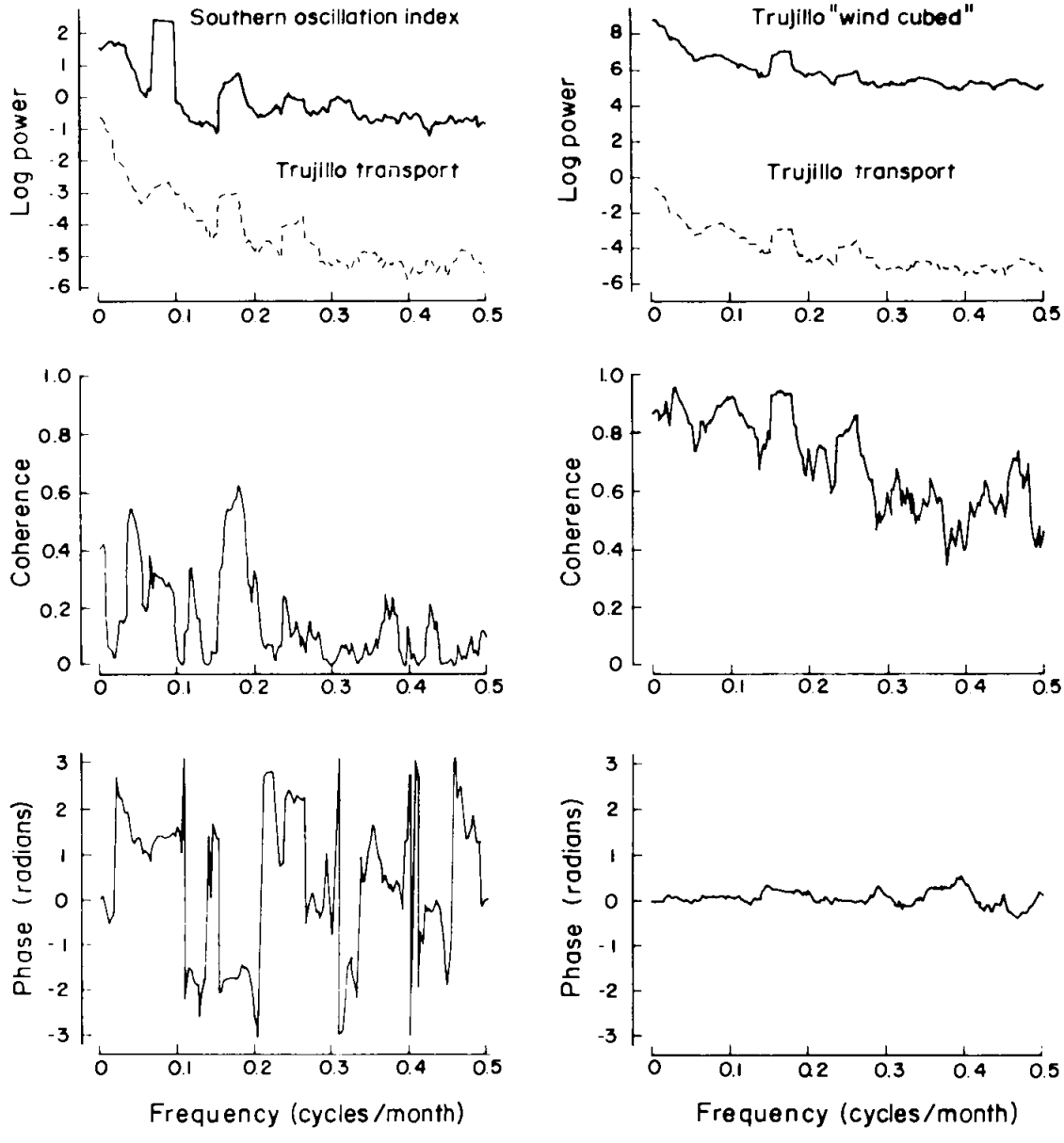

Fig. 6. Spectral analysis of SOI and transport off Trujillo, and of Trujillo transport and turbulence ("wind cubed").
Fig. 6. Análisis espectral del Indice de Oscilación Sur (SOI) y transporte de Trujillo, y del transporte y turbulencia ("viento al cubo") de Trujillo.

Table 1. Estimates of *d*, the fractional differencing parameter, in some environmental series off Peru.
Tabla 1. Estimaciones de d, *parámetro fraccionario diferencial, en algunas series ambientales frente al Perú.*

Series	Method: Geweke and Porter-Hudak (1983)	Method: Kashypa and Eom (1988)
Callao wind cubed	.554	.600
Callao transport	.592	.637
Trujillo wind cubed	.470	.509
Trujillo transport	.603	.652
Oceanic transport	.286	.310
Oceanic wind cubed	.210	.229
SOI	.340	.387

Biological Series

One of the obvious but major problems in studying fisheries is that it is rarely possible to obtain a reliable direct census of the fish population. Instead, "sampling" is used to obtain estimates. Usually the sampling scheme is of no statistical design, but instead depends on uncontrollable factors such as fishermen's behavior. The actual data, or the observables, are things like catch and effort statistics, length distributions, etc. While a variety of schemes have been devised to use this information to estimate characteristics of the population, the inescapable fact is that only the catch, effort, length distribution measurements, etc. are data, while the rest are estimates.

A property of calculating estimates from data is that degrees of freedom are used. In most cohort-analysis schemes, many degrees of freedom are used in calculating population and recruitment estimates. As the schemes are operating on autocorrelated data, they also act as filters on the observed data, changing the importance of different frequencies. When the same algorithm is used to jointly estimate many series, it is likely that just due to the estimation scheme, there will be a certain amount of cross-correlation in the resultant estimates.

It has been common to treat estimates of recruitments and of parents as data with the usual degrees of freedom. (Ultimately I will be forced to do the same (it is all there is to work with), but not without some careful checks on artificially-induced correlation.) In effect, when I use the recruitment estimates to estimate a relationship with another variable, I am fitting a composite function $f(g(x))$ of the original catch, effort and length data, where x is the original data, $g()$ is the operation performed by the cohort analysis, and $f()$ is the final relationship. If two intermediate estimates of this composite process exhibit a strong relationship, it cannot be said for certain that this relationship is real, or is just a product of the estimation scheme. Thus if parents and recruits are strongly related, it may be an artifice of cohort analysis. This will make it difficult to interpret many of the results to follow.

As mentioned previously, in attempting to correct for mortality other than from fishing, the resulting consumption estimates are functions of SST, and this feeds into the recruitment and parent estimates. Thus SST, and any variable highly correlated with SST, will have an unknown degree of spurious correlation with the population estimates. Most of the transport series display a reasonable degree of correlation with SST.

The new estimates of recruitment are shown on Fig. 7, along with the old ones. The new estimates exhibit less relative variation than do the original estimates, as was anticipated by Pauly (1987) who wrote that "it can be hypothesized that the [new] recruitment and biomass [....] will be somewhat smoother". Both series show an increase from 1957 to 1958, during El Niño, but in the original estimates this increase produced a change in mean level in both parent biomass and in recruitment, while in the new estimates the recruitment level drops right after the end of the El Niño. The new estimates start increasing from about 1963 to 1969-1970, after which both the new and old estimates show a similar decrease. The old estimates then show a more significant relative increase than do the new estimates. The parent biomass follows a similar pattern (Fig. 8).

The estimated AR component of the new recruitment estimates (Fig. 9) is relatively less variable than the AR component of the old estimates, particularly during the 1960s. The log of the ratio of recruits to parent biomass three months earlier (Fig. 10) is relatively constant except for the El Niño years of 1972 and 1982-1983. The ratio with the number of eggs shows a similar pattern (not shown), though the decrease during the 1972 El Niño is not as sharp. The spectrum of both the recruit series and the log of the recruits (Fig. 11), is dominated by a red noise component with a weak yearly signal.

The picture presented by these graphs is of a highly persistent, stable series where the only significant change occurred during a one or two year period around 1969. In fact, the trend in the new recruitment estimates mirrors closely what would be expected from the smoothed (5-year averaged) trends in catch and effort in Agüero (1987). After all the corrections, except for questions of scale, the recruitment estimates tend to mirror catch-per-unit-effort (C/f).

Some of the smoothness in the new recruitment estimates are due to mackerel consumption being a surrogate for SST (Pauly 1987). During El Niño years, for example, the catch rate tended to decrease. In the previous models, this results in variability in the recruitment estimate. In the

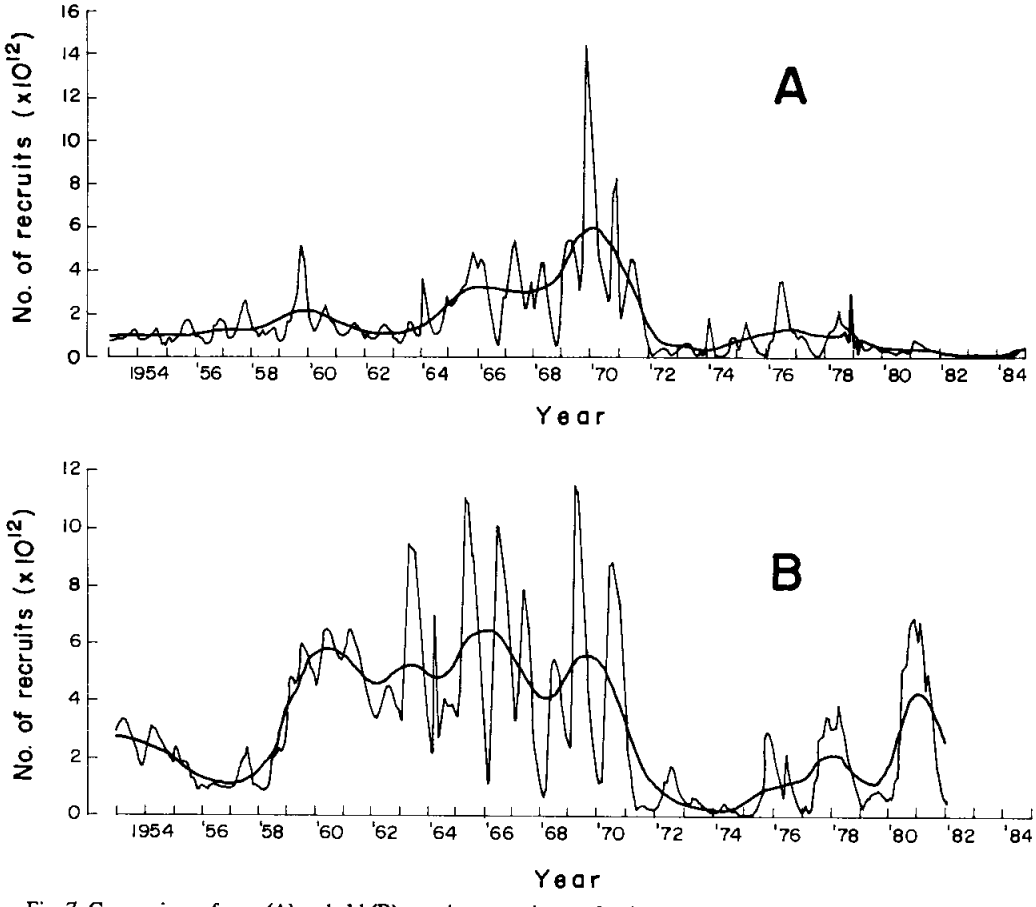

Fig. 7. Comparison of new (A) and old (B) recruitment estimates for the anchoveta, with estimated local trend lines.
Fig. 7. Comparación de las nuevas (A) estimaciones del reclutamiento de la anchoveta y los antiguos (B), con líneas de las tendencias locales estimadas.

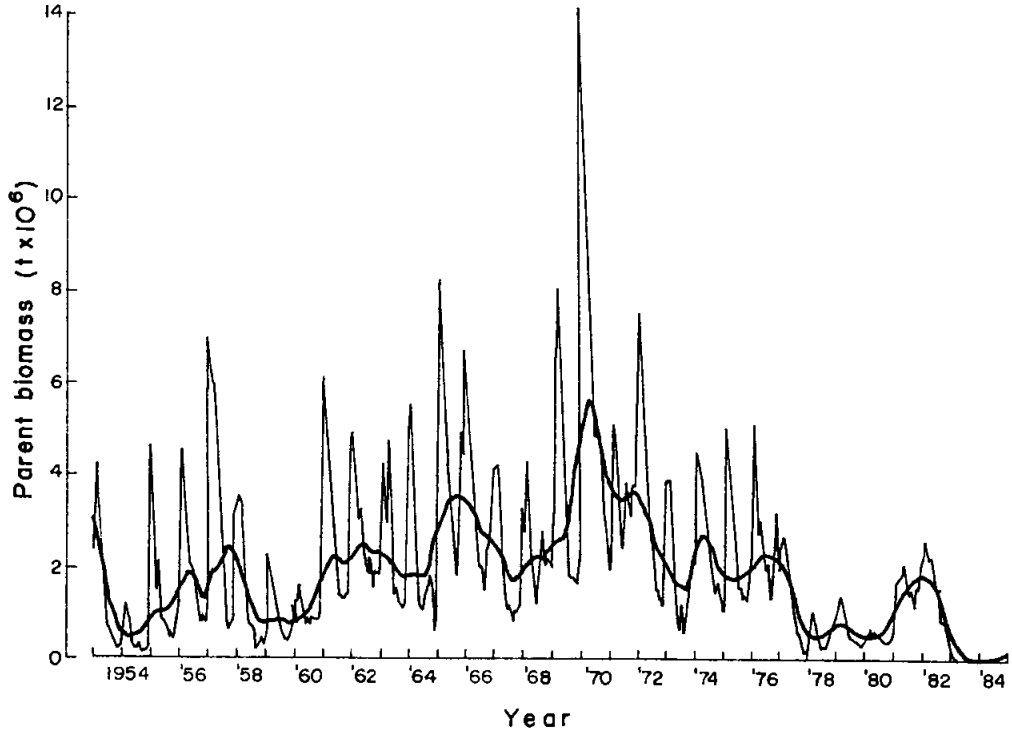

Fig. 8. New estimates of anchoveta parent biomass with estimated local trend.
Fig. 8. Nuevas estimaciones de la biomasa parental de anchoveta con estimación de la tendencia local.

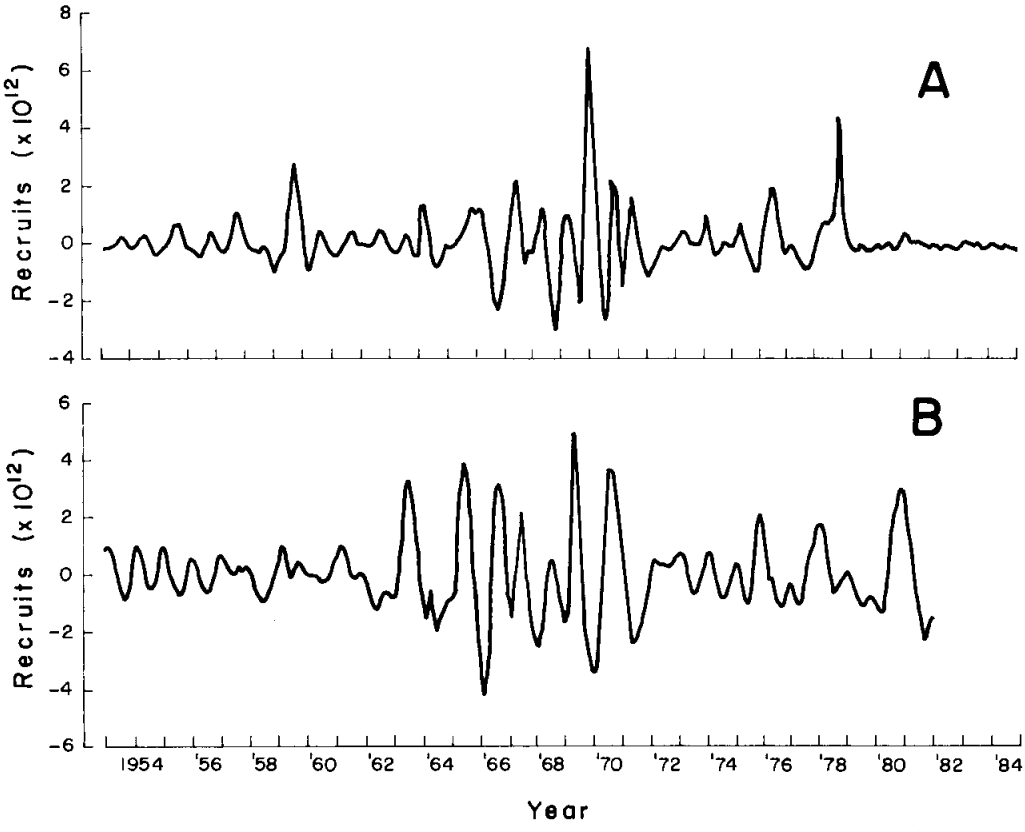

Fig. 9. Stationary (autoregressive) components of the new (A) and old (B) estimates of anchoveta recruitment.
Fig. 9. Componentes estacionarios (autoregresivo) de las nuevas (A) y antiguas (B) estimaciones del reclutamiento de anchoveta.

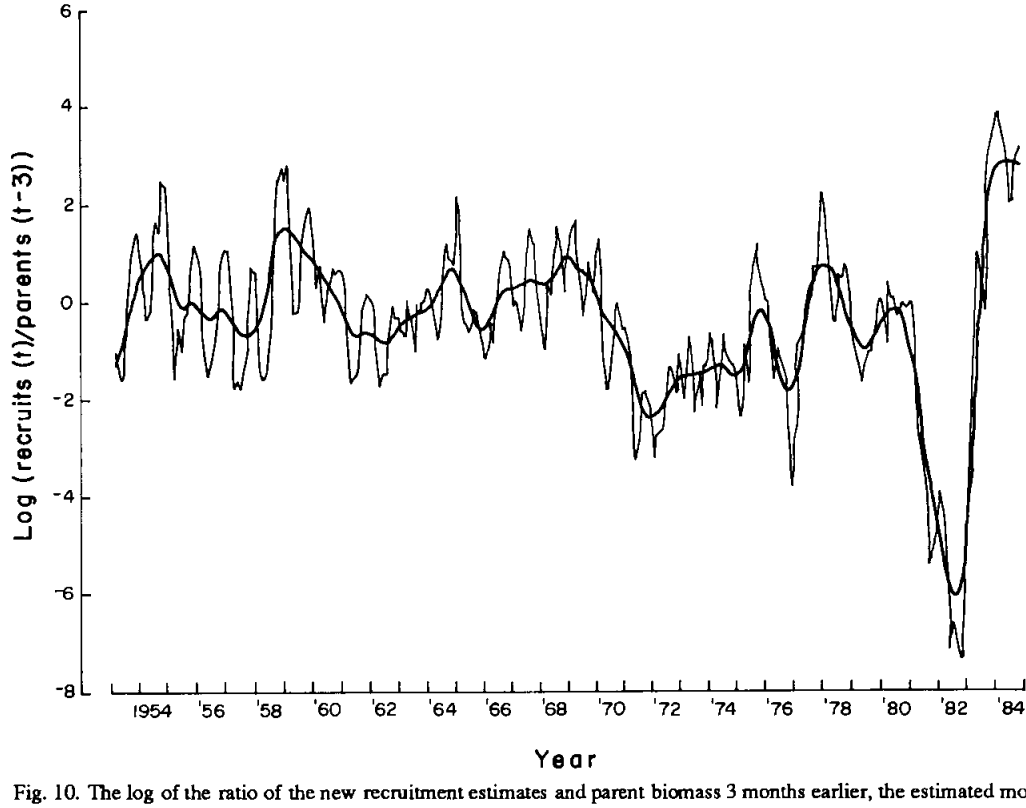

Fig. 10. The log of the ratio of the new recruitment estimates and parent biomass 3 months earlier, the estimated month of hatching.
Fig. 10. Logaritmo de la razón entre la nueva estimación de reclutamiento y biomasa de padres 3 meses antes (mes estimado de eclosión).

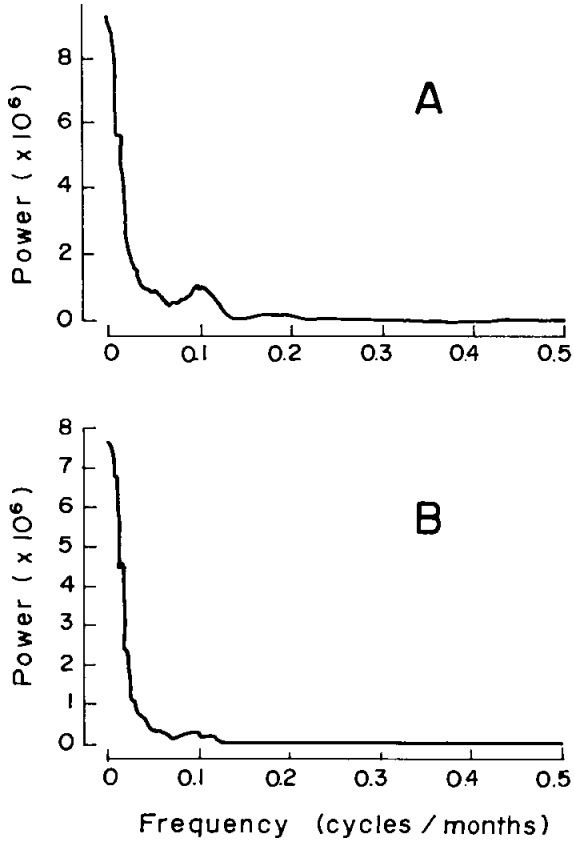

Fig. 11. Estimated power spectra for the new recruitment estimates (A) and for the log of the new recruitment estimates (B).

Fig. 11. Poder espectral estimado para las nuevas estimaciones de reclutamiento (A) y para el log de las nuevas estimaciones de reclutamiento (B).

new series, the mackerel are assumed to come closer to shore as SST warms, increasing mackerel consumption and thereby increasing the estimated population sizes. Mackerel consumption has prewhitened the inputs into the estimation algorithm based on the variation in SST. This does not necessarily mean that prewhitening the inputs is incorrect, but it does explain why there are such differences in the two sets of recruitment estimates.

Comparing the parent series (Fig. 8) with the ratio of recruits to parent biomass (Fig. 10), it is clear that the trend in the log of the ratio is largely explained by changes in the parent biomass, particularly if a mild density dependence is assumed. In the next section I will return to this point more formally, but it brings me back to the initial discussion of this section. If the estimated parent biomass and the estimated recruitment appear to be closely related, is it truly a feature of the population dynamics or a feature of the method that jointly estimates both series?

Data Analysis

In M&M it was found that the monthly recruitment estimates were so highly autocorrelated that it was necessary to examine the monthly series, mildly smoothed (two month nonoverlapping averages), across years. This allowed estimation of the interyear variability as well as to obtain some idea of the intrayear variability. The new recruitment estimates have an autocorrelation of .99 at a lag of 1 month. Even after first differencing, the series is still nonstationary, with the autocorrelations positive and significant at a lag of well over 20 months. This behavior in the autocorrelation function is expected, given the estimated spectrum of the series. Nonoverlapping averages can be formed to try to find a scale at which the series decorrelates and has a more stationary autocorrelation function. However, it is necessary to average almost on a yearly basis to achieve a reasonable degree of stationarity, at which point there is no reason to use anything except the yearly averages.

Following M&M, I have formed 2-month averages of recruitment and parent biomass, as December-January, February-March, etc. The value for December 1952-January 1953 is just the January value, as average, not total values, are used. Each of these series will be examined across

years. Senocak et al. (this vol.), based on the egg survey data in Santander (1987), show that the bulk of the egg distribution throughout the year is inshore rather than offshore. From 1961-1972, for most months the center of the egg distribution is more northerly, around Trujillo rather than Callao. From 1972 onward, the center shifts, being at many times evenly distributed along the coast from Trujillo to Callao, or in some months, clearly centered at Callao. Given the differences in the dynamics of the wind data series analyzed above, this argues for using either the Trujillo or Callao series. As Trujillo is more of a center of the egg distribution in these charts than is Callao, transport at Trujillo, as in M&M, will be used as the environmental variable. As mentioned previously, when a nonlinear analysis is used, this cannot readily be resolved from turbulence at the same location.

Additive models were estimated for the log of recruitment as the response variable, with parent biomass 2 averaged time periods prior (June-July parent biomass predicts October-November recruitment etc.) and Trujillo transport in the previous September and November as the predictor variables. The results in M&M, in Cury and Roy (1989), and the graphical results above all suggest that recruitment should be modeled on a log scale. The span for the transformations of the parent biomass were chosen using cross-validation, which explicitly calculates a tradeoff between the degrees of freedom and the variance of the fit. The estimated transformations of parent biomass (Fig. 12) are approximately that of a log transformation in each case. Thus on a log-log scale, for the period April through November, over 90% of the variance of the recruitment is explained by the parent biomass at the time of birth (Table 2).

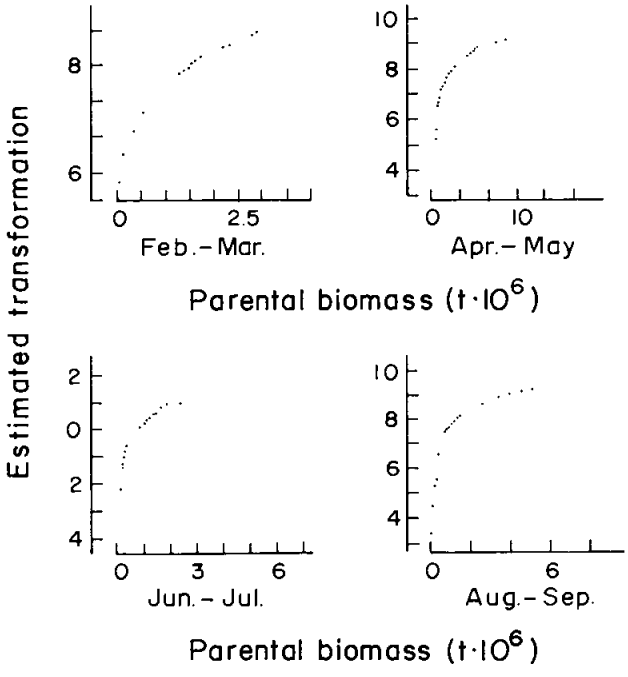

Fig. 12. Estimated transformations of the parent biomass when predicting anchoveta recruitment in a generalized additive model. All four transformations are close to a log transformation.
Fig. 12. Transformaciones estimadas de la biomasa parental cuando se pronostica el reclutamiento de anchoveta en un modelo aditivo generalizado. Las cuatro transformaciones son próximas a la transformacion logaritmica.

For the period from December through March, the estimated r^2 is around .60 (Table 3). The period from December through March is the period of lowest recruitment (Fig. 13A). Therefore the additive models work best during the most important periods of recruitment. On a log scale (Fig. 13B), the monthly recruitment values underline what I have said previously. Recruitment was fairly constant until 1969, with a big peak in 1969, followed by a drop to a new equilibrium

It is entirely possible that recruitment is tightly coupled to parent biomass as these models suggest. That then leaves open the question of why there was such a large parent biomass in 1969. Certainly the recruitment feeding into that year was nothing special compared to previous years; and graphs of the possible environmental factors by month (not shown), do not reveal anything unusual at this time period. The other possibility, of course, is that this is a feature of jointly estimating parents and recruits on such a fine time scale. The added degrees of freedom seemingly brought about from monthly recruitment estimates, at least for the purposes of this

Table 2. Analysis of Deviance for Recruitment-Parent Biomass Models, April-November.
Tabla 2. Análisis de desviaciones para el modelo de Reclutamiento-Biomasa parental, Abril-Noviembre.

response variable .... April-May Recruits
deviance = 10.577 # iterations = 1 #smooths/variable =, 1
average deviance = .353
dof of deviance 26.77 scale estimate .395
r square = 84.01% of a null deviance of 66.169

span	dof	slope	name
--	1	7.3602	s0---the intercept term
.60	2.234	smooth	cv: Dec-Jan Parent Biomass

response variable .... June-July Recruits
deviance = 2.966 # iterations = 1
#smooths/variable =, 1
average deviance = .099
dof of deviance 24.83 scale estimate .119
r square = 95.67% of a null deviance of 68.493

span	dof	slope	name
--	1	7.4202	s0---the intercept term
.30	4.166	smooth	cv: Feb-Mar Parent Biomass

response variable .... August-September Recruits
deviance = 1.569 # iterations = 1
#smooths/variable =, 1
average deviance = .052
dof of deviance 24.67 scale estimate .064
r square = 97.73% of a null deviance of 69.229

span	dof	slope	name
--	1	7.4654	s0---the intercept term
.30	4.331	smooth	cv: Apr-May parent Biomass

response variable .... October-November Recruits
deviance = 5.830 # iterations = 1
#smooths/variable =, 1
average deviance = .194
dof of deviance 24.78 scale estimate .235
r square = 92.62% of a null deviance of 79.032

span	dof	slope	name
--	1	7.3894	s0---the intercept term
.30	4.220	smooth	cv: Jun-Jul Parent Biomass

Table 3. Analysis of Deviance for Recruitment-Parent Biomass Models, December-March.
Tabla 3. Análisis de desviaciones para el modelo de Reclutamiento-Biomasa parental, Diciembre-Marzo.

response variable .... December-January Recruits
deviance = 28.488 # iterations = 1
#smooths/variable =, 1
average deviance = .950
dof of deviance 26.74 scale estimate 1.065
r square = 60.05% of a null deviance of 71.313

span	dof	slope	name
--	1	7.2947	s0---the intercept term
.70	2.257	smooth	cv: Aug-Sep Parent Biomass

response variable .... February-March Recruits
deviance = 26.553 # iterations = 1
#smooths/variable =, 1
average deviance = .885
dof of deviance 26.90 scale estimate .987
r square = 59.44% of a null deviance of 65.465

span	dof	slope	name
--	1	7.3055	s0---the intercept term
.60	2.097	smooth	cv: October-November Parent Biomass

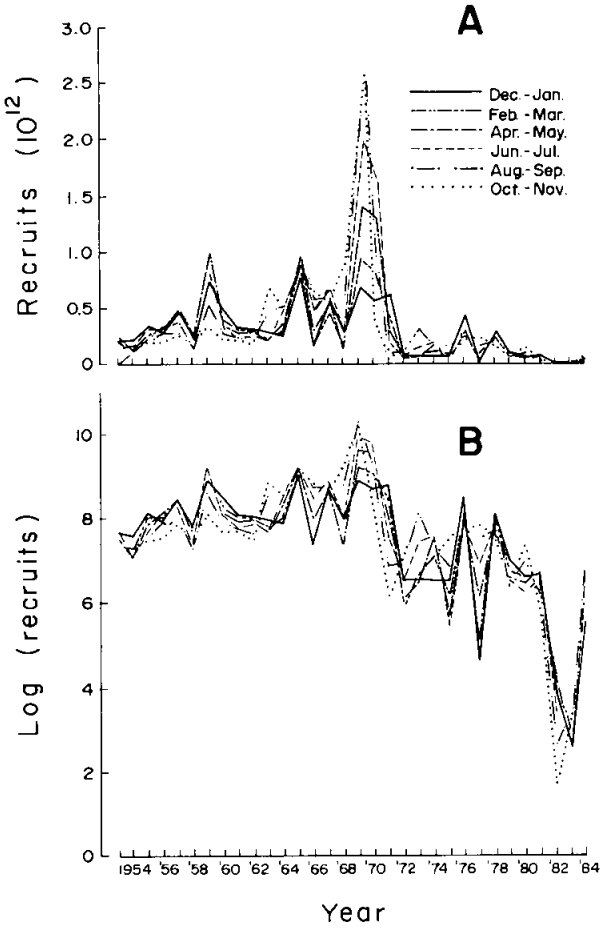

Fig. 13. Time series of bimonthly anchoveta recruitment and the log of bimonthly anchoveta recruitment.

Fig. 13. Serie de tiempo de reclutamiento bimensual de la anchoveta y el logaritmo del reclutamiento bimensual.

paper, do not seem to be there. It appears that all the adjustments in the estimates, while perhaps revealing interesting features in the dynamics of anchoveta recruitment, have also limited the amount of independence in the data.

Cury and Roy (1989) estimate transformations for the yearly averages for the old estimates using the ACE algorithm of Breiman and Friedman (1985). For completeness, I have redone this for the new recruitment estimates (Fig. 14A). Cury and Roy's basic conclusions remain unchanged. The ACE algorithm does not provide an analysis of variance, and given the correlation between transport and turbulence at Trujillo, starting with the variable of lower dimension appears wise. For this reason I refit this model using generalized additive models.

The analysis of deviance for a span of .20 (Table 4) shows that the single best predictor is transport, which for this choice of span explains 60% of the variance. With so few data points, the fit does vary with the choice of span, from roughly 50% to 60%. In all cases, however, the fit due to transport was much higher than that due to parent biomass. When both variables are included, the r^2 increases to .78, which suggests that there is also strong intercorrelation between the parent biomass estimate and turbulence. The range of r^2 for different values of the span was .68 to .78.

The estimated transformations (Figs. 14B and 14C) for both variables resemble a log transformation, and the 95% confidence intervals (Hastie and Tibshirani 1985) are reasonably tight around the mean and preserve the same shape. While the choice of span affects the estimated degrees of freedom, the shape of the transformation is unaffected by the choice of span.

The effect of the transformations can also be viewed by fitting a smoothed surface to the 3-dimensional data (Fig. 15). (This is also a phase plot of recruitment for both datasets). The transformed surface is unimodal and smoother. It is clear that the relationships on the raw scale are nonlinear, while those on the transformed scale are linear in each dimension. While the model is only an additive approximation, it has caught the essence of what information is contained in the data.

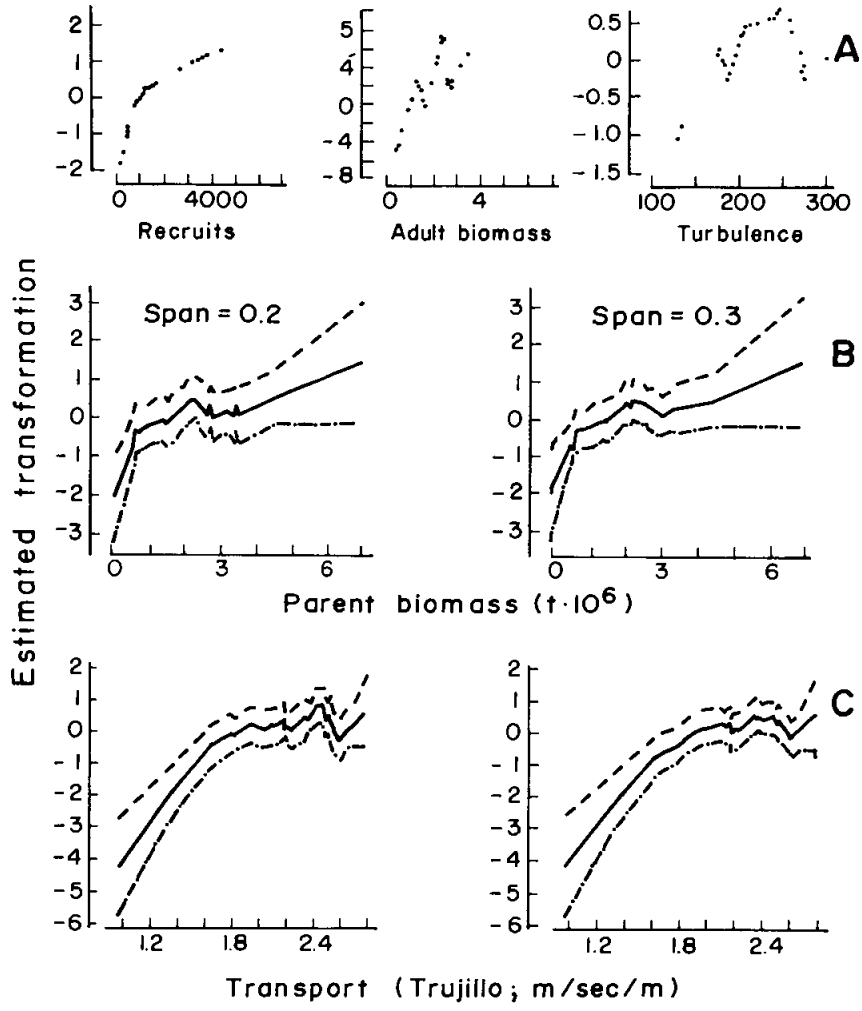

Fig. 14. Estimated transformations (A) from the ACE algorithm, redoing the analysis of Cury and Roy (1989) for the new recruitment estimates. (B) Parent biomass in a generalized additive model for predicting yearly anchoveta recruitment. Dashed lines are 95% confidence intervals for the transformations. (C) Trujillo transport in a generalized additive model for predicting yearly anchoveta recruitment. Dashed lines are 95% confidence intervals for the transformations.

Fig. 14. Transformaciones estimadas (A) del algoritmo ACE, rehaciendo el análisis de Cury y Roy (1989) para las nuevas estimaciones del reclutamiento. (B) Biomasa parental en un modelo aditivo generalizado para predecir el reclutamiento anual de la anchoveta. Las lineas punteadas representan el intervalo de confianza del 95% para las transformaciones. (C) Transporte de Trujillo en un modelo aditivo generalizado para predecir el reclutamiento anual de la anchoveta. Las lineas punteadas representan el intervalo de confianza del 95% para las transformaciones.

Discussion

I have shown that the new estimates of recruitment are much smoother than the previous estimates, with different trends, except for the sharp decrease following 1969 evident in both sets of estimates. Part of the difference between the two sets of recruitment estimates appears to be due to the fact that several estimates of anchoveta consumption, particularly that for mackerel, are surrogates for SST and tend to cause the recruitment estimates to be filtered (smoothed) based on the variation in the SST series.

The new recruitment estimates, even more so than the previous estimates, are highly autocorrelated, even after differencing. Essentially all of the variance in the monthly recruitment series can be modeled by a simple AR(1) model. It is questionable that this represents the true dynamics of recruitment, and certainly would follow, rather than predict, any sudden changes in the population dynamics. Nonoverlapping time averaging requires forming yearly averages to achieve a satisfactory level of stationarity.

Table 4. Analysis of Deviance for Recruit-Parents-Transport Model, Yearly Data.
Tabla 4. Análisis de desviaciones para el modelo de Reclutamiento-Padres-Transporte, datos anuales.

response variable .... LOG (RECRUITS)
deviance = 32.239 # iterations = 1
#smooths/variable =, 1
average deviance = 1.007
dof of deviance 25.27 scale estimate 1.276
r square = 45.37% of a null deviance of 59.017

span	dof	slope	name
--	1	6.8277	s0---the intercept term
.20	5.729	smooth	PARENT BIOMASS

response variable .... LOG (RECRUITS)
deviance = 22.121 # iterations = 1
#smooths/variable =, 1
average deviance = .691
dof of deviance 25.57 scale estimate .865
r square = 62.52% of a null deviance of 59.017

span	dof	slope	name
--	1	6.8277	s0---the intercept term
.20	5.435	smooth	TRANSPORT

response variable .... LOG (RECRUITS)
deviance = 12.714 # iterations= 1
#smooths/variable =, 6
average deviance = .397
dof of deviance 19.84 scale estimate .641
r square = 78.46% of a null deviance of 59.017

span	dof	slope	name
--	1	6.8277	s0---the intercept term
.20	5.729	smooth	PARENT BIOMASS
.20	5.435	smooth	TRANSPORT

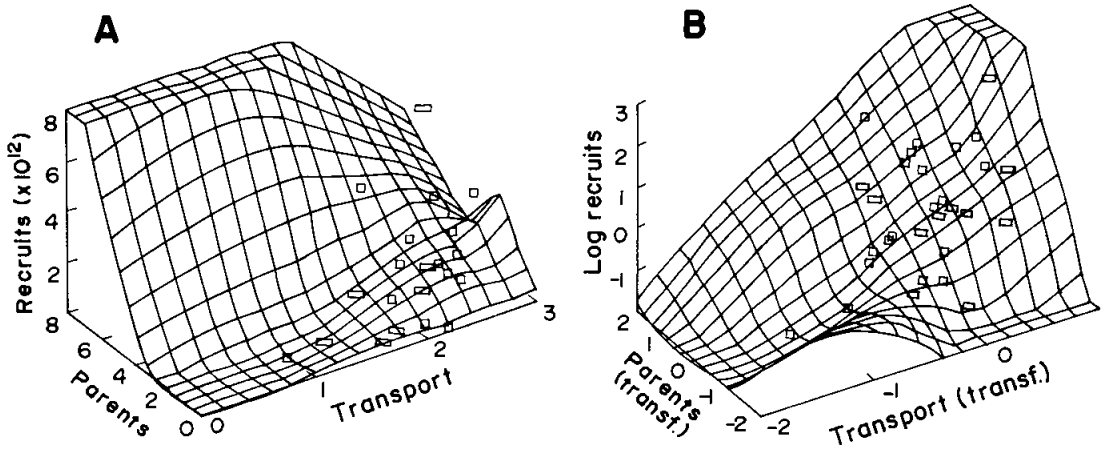

Fig. 15. Estimated smoothed surfaces for (A) yearly anchoveta recruitment, yearly parent biomass and Trujillo transport and (B) the estimated transformed data for the same variables. The small rectangles are the observed points. The effective linearization brought about by the transformations is immediate.
Fig. 15. Superficies suavizadas estimadas para (A) reclutamiento anual de la anchoveta, biomasa parental anual y transporte en Trujillo y (B) estimado de los datos transformados para las mismas variables. Los rectángulos pequeños son los puntos observados. La linealización efectiva producida por las transformaciones es inmediata.

Bimonthly averages of recruitment, viewed across years, are extremely correlated with the log of parent biomass when the recruits were born. The high degree of fit is suspicious, and may be due to the fact that both series were jointly estimated. This left little choice but to analyze yearly averages.

A generalized additive model was then estimated for the yearly averages, using the average parent biomass over the year, and the average transport at Trujillo. The resulting estimates suggest that on a nonlinear scale, about 75% of the variance in the recruitment estimates can be explained by these two series. The analysis suggests that large parent biomass, and a reasonable level of transport produce the best recruitment. Evidence is presented that these nonlinear estimates are relatively stable.

Parrish et al. (1984) argue that transport should be an important variable in the Peruvian system, but due to the dominance of wind in a single direction, it is not possible to resolve whether it is transport, turbulence or some combination of the two (as argued by Cury and Roy 1989) affecting the fish. Even at the yearly scale it is not possible to say what part of the relationship between the parent biomass and the recruitment estimates are due to correlation from their joint estimation. This is compounded by the fact that transport is correlated with SST, and all the population estimates have been influenced by changes in SST.

Unlike in M&M, the present model, if valid, has much explanatory power but little predictive use since all terms are contemporaneous and are averaged over a year. It may well be possible to construct models that will forecast using lagged terms to approximate the proper model, but it would be premature to do so at this time. More important at the moment is to study the various methods of cohort analysis to obtain either theoretical or empirical estimates of the expected cross-correlation functions between recruits and parents due to the fact that they are being jointly estimated in a model that uses up most of the degrees of freedom in the data. (Simulations based on model-generated data with recruitment a random variable, possibly autocorrelated, could give estimates of the expected level of correlation when none is present.) Further, some estimates of the likely base level of correlation with any environmental variable correlated with SST should also be ascertained.

With these results, more valid estimates of significance of a model would be possible. The yearly model in this paper, on the surface, has an intuitive biological interpretation, but this does not guarantee its validity. If all the new population estimates are valid, the existing interpretations of what has occurred in the anchoveta fishery would have to be greatly modified. The new estimates suggest a population that essentially stays in equilibrium until some single event changes the mean level. A new mean level is then found, until another shock comes to the system. The most likely cause of these shocks are environmental changes, but as examined here and in Bohle-Carbonell (this vol.), the environment around Peru exhibits long-term memory, so that monitoring of the environment would have to become an important part of the predictive process.

This implies that once local mechanistic models can be validated, then the use of surrogate variables, such as SOI, that may "monitor" the ocean further ahead, could be useful in forming a predictive model. I have not examined this possibility in detail, but I have presented evidence based on the interrelationship between the SOI and oceanic transport, that this longer lead prediction is at least physically plausible.

Acknowledgements

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References

Akaike, H. 1977. On entropy maximisation principle, p. 27-41. *In* P.R. Krishnaiah (ed.) Applications of Statistics. North-Holland, Amsterdam.

Agüero, M. 1987. A bioeconomic model of the Peruvian pelagic fishery, p. 307-324. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953-84, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bakun, A. and R.H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. CalCOFI Rep. 23: 99-112.

Bloomfield, P. 1976. Fourier analysis of time series: an introduction. John Wiley and Sons, New York. 258 p.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984, p. 14-45. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Breiman, L. and J.H. Friedman. 1985. Estimating optimal transformations for multiple regression and correlation (with discussion). J. Am. Stat. Assoc. 80: 580-619.

Cleveland, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Am. Stat. Assoc. 74: 829-836.

Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. and Aquat. Sci. 44: 670-680.

Geweke, J. and S. Porter-Hudak. 1983. The estimation and application of long memory time series models. J. Time Series Anal. 4: 221-238.

Granger, C.W.G. and R. Joyeux. 1980. An introduction to long memory time series models and fractional differencing. J. Time Series Anal. 1: 15-29.

Hastie, T. 1987. A closer look at deviance. The Am. Stat. 41: 16-20.

Hastie, T. and R. Tibshirani. 1985. Generalized additive models: some applications, p. 66-81. *In* R. Gilchrist, B. Francis, and J. Whittaker (eds.) Generalized Linear Models. Springer-Verlag Lecture Notes in Statistics 32. Springer, New York.

Hastie, T. and R. Tibshirani. 1986. Generalized additive models (with discussion). Statistical Science 1: 297-318

Hosking, J.R.M. 1981. Fractional differencing. Biometrika 68: 165-176.

Hurst, H.E. 1951. Long term storage capacity of reservoirs. Trans Am. Soc. Civil. Engrs. 116: 770-799.

Kashypa, R.L. and Kie-Bum Eom. 1988. Estimation in long-memory time series models. J. Time Series Anal. 9: 35-42.

Kitagawa, G. and W. Gersch. 1984. A smoothness priors - state space modeling of time series with trend and seasonality. J. Am. Stat. Assoc. 79: 378-389.

Kohn, R. and C.F. Ansley. 1988. The equivalence between Bayesian smoothness priors and optimal smoothing for function estimation, p. 393-430. *In* J. Spell (ed.) Bayesian Analysis of Time Series and Dynamic Models, Marcel Dekker, New York.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 173:212-230.

Mandelbrot, B.B. 1971. A fast fractional Gaussian noise generator. Water Resour. Res. 7: 543-553.

Mandelbrot, B.B. 1983. The Fractal Geometry of Nature. W.H. Freeman and Company, New York. 468 p.

Mandelbrot, B.B. and J.W. Van Ness. 1968. Fractional Brownian motion, fractional noises and applications. SIAM Review 10: 422-437.

Mendo, J., L. Pizarro and S. Castillo. 1987. Monthly turbulence and Ekman transport indexes, 1953 to 1985, based on local wind records from Trujillo and Callao, Peru. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling Ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and H. Fuentes. 1987. Sea Lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and G. Sánchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. 1987. Managing the Peruvian upwelling ecosystem: a synthesis, p. 325-342. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., A. Ch. Vildoso, J. Mejía, M. Samamé and M.L. Palomares. 1987. Population dynamics and estimated anchoveta consumption of bonito *(Sarda chiliensis)* off Peru, 1953-1982, p. 248-267. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Parrish, R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1984. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction, p. 731-777. *In* G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species of Neritic Fish Resources. San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291 (Vol. 3).

Porter-Hudak, S.L. 1982. Long-term memory modeling - a simplified approach. Ph.D. thesis, Dept. of Statistics, University of Wisconsin, Madison.

Santander, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru, 4-14 S. p. 179-207. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Schwarz, G. 1978. Estimating the dimension of a model. Ann. Statist. 6: 461-464.

Major Trends in the Pelagic Ecosystem off Peru and Their Implications for Management*

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Abstract

This paper summarizes the observations on changes in biomass, individual growth, species dominance, feeding strategy and oceanographic parameters reported from the Peruvian upwelling ecosystem from 1953 to 1987. It is concluded that overfishing of the Peruvian anchoveta (*Engraulis ringens*) is the key factor behind the observed biomass changes in all important species in the system. The hypothesis is presented that stronger exploitation of horse mackerel (*Trachurus murphyi*), a major anchoveta predator, could help alleviate the present disequilibrium between predators and prey fishes, and lead to higher sustained multispecies yield.

Resumen

Esta contribución sumariza las observaciones sobre cambios en biomasa, crecimiento individual, dominancia de especies, estrategia de alimentación y parámetros oceanográficos del ecosistema de afloramiento peruano reportados de 1953 a 1987. Se concluye que la sobrepesca de la anchoveta peruana (*Engraulis ringens*) es el factor determinante en los cambios de biomasa observados en todas las especies importantes del sistema. Se presenta la hipótesis de que una más fuerte explotación del jurel (*Trachurus murphyi*), un gran predador de la anchoveta, ayudaría a aliviar el desequilibrio actual entre los peces predadores y presa, y conducir a un mayor rendimiento sostenido multiespecifico.

Introduction

This contribution presents a review of the major trends of biotic and abiotic factors in the Peruvian upwelling ecosystem, for the years 1953 to 1987, based on the time series data in Pauly and Tsukayama (1987) and ancillary data recently collected by IMARPE and PROCOPA staff.

The aim of this contribution is to enable fishery scientists and managers to obtain an understanding of the complexity of, and of the interactions within the Peruvian upwelling ecosystem. Such understanding is necessary for economic management of the Peruvian pelagic fisheries, which are linked to the marine ecosystem through various feedback loops.

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*PROCOPA Contribution No. 90.

Materials and Methods

The following atmospheric and oceanographic parameters are available as monthly time series, for the period 1953 to 1982 or later:

- Solar radiation (Bakun 1987)
- Atmospheric pressure (Bakun 1987)
- Southern Oscillation Index (Brainard and McLain 1987)
- Total cloud amount (Bakun 1987)
- Wind stress on sea surface (Bakun 1987)
- Offshore Ekman transport (i.e., upwelling) (Mendo et al. 1987; Bakun and Mendelssohn, this vol.)
- Offshore Ekman velocity (Bakun 1987)
- Turbulence (Bakun 1987; Mendo et al.1987)
- Sea surface temperature (Pauly and Tsukayama 1987b; Bakun 1987; Tsukayama, this vol.)
- Depth of SST -2°C (Brainard and McLain 1987)
- Depth of SST -14°C, i.e, thermocline (Brainard and McLain 1987)
- Radiative heat loss (Bakun 1987)
- Evaporative heat loss (Bakun 1987)
- Net heat exchange (Bakun 1987)
- Heat content to depth of SST -2°C (Brainard and McLain 1987)
- Potential new primary production (Chavez et al., this vol.; Mendo et al., this vol.).

Table 1 summarizes the time series data of biomass used here for inferences concerning the major species of fish, mammals and birds inhabiting the Peruvian upwelling ecosystem. Table 2 summarizes some fishery statistics, to be discussed further below as well as some of the abovementioned oceanographic time series, all put on an annual basis.

These data refer to the area off Peru ranging from 4°-14°S, and about 75 km offshore. This area of approximately 100,000 km^2 shall be called here the Main Anchoveta (distribution) Area, or MAR.

The "match" between time series was quantified using two approaches. The first of these was to convert the time series in Tables 1 and 2 into series of signs, depending on whether interannual changes reflected an increase (+) or a decrease (-). Testing was based on the assumption that when there is no significant match between two time series, the occurrence of each of the four possible combinations of signs (- -; + +; + - and - +) should be equal. Or more generally: the sum of pairs with different signs (- + or + -) should be equal to the sum of pairs with the same sign (- - or + +); this can be tested using a chi-square test.

The other approach, also based on counting signs, involved the definition of a degree of coincidence (DC), computed from

$$DC = | 50 - Obs | \qquad ...1)$$

where 50 refers to the expected percentage of - - or + + pairs for interyear changes, and Obs refers to the observed percentage of such pairs. DC thus has a value of 50 when all (i.e., 100%) of the paired signs are of the type + -, - + or + +, - -, and a value of zero when the paired signs are equal in numbers. DC values have been estimated for lags of 0 and 1 year.

Results and Discussion

Means and Coefficients of Variation

Table 1 and Fig. 1 show that the MAR was (and in fact still is) dominated by anchoveta, followed by sardine and horse mackerel, each of them representing about 25% of the biomass of anchoveta. Hake and mackerel, finally contribute(d) about 10% of the biomass of anchoveta.

The biomass of bonito, guano birds (three species) and pinnipeds (two species) are, in this context, negligibly small: each of them contributed less than 1% of the biomass of anchoveta.

Table 1. Annual time series of the biomasses of major elements of the Peruvian upwelling ecosystem (adjusted to 4-14°S), as used to discuss trends.
Tabla 1. Series de tiempo anuales de la biomasa de los principales elementos del ecosistema de afloramiento peruano (ajustados a 4-14°S), usados para discutir tendencias.

Year	A	B	C	D	E	F	G	H	I	J	K	L	M
1953	6.10	1.66	0.064	0.23	1.04	0.270	0.310	0.018	27.20	2.55	2.38	9.36	9.39
1954	9.51	1.05	0.065	0.16	0.73	0.260	0.340	0.020	40.80	3.06	2.94	11.77	11.82
1955	8.28	1.27	0.064	0.18	0.82	0.230	0.360	0.023	40.00	3.47	3.24	10.84	10.89
1956	5.07	1.84	0.061	0.19	0.88	0.210	0.390	0.027	34.30	3.49	2.69	8.25	8.29
1957	2.90	2.23	0.052	0.28	1.25	0.250	0.410	0.030	17.90	1.69	0.94	6.96	6.98
1958	3.75	2.08	0.051	0.23	1.05	0.260	0.440	0.035	12.30	1.50	1.37	7.42	7.43
1959	7.42	1.42	0.056	0.21	0.97	0.190	0.470	0.041	22.40	1.86	2.86	10.27	10.29
1960	11.9	0.620	0.053	0.19	0.85	0.210	0.510	0.048	21.00	2.30	2.39	13.84	13.87
1961	16.7	0.300	0.048	0.19	0.87	0.240	0.540	0.055	26.50	2.29	1.89	18.37	18.40
1962	14.9	0.300	0.046	0.18	0.80	0.400	0.580	0.064	25.20	2.55	1.65	16.59	16.62
1963	13.3	0.370	0.046	0.20	0.89	0.450	0.620	0.075	21.10	2.16	1.87	15.24	15.27
1964	14.4	0.300	0.050	0.17	0.76	0.490	0.670	0.088	25.80	2.41	1.47	16.16	16.19
1965	13.3	0.380	0.046	0.24	1.06	0.470	0.720	0.102	7.50	1.46	2.00	15.46	15.47
1966	15.5	0.300	0.049	0.19	0.84	0.450	0.770	0.119	4.40	1.45	1.39	17.34	17.35
1967	19.0	0.300	0.044	0.17	0.75	0.430	0.820	0.139	5.50	1.32	2.27	20.69	20.70
1968	13.1	0.300	0.040	0.16	0.74	0.370	0.880	0.149	5.80	1.47	1.99	14.68	14.69
1969	13.6	0.320	0.029	0.22	1.00	0.320	0.950	0.144	3.70	1.65	1.00	15.48	15.49
1970	14.7	0.300	0.020	0.20	0.92	0.280	1.02	0.140	4.00	1.65	1.36	16.46	16.47
1971	13.8	0.300	0.017	0.21	0.93	0.200	1.09	0.126	5.90	1.91	1.21	15.41	15.42
1972	3.16	2.18	0.020	0.29	1.32	0.260	1.14	0.112	2.10	0.97	1.30	7.24	7.24
1973	3.14	2.18	0.021	0.20	0.92	0.410	1.18	0.118	1.40	1.15	1.30	6.88	6.88
1974	3.46	2.13	0.019	0.19	0.83	0.380	1.18	0.124	1.60	1.69	1.32	7.01	7.01
1975	2.83	2.24	0.011	0.18	0.82	0.360	1.18	0.133	2.00	1.73	0.60	6.44	6.45
1976	4.26	1.98	0.004	0.25	1.11	0.500	1.22	0.156	1.70	1.70	0.71	8.11	8.12
1977	1.25	2.52	0.001	0.22	0.99	0.610	1.30	0.183	2.20	1.96	0.78	5.59	5.60
1978	3.98	2.03	0.001	0.19	0.85	0.670	1.37	0.210	2.20	2.97	1.78	7.72	7.73
1979	1.45	2.49	0.001	0.20	0.90	0.360	1.46	0.241	3.40	2.30	1.86	5.40	5.41
1980	2.71	2.57	0.001	0.20	0.89	0.320	1.58	0.282	4.10	2.18	1.21	4.97	4.98
1981	1.00	2.57	0.001	0.19	0.84	0.180	1.70	0.332	5.40	2.50	0.96	4.77	4.78
1982	1.00	2.57	0.002	0.22	1.01	0.150	1.81	0.386	6.10	2.33	1.10	4.95	4.96
1983	1.00	4.84	0.003	0.37	1.68	0.240	1.71	0.260	4.21	2.15	1.33	8.13	8.14
1984	1.25	4.13	0.004	0.17	0.77	0.350	1.75	0.230	2.29	1.97	1.56	6.67	6.68
1985	5.43	2.10	0.004	0.16	0.70	0.500	1.81	0.386	2.31	1.80	2.11	9.66	9.67
1986	3.13	2.36	-	0.18	0.81	0.700	1.81	0.386	1.66	2.10	2.64	6.91	6.91
1987	0.70	3.80	-	0.24	1.07	0.770	1.81	0.386	2.26	2.23	2.24	6.93	6.93
1988	3.77	4.54	-	-	-	-	-	-	-	-	-	-	-
Mean	7.24	1.75	0.03	0.21	0.93	0.364	1.03	0.15	11.32	2.06	1.71	10.51	10.53
s.d.	5.58	1.26	0.02	0.04	0.19	0.153	0.50	0.11	11.85	0.58	0.67	4.56	4.57
C.V.	77.1	72.0	76.4	20.3	20.3	42.0	48.9	74.2	104.7	28.4	39.1	43.4	43.4

A = anchoveta *Engraulis ringens*; 1953 to 1980: based on VPA (from Pauly et al. 1987a); 1980-1983 interpolated; 1984-1987 based on echoacoustics (from Vilchez et al. 1988); 1988 based on echoacoustics (IMARPE, unpublished); in $t*10^6$.
B = sardine *Sardinops sagax*; 1953 to 1982 based on egg surveys (from Muck et al. 1987); 1983-1987 based on echoacoustics (from Vilchez et al. 1988); 1988 based on echoacoustics (IMARPE, unpublished); in $t*10^6$.
C = bonito *Sarda chiliensis*; 1953-1982 based on catch and ancillary data on "large" bonito (from Pauly et al. 1987b); 1983-1987: based on IMARPE catch data; in $t*10^6$.
D = nearshore (≤ 75 km) population of mackerel *Scomber japonicus*; based on larval survey, acoustics and population model (from Muck et al. 1987 and Muck and Sanchez 1987); in $t*10^6$.
E = nearshore (≤ 75 km) population of horse mackerel *Trachurus murphyi*; based on larval survey, acoustics and population model (from Muck et al. 1987 and Muck and Sanchez 1987); in $t*10^6$.
F = hake *Merluccius gayi*; based on VPA (from Espino and Wosnitza-Mendo, this vol.); in $t*10^6$.
G = sea lion *Otaria byronia* based on beach counts and population model (1953-1984 from Muck and Fuentes 1987; 1985-1987 assumed equal to 1982 level; P. Majluf, pers. comm.); in $t*10^3$.
H = fur seal *Arctocephalus australis*; based on beach counts and population model (1953-1984 from Muck and Fuentes 1987; 1985-1987 assumed equal to 1982 level; P. Majluf, pers. comm.); in $t*10^3$.
I = cormorant *Phalacrocorax bougainvillii*; monthly counts (1953-1982 Tovar et al. 1987) converted to biomass using relationships in Muck and Pauly 1987; 1984-1987 courtesy of H. Tovar; in $t*10^3$.
J = booby *Sula variegata*; monthly counts (1953-1982 Tovar et al. 1987) converted to biomass using relationships in Muck and Pauly 1987; 1984-1987 courtesy of H. Tovar; in $t*10^3$.
K = pelican *Pelecanus thagus*; monthly counts (Tovar et al. 1987) converted to biomass using relatioships in Muck and Pauly 1987; 1984-1987 courtesy of H. Tovar; in $t*10^3$.
L = All teleosts (A to F); in $t*10^6$.
M = All species (A to K); in $t*10^6$.

Tables 1 and 2 also include information on the relative variability of each time series as expressed by its % coefficient of variation (C.V. = s.d. * 100/$\overline{X}$). As might be seen, the lowest observed C.V. values were those of the oceanographic parameters, with temperature (C.V. = 6%) being the least, and upwelling (C.V. = 40%) being the most variable time series. The variation of biomass in Table 1 tends to be higher: mackerels (C.V. = 20.3%) varied least while the cormorants (C.V. = 105%) varied most.

Table 2. Selected time series on the Peruvian pelagic fisheries and the upwelling ecosystem.
Tabla 2. Series de tiempo seleccionadas sobre la pesquería pelágica peruana y el ecosistema de afloramiento.

Year	A	B	C	D	E	F	G	H	I	J	K	L
1953	52	25.0	0.080	0.045	0.010	18.8	192	31.0	179	29.0	2.10	2.47
1954	137	25.0	0.100	0.053	0.010	16.6	236	28.0	229	31.0	2.10	5.65
1955	12	27.0	0.130	0.076	0.010	17.3	256	31.0	251	36.0	2.15	7.02
1956	238	30.0	0.210	0.139	0.030	17.8	261	28.0	259	36.0	2.40	4.70
1957	29	34.0	0.390	0.336	0.120	20.0	277	62.0	291	87.0	2.38	4.24
1958	354	38.0	0.820	0.737	0.200	18.9	239	48.0	221	73.0	2.10	3.16
1959	414	51.0	2.04	1.95	0.250	18.4	233	47.0	212	70.0	1.75	3.11
1960	667	42.0	3.42	3.32	0.280	17.6	220	30.0	199	43.0	1.65	3.52
1961	756	57.0	5.13	5.01	0.300	17.7	219	31.0	195	59.0	1.75	3.82
1962	1069	88.0	6.80	6.69	0.450	17.2	217	24.0	188	54.0	2.10	5.20
1963	1655	100	6.74	6.63	0.500	17.9	412	27.0	185	53.0	2.30	3.74
1964	1744	100	8.95	6.86	0.620	16.9	217	28.0	185	60.0	2.50	5.66
1965	1623	110	7.32	7.24	0.550	19.0	214	37.0	180	57.0	2.40	2.57
1966	1650	120	8.61	8.53	0.550	17.5	250	47.0	221	56.0	2.38	4.37
1967	1569	130	9.91	9.83	0.520	16.8	248	41.0	218	54.0	2.15	5.52
1968	1490	130	10.32	10.26	0.790	16.7	278	56.0	273	79.0	2.23	5.94
1969	1455	155	9.03	8.97	0.660	18.6	245	71.0	225	96.0	1.90	3.15
1970	1499	161	12.35	12.3	0.830	18.1	268	54.0	250	78.0	1.90	5.78
1971	1473	175	10.38	10.3	0.750	18.2	233	54.0	206	71.0	2.23	5.28
1972	1399	181	4.55	4.48	1.42	20.4	254	76.0	239	90.0	2.30	2.49
1973	1256	188	1.79	1.77	0.560	18.1	258	60.0	243	76.0	2.50	4.59
1974	795	217	3.86	3.58	1.04	17.5	177	57.0	148	68.0	2.80	3.31
1975	785	218	3.20	3.08	1.09	17.3	250	64.0	252	78.0	2.65	6.39
1976	556	256	4.14	3.86	0.910	19.3	251	72.0	238	84.0	2.30	3.19
1977	514	260	2.22	0.792	0.630	18.5	216	76.0	190	107	2.15	2.66
1978	504	261	2.94	1.19	0.300	17.6	202	54.0	163	80.0	2.35	3.02
1979	484	262	3.36	1.36	0.940	18.0	207	59.0	178	89.0	2.40	2.81
1980	403	254	2.39	0.720	0.720	17.9	181	52.0	201	76.0	2.35	2.69
1981	-	254	2.49	1.23	1.23	17.5	136	51.0	138	85.0	2.30	2.00
1982	-	254	3.32	1.72	1.72	18.7	97.0	79.0	76.0	119	2.15	0.75
1983	-	254	1.20	0.118	0.120	21.9	222	125	203	157	1.90	-
1984	-	254	2.85	0.025	0.020	16.9	163	78.0	139	116	2.00	-
1985	-	254	3.92	0.762	0.120	16.4	146	66.0	121	84.0	-	-
1986	-	254	5.02	3.31	1.16	17.2	-	-	-	-	-	-
1987	-	254	4.05	1.70	1.62	19.0	-	-	-	-	-	-
Mean	878	156	4.37	3.68	0.60	18.1	227	52.8	203	73.7	2.21	3.96
s.d.	577	88.6	3.35	3.58	0.46	1.13	52.4	21.0	45.3	26.6	0.255	1.46
c.v.	65.7	56.6	76.6	97.2	76.8	6.3	23.1	39.8	22.3	36.1	11.6	37.0

A = number of purse seiners (from Agüero 1987).
B = fleet capacity (tonnes/vessel) (1953-1969: adjusted from Jordan 1982; 1970-1980: from Agüero 1987; 1981-1987: M. Agüero, pers. comm.).
C = total catch of pelagic fishes (= anchoveta + sardine + bonito + mackerel + horse mackerel, in t * 10^6) (IMARPE, unpublished data).
D = nominal catch of anchoveta (1953-1983: from Agüero 1987; 1984-1987: IMARPE, unpublished data).
E = exploitation rate of anchoveta (= annual catch/biomass; biomasses from Pauly et al. 1987a).
F = sea surface temperature in °C, Peruvian coast from 4-14°S; 1953-1982 from Pauly and Tsukayama (1987); 1983-1987 from IMARPE (unpublished data).
G = Ekman transport (i.e., upwelling) near Trujillo, in m^3/sec/100m coastline; from Mendo et al. (1987).
H = Ekman transport (i.e., upwelling) near Callao, in m^3/sec/100m coastline; from Mendo et al. (1987).
I = Turbulence index (i.e., "wind cubed") near Trujillo, in m^3/sec^3; from Mendo et al. (1987).
J = Turbulence index (i.e., "wind cubed") near Callao, in m^3/sec^3; from Mendo et al. 1987.
K = potential new production off Peru, in gC/m^2/day, as estimated by Chavez et al. (this vol.).
L = potential new production near Trujillo, in gC/m^2/day, as given in Table 3 of Mendo et al. (this vol.).

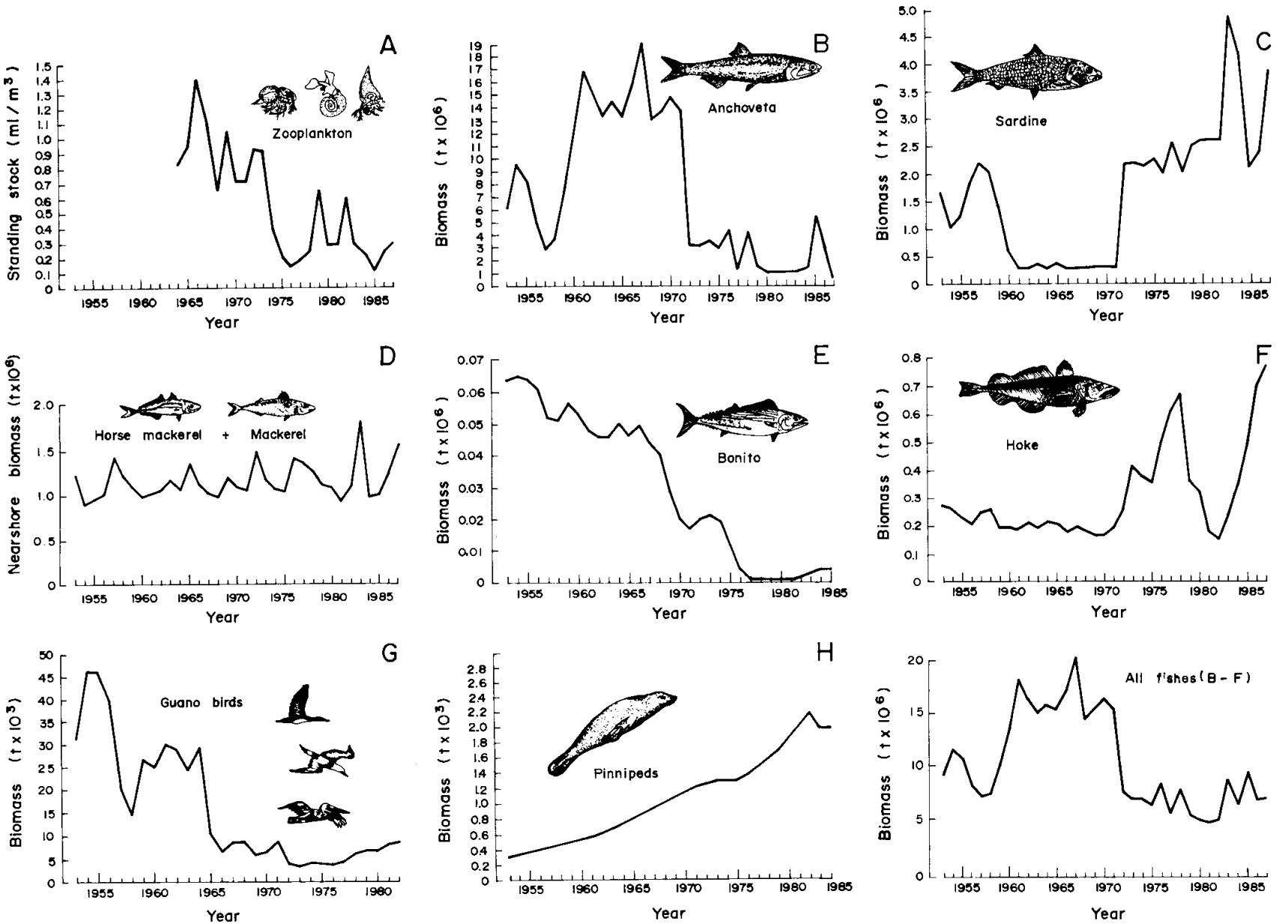

Fig. 1. Mean annual biomass of major species/groups (A-H) in the main anchoveta distribution area, 4-14°S (see Table 1).

Fig. 1. Biomasa promedio anual de las especies/grupos (A-H) más importantes en el área principal de distribución de la anchoveta, 4-14°S (ver Tabla 1).

Major Trends

Before 1975, the Peruvian pelagic fishery was aiming almost exclusively at anchoveta, due to the ease with which anchoveta-derived products (oil, fish meal) could be marketed outside of Peru. The size of the fleet of purse seiners ("bolicheras") aiming at anchoveta roughly reflects the catch trends: a rapid increase from less than 100 units in 1953 to 1700 in the early 1970s; then following the 1971/72 collapse of anchoveta recruitment, a rapid decrease occurred in the early 1980s (the more recent trend is again increasing).

Fig. 1 illustrates the change in biomass of some major species in the MAR. This figure includes three types of plots:

(i) plots with increasing trend,
(ii) plots with no clear trend, and
(iii) plots with decreasing trend.

Fig. 2 compares the mean initial biomass (1955-1965) with the (1975-1985) biomass in terms of their relative changes, by species/groups. The two extremes are bonito and pinnipeds; with the former decreased by a factor of 17, while the latter increased by a factor of 3.

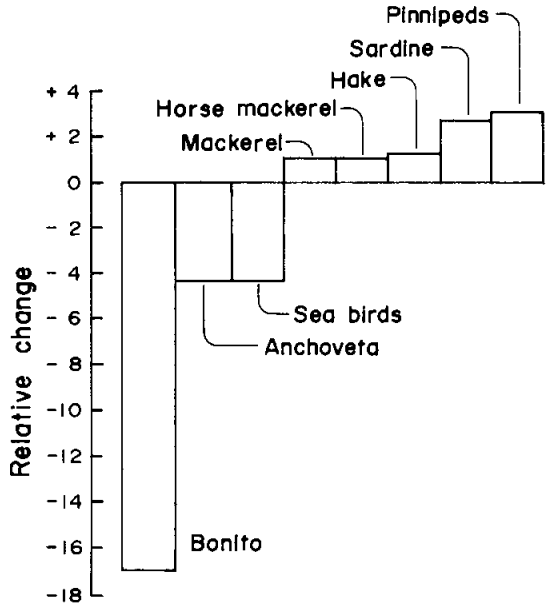

Fig. 2. Relative change in biomass of major species/groups in the main anchoveta distribution area, comparing the period 1955-1965 with the period 1975-1985.

Fig. 2. Cambio relativo en biomasa de las principales especies/grupos en el área principal de distribución de la anchoveta.

Fig. 1 also summarizes our scanty knowledge on zooplankton biomass off Peru, i.e., on one of the key elements of the ecosystem (see Carrasco and Lozano, this vol.). Although "ml/m^3" is probably not the best index of total abundance, the data at hand indicate a clear, declining trend: zooplankton biomass during the 1980s is only about 25% of what it was in the 1960s.

Generally, the available oceanographic time series are characterized by marked interyear variations, El Niño-related anomalies (Fig. 3) as by strong seasonal cycles (see Brainard and McLain 1987). Long term increasing trends have been observed for offshore SST and offshore Ekman transport, velocity, turbulence and upwelling off Callao.

Overall the Peruvian waters are on the average 2°C warmer today than 30 years ago and water mixing and transport processes are more intensive than in the past. The consequences of these changes for evolutionary adaptations of life cycles, strategies and processes are largely unknown, although some general inferences can be made. Thus, a temperature increase, for example, will increase the turnover rate of all organisms, and favor a shift in species composition toward warm-adapted forms.

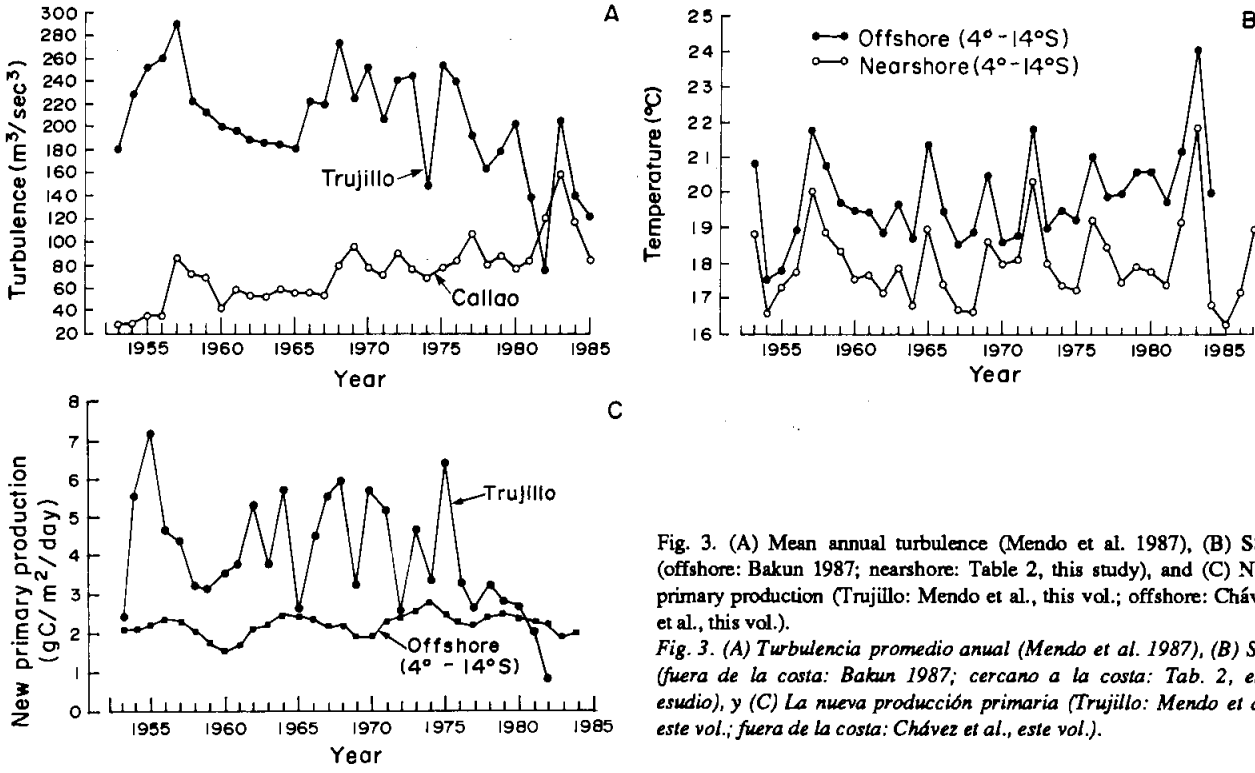

Fig. 3. (A) Mean annual turbulence (Mendo et al. 1987), (B) SST (offshore: Bakun 1987; nearshore: Table 2, this study), and (C) New primary production (Trujillo: Mendo et al., this vol.; offshore: Chávez et al., this vol.).

Fig. 3. (A) Turbulencia promedio anual (Mendo et al. 1987), (B) SST (fuera de la costa: Bakun 1987; cercano a la costa: Tab. 2, este esudio), y (C) La nueva producción primaria (Trujillo: Mendo et al., este vol.; fuera de la costa: Chávez et al., este vol.).

The observed change of various oceanographic parameters has also resulted in the reduction of some gradients. Thus upwelling and turbulence, which were previously different off Callao and Trujillo, have now become very similar in value (Mendo et al.1987).

This long-term "flattening" of gradients within the MAR might have important implication for fishes of various life stages. What is good for larvae (low turbulence, upwelling of offshore transport = stable food patches, low drift mortality) is not necessarily good for the adults, because it corresponds to low primary and secondary production (Navaluna and Pauly 1986; Pauly 1987). Thus, the chance for organism, particularly larvae, to find (or to occur at) the optimal "spot" along a gradient may nowadays be lower than earlier.

Change in the Growth Patterns of Individual Fishes

During the 1970s and 1980s, anchoveta grew faster, and reached larger sizes than during the 1950s and 1960s (Palomares et al.1987 and see Fig. 4A). These authors suggested that the decline of anchoveta biomass enhanced the individual growth of anchoveta, i.e., that growth was originally density-limited. Recent studies (Fig. 4B) also suggest density-dependent effect on sardine, albeit in opposite direction. This is reasonable in view of the recent surge of biomass in this species.

Shifts in Species Dominance

Two cases of species replacements (Daan 1980) or at least of shifts in species dominance occurred in the Peruvian ecosystem in the last decades.

A clear shift of species dominance occurred among the guano birds. In the 1980s and early 1960s, cormorants represented over 80% of the guano birds of Peru; when total bird numbers

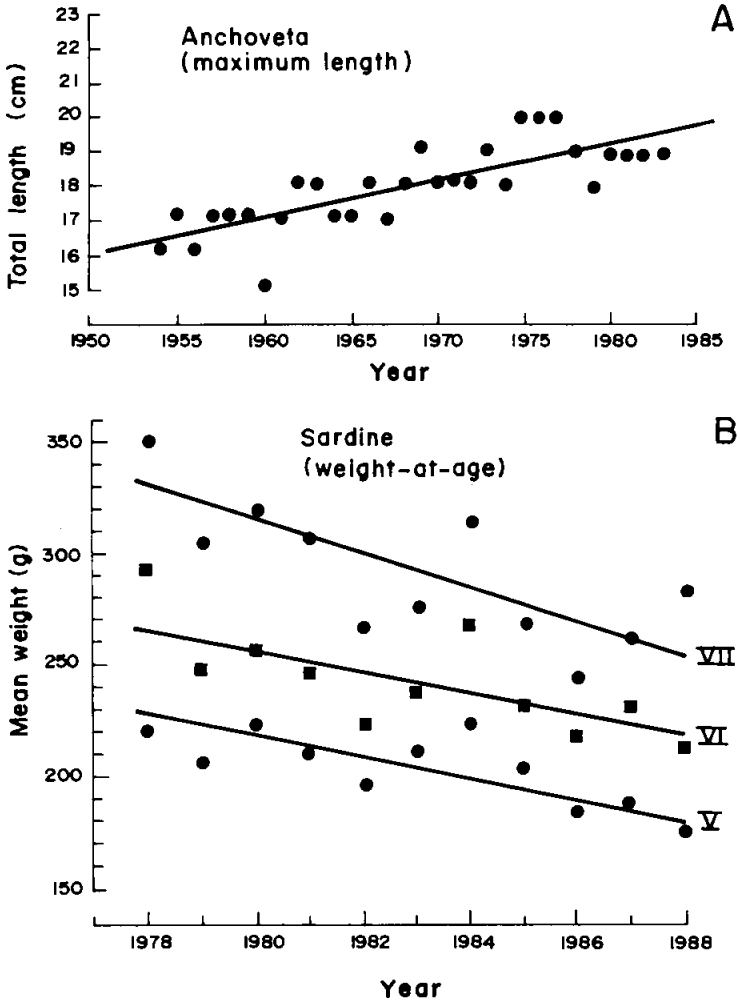

Fig. 4. (A) Changes in the maximum length of anchoveta, and (B) the weight-at-age of adult sardine. (Sardine data courtesy of Dr. A.C. Burd and Mr. J. Zuzunaga).
Fig. 4. (A) Cambios en la longitud máxima de anchoveta y (B) el peso a la edad de sardina adulta. (Datos de sardina cortesía del Dr. A.C. Burd y Sr. J. Zuzunaga).

were reduced by the anchoveta fishery, boobies experienced a relative increase, and became dominant in 1972, a situation which lasted until the late 1970s (Tovar et al.1987).

Another better-known example is the partial replacement of anchoveta by sardine (see Fig. 1), which is based on mechanisms discussed in Ursin (1980) and Muck et al.(1987). Mutual predation on eggs and larvae between anchoveta and sardine should have comparable effects on both stocks. However, detailed analysis of filtering rates shows that anchoveta have a gape 4.4 times larger than sardine of the same size. Also, the growth efficiency of anchoveta is higher than that of sardine (Villavicencio and Muck 1983a), a consequence of difference in the swimming mode of the two species (Weihs 1974). Hence, anchoveta should usually have a greater impact on sardine than *vice versa*. This would explain the near permanent dominance, of anchoveta in geological time, (De Vries and Pearcy 1982) and identify the fishery as the key factor for the altered dominance pattern prevailing to date.

The third example to be presented here of changes in species dominance involves the relationship between anchoveta and hake. The contribution of Espino and Wosnitza-Mendo (this vol.) suggests that high anchoveta biomass correlate with low hake biomass. Negative interactions between hake and anchoveta are further illustrated in Sandoval et al.(this vol.), where high hake larvae densities are shown to correlate negatively with high anchoveta biomasses.

Anchoveta thus influence the biomasses of both their competitors (sardines) and at the least one of their predators (hake). Strong reduction, through fishing, of the anchoveta biomass thus had a strong impact on dominance patterns.

Shifts in Feeding/Fishing Strategy

Changes in diet composition reflecting changes in anchoveta availability were found in fur seals and sea lions, with sardine replacing anchoveta (Majluf 1985). Similarly, mackerel and horse mackerel shifted to zooplankton when anchoveta became scarce (Fig. 5). The latter shift, together with the increase of sardine (a zooplankton feeder) may be the reason for the decreasing trend of zooplankton (c.f. Fig. 1).

The purse seiners fleet, in analogy to the anchoveta predator also shifted from its former unique "prey" to a mixture of sardine and anchoveta as the anchoveta declined. In fact, the drop in catch per effort which the purse seiners experienced in from 1972 to 1974 (Fig. 6) can be attributed to the time it took for the fleet to switch to its new "prey" (sardine).

Population Dynamics of Anchoveta

The El Niño events which occurred off Peru since 1953 (i.e., in 1953, 1957-1958, 1965, 1969, 1972-1973, 1977, 1982-1983 and 1987) have all affected the biomass of anchoveta (see Fig. 7B). However, anchoveta population growth is usually high following such event and it appears that whatever El Niño events "do" to the anchoveta, it has no-long term consequence,

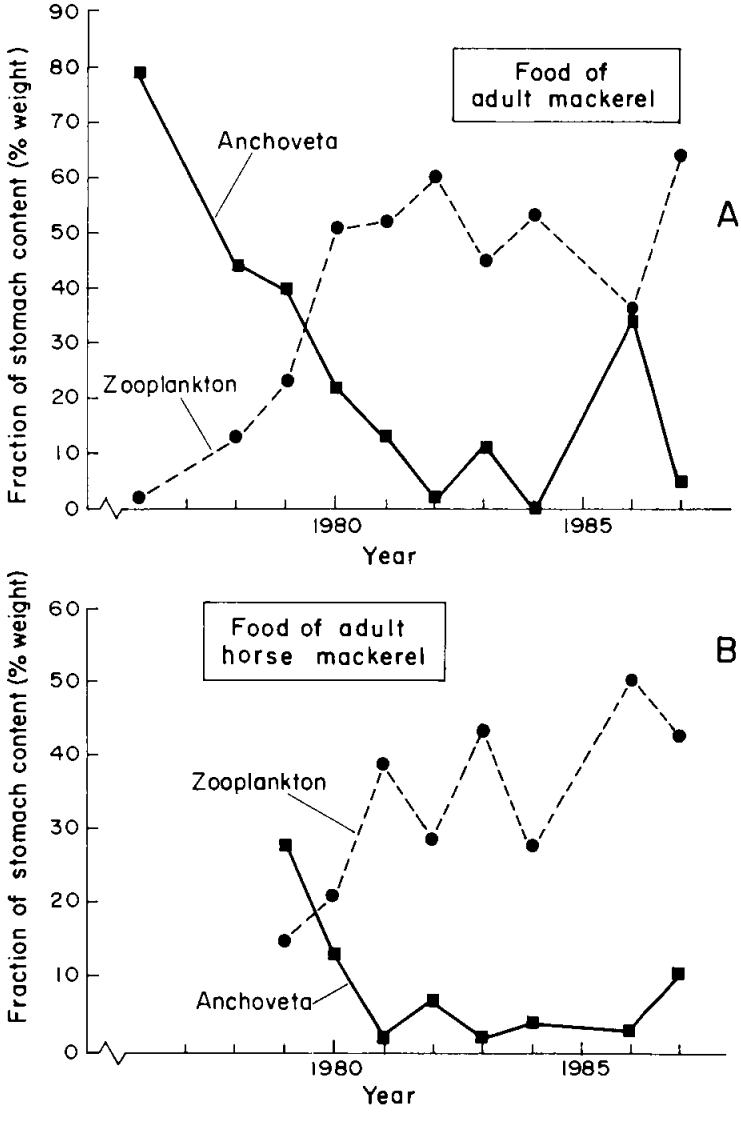

Fig. 5. Changes in diet composition of adult (>30 cm) mackerel (A) and horse mackerel (B).
Fig. 5. Cambios en la composición de la dieta de adultos de caballa (A) y jurel (B) (>30 cm).

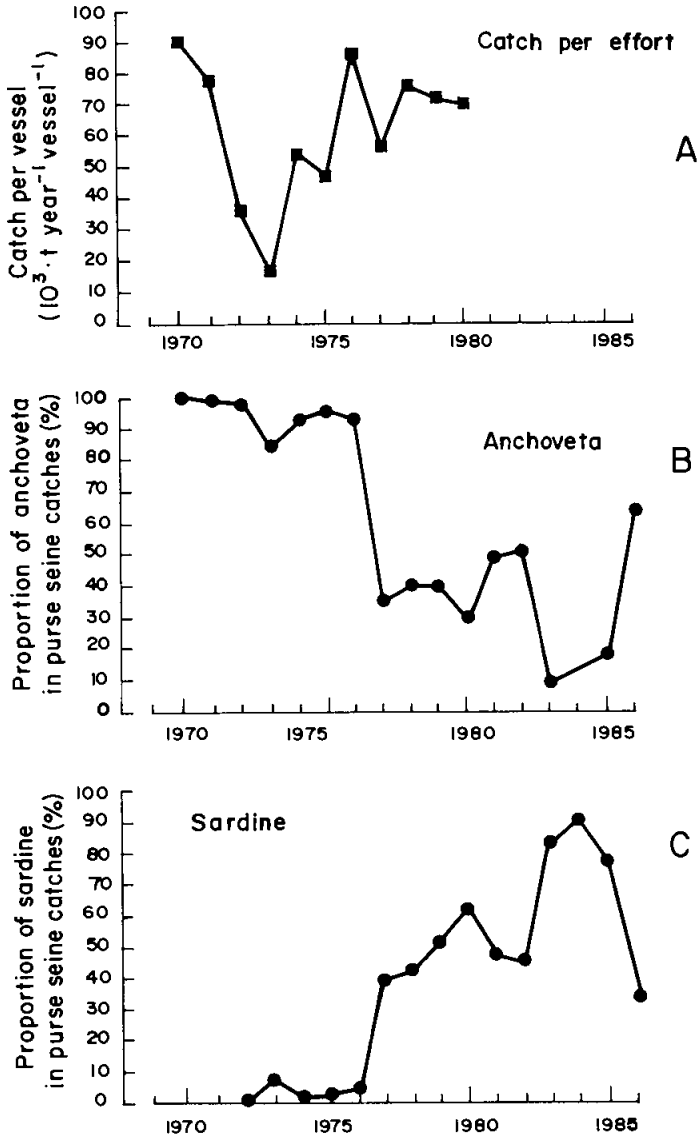

Fig. 6. (A-C) Changes in catch per effort and catch composition in the Peruvian pelagic fishery.
Fig. 6. (A-C) Cambios en la captura por unidad de esfuerzo y en la composición de capturas en la pesquería pelágica peruana.

because biomass losses are rapidly compensated for, at least in the absence of a fishery (see below).

It is nowadays generally assumed that it was the combined effects of a strong fishery plus El Niño events which control anchoveta population dynamics and that a combination of effects was responsible for the collapse, in 1972-1973 of anchoveta recruitment and biomass. The continuously increasing trend of anchoveta exploitation even after the 1972-1973 collapse (Fig. 7C) suggests that it was mainly the fishery which prevented a recovery of anchoveta biomass in the 1970s. However, the available time series also show that a moderately strong fishery does not preclude an increase of anchoveta biomass: during the period for 1958 to 1961, anchoveta catches increased from 1 to 5 t x 10^6 within two years while anchoveta biomass increased from 4 to 17 x 10^6 t. A similar situation also occurred for 1965 to 1967 when catches were increasing from 7 to 10 x 10^6 t while anchoveta biomass increased from 13 to 19 x 10^6 t, and from 1982 to 1985, when catches increased from 0.1 to 0.8 x 10^6 t while anchoveta biomass increased from about 1 to 6 x 10^6 t.

Much earlier work on the dynamics of the Peruvian anchoveta was based on the assumption that the guano birds were the major predators of anchoveta (Jordan 1967, Schaefer 1970; Murphy 1972; Furness 1982). However, the studies in Pauly and Tsukayama (1987), notably those of Pauly et al. (1987a), Muck and Sánchez (1987) and Muck and Pauly (1984) show that

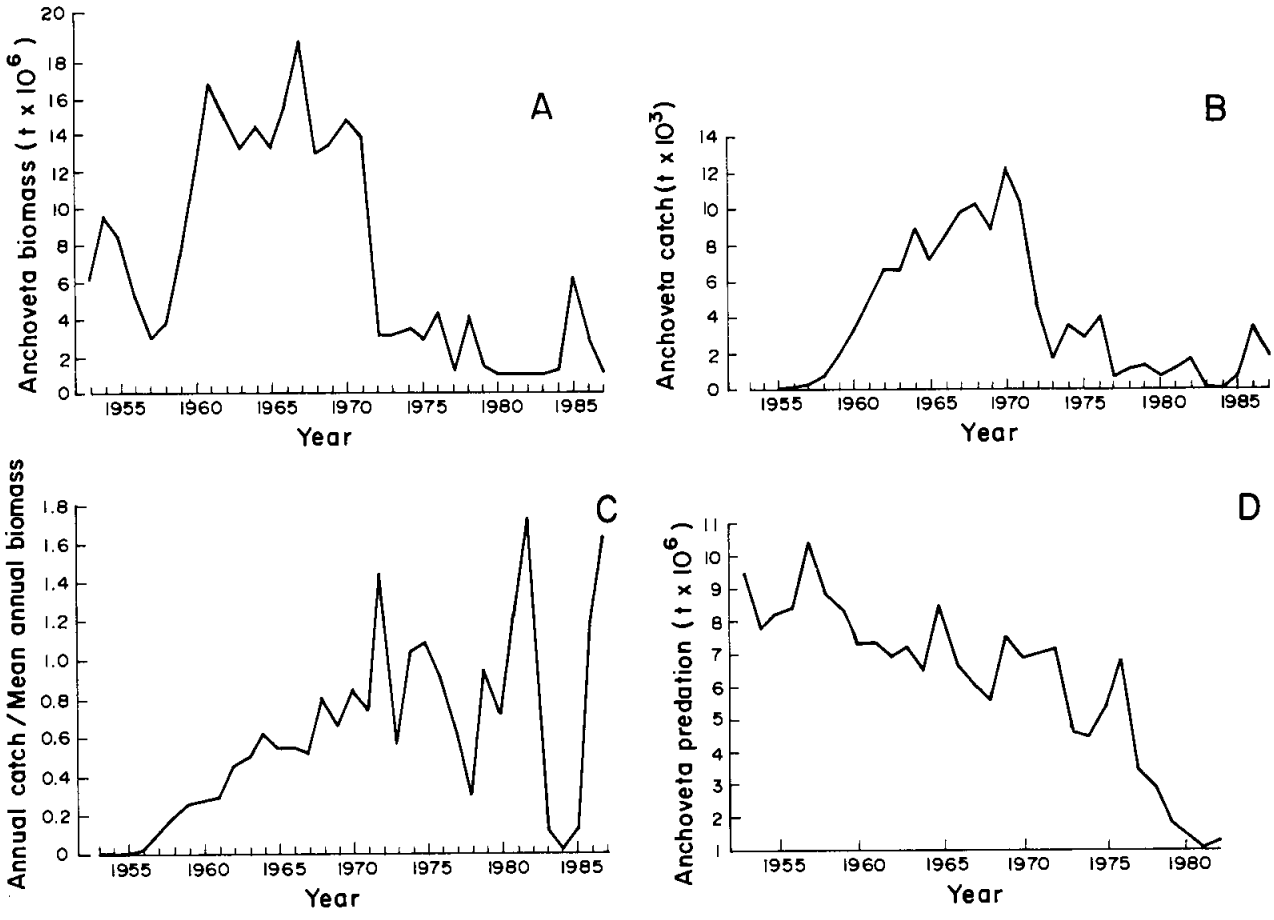

Fig. 7. Anchoveta biomass (A) and the parameters influencing it: catch (B), El Niño (C), predation (D).
Fig. 7. Biomasa de la anchoveta (A) y los parámetros que la influencian: captura (B), El Niño (C), predación (D).

teleosts, especially horse mackerel *Trachurus murphyi* consume far more anchoveta than the guano birds, and *ipso facto* also more than the pinnipeds (see Pauly and Palomares, this vol.). Indeed, horse mackerel predation exceeded fishery catches throughout the 1950s and in the mid 1970s as well (see Muck and Sanchez 1987). Thus, studies of the population dynamics of anchoveta must consider fish predation if they are to lead to useful management advice.

Table 3 summarizes the results of matches between changes in anchoveta biomass (+ or -) with changes of other parameters hypothesized to be linked (causally or otherwise) to anchoveta biomass.

Some of the significant matches in Table 3 are straightforward to explain, i.e., one should expect a relationship between changes in anchoveta biomass and fishery catches. Other matches are more difficult to explain, e.g., that between anchoveta biomass changes and upwelling off Trujillo. The Northern/Central stock of anchoveta has a distribution and spawning area expending over more than 1000 km, and it is surprising that its biomass changes should be so closely correlated with local upwelling.

The data of Table 3 support the hypothesis that offshore transport has a negative effect on anchoveta (Bakun 1987). Mendelssohn and Mendo (1987) showed, on the other hand, that neither upwelling nor turbulence correlated directly with anchoveta recruitment. They concluded that "Lasker events" (i.e., 4-day periods of reduced turbulence) do not have, in the Peru system, the positive effect on engraulid recruitment which they appear to have along the California coast (Peterman and Bradford 1987). Overall, the question of the impact of wind-driven processes (i.e., turbulence, upwelling, offshore transport) is in need of further work.

Table 3. Test results of matches between (i) time series of anchoveta biomass and (ii) another time series.[a]

Tabla 3. Resultados de pruebas comparativas entre (i) series de tiempo de biomasa de anchoveta y (ii) otra serie de tiempo.

Time series tested (ii)	Years used for comparison (n)	Chi-square	Hypothesis rejected ($P < 0.05$)
Hake biomass	31	0.03	no
Sea lion biomass	26	0.04	no
Fur seal biomass	28	0.05	no
Booby biomass	26	0.15	no
Pelican biomass	26	0.15	no
Bonito biomass	26	0.15	no
Cormorant biomass	27	0.33	no
Primary production I[b]	27	0.33	no
Primary production II[c]	28	1.29	no
Turbulence off Callao	28	1.29	no
Turbulence off Trujillo	28	3.57	no
Upwelling off Callao	28	3.57	no
Anchoveta catch	31	3.90	yes
Upwelling off Trujillo	29	4.77	yes
Sea surface temperature	31	5.85	yes
Mack. + horse mack. biomass	31	5.85	yes
Sardine biomass[d]	31	n.a.[d]	yes[d]

[a]Time series used here are documented in Tables 1 and 2 and/or above in the text; the hypothesis tested was that the +-, -+ and ++; pairs are normally distributed (see Materials and Methods section). The critical chi-square value was 3.84 for 1 d.f.

[b]From Chávez et al. (this vol.).

[c]From Mendo et al. (this vol.).

[d]Sardine biomass was here estimated as an inverse function of anchoveta biomass. Hence χ^2 value is inflated.

The significant correlation between interannual changes of anchoveta biomass and SST probably does not indicate any direct effect. Rather, temperature mediates the distribution of mackerel and horse mackerel (Muck et al.1987), which prey heavily on anchoveta when their distribution area overlap (Muck and Sánchez 1987), and recent biomass estimates obtained during 1983-1987 using echoacoustics confirm the SST-driven model used by Muck and Sánchez (1987) to estimate anchoveta consumption by mackerel and horse mackerel.

Thus overall, it does appear that anchoveta mortality, as controlled by the pelagic fishery and anchoveta predators plays the crucial role in anchoveta dynamics. These considerations allow the identification of three periods since the onset of the anchoveta fishery in 1953. 1958 to 1960, 1961-1971 and 1972-1987, documented in Table 4.

The data in this table confirm that the increasing and decreasing interannual changes of anchoveta biomass are largely due to changes in mortality, themselves due to fishing and predation. Table 4 also documents how in the mid 1960s the pelagic fishery replaced horse mackerel as a major source of mortality for anchoveta.

Interestingly, no correlation was found between interannual changes of anchoveta biomass and guano birds, although one should expect the guano birds to depend strongly on anchoveta production.

The probable explanation for this is that the sea birds are affected more by changes in vulnerability (an SST-mediated variable) than by changes of anchoveta biomass itself (Muck and Pauly 1987).

One can expect the sea birds depending on anchoveta to be also mediated via the fishery catches and by fish predation; this all suggests that comparison of signs of the biomass changes in two time series may not be the appropriate approach in the case of the guano birds.

Table 4. Interannual changes of three time series (+ = increase; - = decrease) pertaining to anchoveta (*Engraulis ringens*) and horse mackerel (*Trachurus murphyi*) + mackerel (*Scomber japonicus*).
Tabla 4. Cambios interanuales de tres series de tiempo (+ = incremento; - = decremento) perteneciente a la anchoveta (Engraulis ringens) *y jurel* (Trachurus murphyi) + *caballa* (Scomber japonicus).

Years	Anchoveta biomass (A)	Anchoveta catch (B)	Horse mackerel and mackerel biomass (C)	Major El Niño events (anomaly > 0.8°C)	Coincidence of time series (DC)[a]	Status of anchoveta
1953-54	+	+	-			
1954-55	-	+	+			
1955-56	-	+	+			
1956-57	-	+	+	1	A&B = 7(7) A&C = 50(21)	high anchoveta biomass, low catch/biomass ratio (0.1)
1957-58	+	+	-			
1958-59	+	+	-			
1959-60	+	+	-			
1960-61	+	+	+			
1961-62	-	+	-			
1962-63	-	-	+			
1963-64	+	+	-			
1964-65	-	-	+			
1965-66	+	+	-	1	A&B = 32(5) A&C = 10(30)	very high anchoveta high catch/biomass ratio (0.6)
1966-67	+	+	-			
1967-68	-	-	-			
1968-69	+	-	+			
1969-70	+	+	-			
1970-71	-	-	+			
1971-72	-	-	+			
1972-73	-	-	-			
1973-74	+	+	-			
1974-75	-	-	-			
1975-76	+	+	+			
1976-77	-	-	-			
1977-78	+	+	-			
1978-79	-	+	+	4	A&B = 27(41) A&C = 12(17)	low anchoveta biomass, very high catch/biomass ratio (0.8)
1979-80	-	-	-			
1980-81	?	+	-			
1981-82	?	+	+			
1982-83	?	-	+			
1983-84	+	-	-			
1984-85	+	+	-			
1985-86	-	+	+			
1986-87	-	-	+			

[a]See Materials and Methods section for definition of DC whose first value pertains to a lag of 0 year, while the values in bracket pertain to a lag of 1 year.

Predator-Prey Disequilibrium

The anchoveta predators in the Peruvian upwelling system (see Fig. 8) may be grouped as follows:

Opportunists	Specialists
mackerel	cormorant
horse mackerel	booby
sea lion	pelican
fur seal	bonito
hake	

The purse seiners exploiting anchoveta can also be identified by these two categories: with regard to their capacity, they reacted to changes of anchoveta abundance like the opportunist

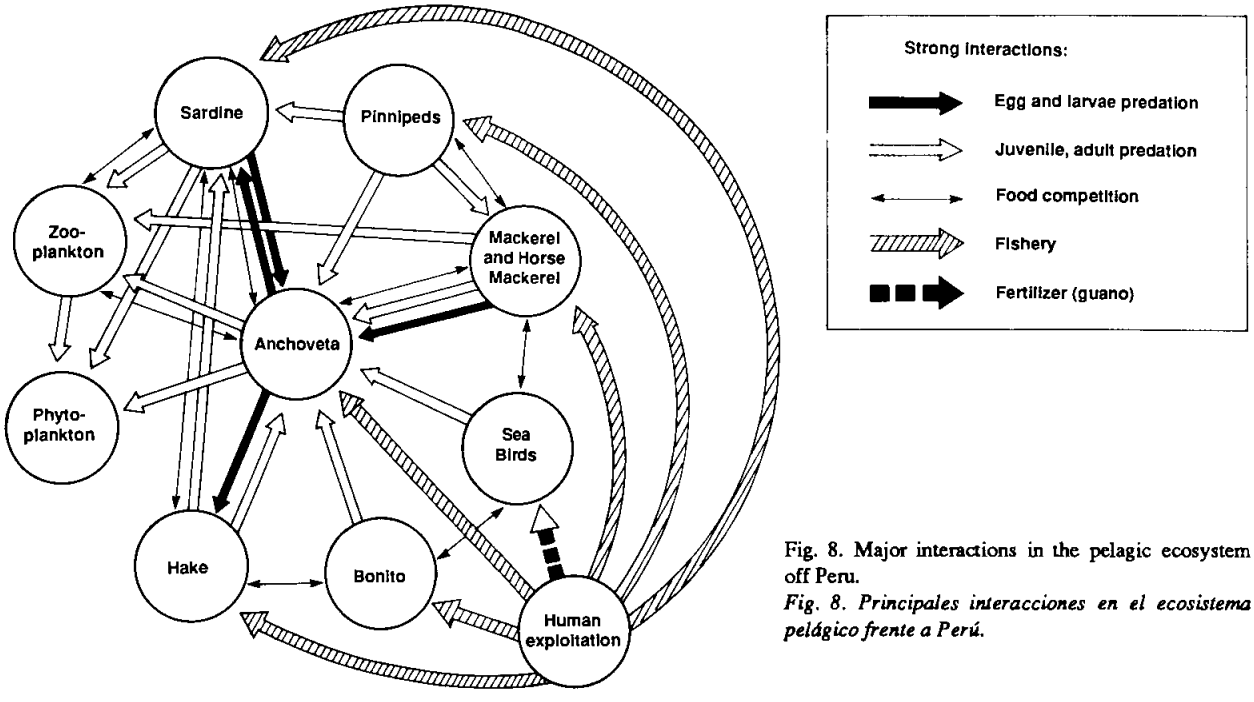

Fig. 8. Major interactions in the pelagic ecosystem off Peru.
Fig. 8. Principales interacciones en el ecosistema pelágico frente a Perú.

predators, i.e., they increased. With regard to their numbers, however, the purse seiners declined in reaction to changes of anchoveta abundance, just as the specialists did (see Table 2, and data in Agüero 1987).

As a result, the present sum of predation + harvesting capacity is equal to what it was in the 1960s, although anchoveta has now only one fourth of the biomass it then had. Or put differently: the total annual capacity of the Peruvian upwelling ecosystem to "consume" anchoveta is about 5 times the average biomass, *vs* one time in the 1960s.

This again means that the pressure on the anchoveta stock is nowadays much higher than in the past. This disequilibrium suggests that, overall, the anchoveta may have difficulties regaining its past high biomasses.

Still, the experience of 1985 is encouraging: after a period of extremely low biomasses (1980-1983, see Fig. 1B), biomass estimates based on two independent approaches (echo acoustics and the egg production method) indicated a dramatic increase. Detailed analysis of the context makes this understandable:

i) from 1983 to 1985 the catch/biomass ratio of anchoveta was low (Fig. 7C),
ii) mackerel and horse mackerel biomass within the MAR - and hence anchoveta predation - were extremely low in 1984-1985 (Fig. 9), a consequence of the abnormally low SST, and
iii) low temperatures allowed anchoveta to disperse into a larger habitat (see Muck et al, this vol.), thus reducing density dependent checks on anchoveta growth.

In other words, the period between the 1982/83 El Niño event and 1985 was the most favorable for anchoveta since the collapse of 1971/72.

The response of the Peruvian purse seiner fleet to the 1984/85 increase of anchoveta biomass was to drastically increase the exploitation of this fish, which resulted in 1987 having one of the highest annual catch/biomass ratios ever recorded off Peru (see Fig. 7C).

This excessive level of effort, combined with the reoccurrence of the high SST associated with the weak El Niño of 1987 and hence of large quantities of mackerel and horse mackerel within the MAR predictably reduced anchoveta back to their present low level.

To summarize the preceding paragraphs on the population dynamics of anchoveta, we thus note:

i) the fishing and predation mortality of anchoveta can be straightforwardly expressed as function of fishing effort, anchoveta vulnerability (and predator biomass in the case of

predation); fishing and predation mortality largely determine the extent (if any) of anchoveta population growth;

ii) high SST impacts anchoveta directly (e.g., by reducing habitat size) and indirectly (by creating appropriate conditions for the invasion of the coastal waters by anchoveta predators (see Fig. 9). High SST occur in summer and especially during El Niño events;

iii) reduction of habitat size increase the vulnerability of anchoveta to purse seiners (see also Csirke, this vol.);

iv) the high SST brought about by El Niño events also impact anchoveta via a variety of biological mechanisms such as: increase of (density- dependent) egg and larval cannibalism, increase of metabolic costs, food scarcity, etc.;

v) thus, the SST-mediated distribution patterns of anchoveta and of its predators largely determine the dynamics of anchoveta, and the ultimate fate of the fishery (Fig. 10).

It is now obvious that the Peruvian pelagic fishery failed to account for these interrelationships and this explains both the crucial 1971-1972 collapse, and the non-recovery of the stock thereafter.

This makes the human factor the decisive one, and strengthens the argument for an ecosystem-oriented management scheme.

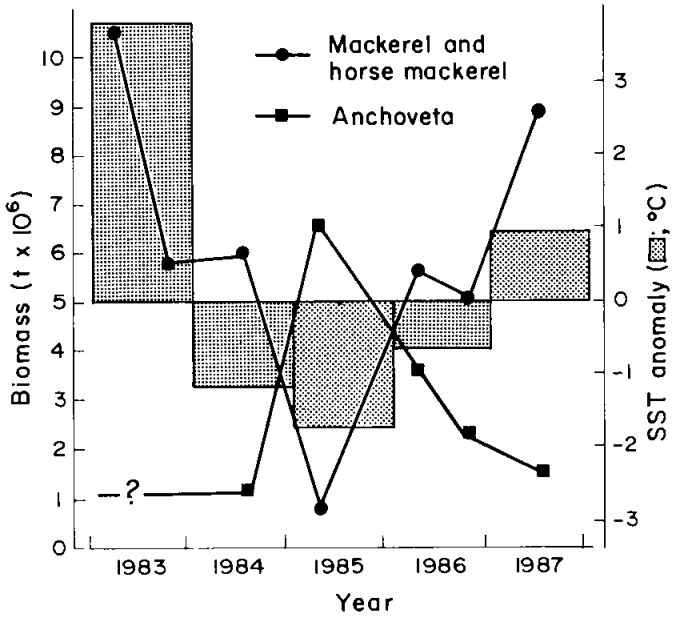

Fig. 9. Mean annual SST-anomalies (bars) and biomass estimates (acoustic surveys) of anchoveta, mackerel and horse mackerel.
Fig. 9. Promedio anual de las anomalías de TSM (barras) y estimaciones de biomasa (evaluaciones acústicas) de la anchoveta, caballa y jurel.

Options for Management

Comparison of the present biomass of the six major species in the Peruvian ecosystem with those of the 1960s shows a deficit of 10 million tons, i.e., the Peruvian fishing industry has now at its disposal only half of the reserves it has 30 years ago, when the Peruvian population was half its present size. The data presented above strongly suggests that the reduction of the biomass of harvestable fish in the Peruvian sea is the result of overfishing, or more precisely, of a lack of synchronization of the fishing with periods of high anchoveta production.

The same data also suggest, however, that the present knowledge on the dynamics of anchoveta is sufficient to design a rational exploitation strategy. Such strategy would be based on the observation that the anchoveta stock can recover after a collapse if conditions are "favorable". Favorable conditions occur if fishing pressure is low and predation pressure is low.

Reducing the predation pressure on anchoveta involves applying a high fishing pressure on anchoveta predators, notably horse mackerel and mackerel. Exploiting these species at the right time is straightforward because these species move inshore when SSTs are high.

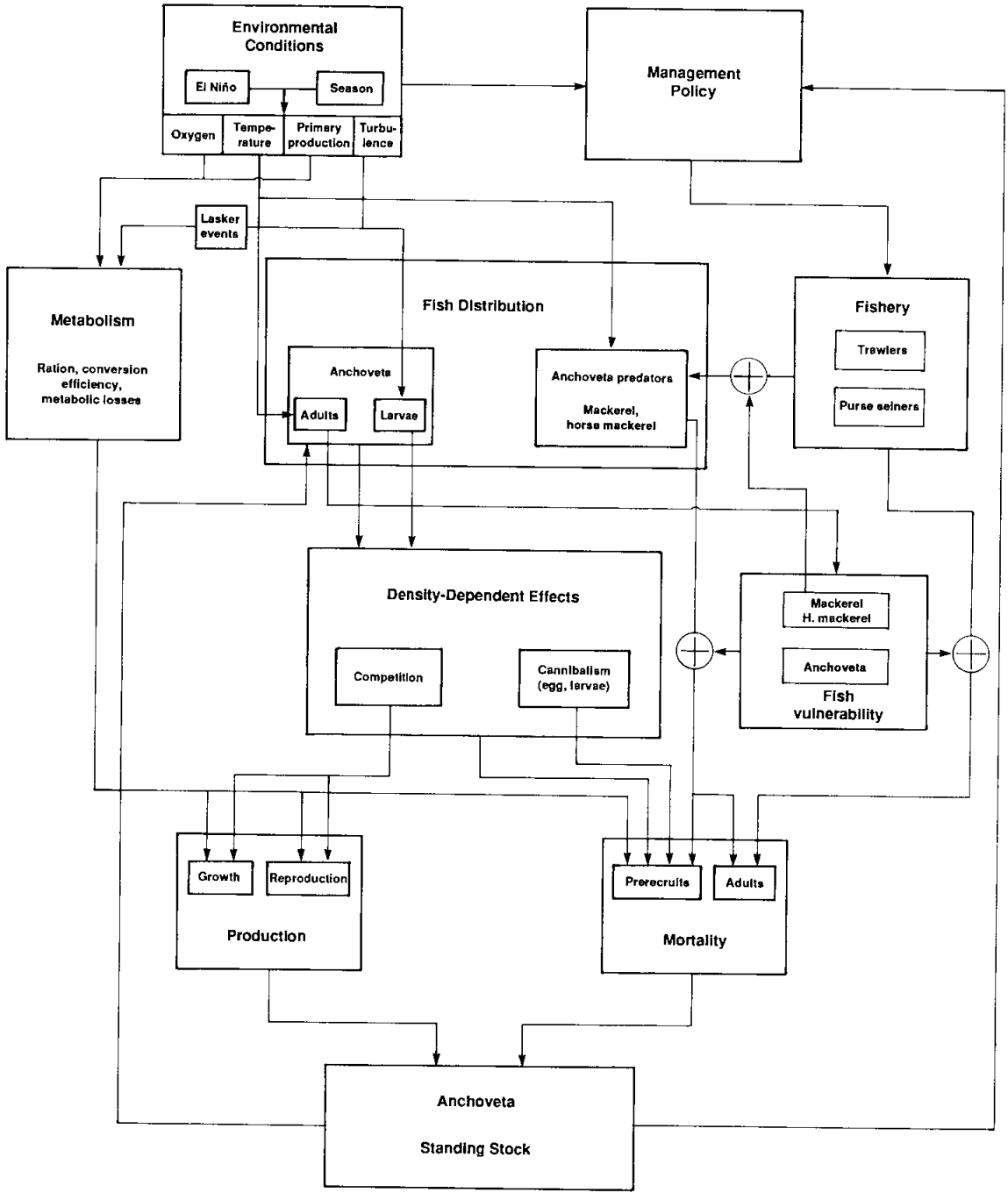

Fig. 10. Schematic representation of the guiding mechanisms and feedback loops which can affect anchoveta population size and fishery.
Fig. 10. Esquema de los mecanismos guias y enlaces de la retroalimentación que pueden afectar el tamaño poblacional y la pesquería de la anchoveta.

A rational exploitation scheme for the multispecies stock off Peru would thus involve an alternance between exploitation of anchoveta (when biomasses of anchoveta are high and SST are low) and of horse mackerel and mackerel (when SST are high).

The species composition of the multispecies complex off Peru provides three different options for the fisheries sector:

i) production of fish meal and fish oils
ii) production of fish for direct human consumption
iii) some mixture of (i) and (ii)

Option (i) prevailed until the 1971/72 collapse and is now discredited, option (ii) being now declared government policy. However, use of pelagic fishes for direct human consumption (e.g., via canning or (iced) fresh fish) is still very much less than use of anchoveta (and sardine) for fish meal and oils.

The main reason for this gap between stated policy and the present reality is the fact that fish meal can be easily marketed internationally, and that its price tends to increase, while domestic marketing of mackerel, horse mackerel and hake is hampered by low market prices relative to harvesting costs and the absence of an efficient cold chain along the Peruvian coast and into the hinterland.

Thus, option (ii), meant to help solve the protein deficiency of low-income Peruvians (the overwhelming majority of the population), can probably not be implemented without subsidies.

Option (iii) is proposed here as alternative: profits realized by Pesca-Perú, the state fishing enterprise from fish meal exports could be used to gradually acquire the capacity to economically harvest and market mackerel and horse mackerel. This would reduce predation pressure on the anchoveta, of which more would then become available for fish mean production. All data reviewed above suggest that such positive feedback loop could be made to contribute to the rehabilitation of the Peruvian fisheries.

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References

Agüero, M. 1987. A bioeconomic model of the Peruvian pelagic fishery, p. 307-324. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Phiippines.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Phiippines.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984, p. 14-45. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Phiippines.

Daan, N. 1980. A review of replacement of depleted stocks by other species and mechanisms underlying such replacement, p. 405-421. *In* A. Saville (ed.) The assessment and management of pelagic fish stocks. Rapp. P.-v. Réun. CIEM (177).

De Vries, T.J. and W.G. Pearcy. 1982. Fish debris in sediments of the upwelling zone off central Peru: a late quarternary record. Deep Sea Res. 28(1A): 87-109.

Furness, R.W. 1982. Competition between fisheries and seabird communities. Adv. mar. Biol. 20:225-307.

Jordan, R. 1967. The predation of Guano birds on the Peruvian anchoveta (*Engraulis ringens* Jenyns). CalCOFI. Rep. 11:105-109.

Jordan, R. 1982. La anchoveta y su captura frente a las costa del Perú. Monografías Biológicas (2), p. 51-63. *In* J.C. Castilla (ed.). Segundo seminario taller. Bases biológicas para el uso y manejo de recursos naturales renovables.

Majluf, P. 1985. Comportamiento de lobo de Sudamérica *(Arctocephalus australis)* en Punta San Juan, Perú, durante "El Niño" 1982/83, p. 187-193. *In* W. Arntz, A. landa and J. Tarazona (eds.). El Niño: Su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen extraordinario.

Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Mendo, J., L. Pizarro and S. Castillo. 1987. Monthly turbulence and Ekman transport indexes 1953 to 1985, based on local wind records from Trujillo and Callao, Peru, p. 75-88. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and G. Sanchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P., M. Espino, H. Fuentes, C. Wosnitza-Mendo and M. Esquerre. 1988. Predación de la merluza Peruana *(Merluccius gayi peruanus)* sobre la anchoveta *(Engraulis ringens)*, p. 249-253. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento Peruano. Bol. Inst Mar Perú-Callao, Volumen Extraordinario. 382 p.

Muck, P., O. Sandoval de Castillo and S. Carrasco. 1987. Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Peru, p. 268-275. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, Z. and P. Muck. 1986. La importancia del cambio de la temperatura y de la biomasa planctónica para la producción y mortalidad de anchoveta (*Engraulis ringens*) y sardina (*Sardinops sagax*), p. 119-128. *In* W. Amtz, A. Landa and J. Tarazona (eds.) El Niño: Su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao. Volumen extraordinario

Murphy, G.I. 1972. Fisheries in upwelling regions with special reference to peruvian waters. Geoforum 11/72:63-71.

Navaluna, N.A. and D. Pauly. 1986. Seasonality in the recruitment of Philippine fishes as related to monsoon wind patterns, p. 167-179. *In* A. Yañez-Arancibia and D. Pauly (eds.) Proceedings of the IREP/OSLR Workshop on the Recruitment of Coastal Demersal Communities, Campeche, Mexico, 21-25 April 1986. IOC (UNESCO) Workshop Rep. No. 44.

Palomares, M.L., P. Muck, J. Mendo, E. Chumán, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1982, p. 117-141. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama (eds.). 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., A. Ch. De Vildoso, J. Mejía, M. Samamé and M.L. Palomares. 1987b. Population dynamics and estimated anchoveta consumption of bonito (*Sarda chilensis*) off Peru, 1953 to 1982, p. 248-267. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., M. Palomares and F. Gayanilo. 1987a. VPA estimates of the monthly population length composition, recruitment, mortality, biomass and related statistics of peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., A. Ch. De Vildoso, J. Mejía, M. Samamé and M.L. Palomares. 1987b. Population dynamics and estimated anchoveta consumption of bonito (*Sarda chilensis*) off Peru, 1953 to 1982, p. 248-267. *In* D. Pauly and I. Tsukayama (eds.). the Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p.

Peterman, R.M. and M.J. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy *(Engraulis mordax)*. Science 235: 354-356.

Schaefer, M.B. 1970. Men birds and anchovies in the Peru current - dynamic interactions. Trans. Am. Fish. Soc. 9: 461-467.

Tovar, H., V. Guillen and M.E. Nakama. 1987. Monthly population size of three guano birds species off Peru, 1953 to 1982, p. 208-218. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Ursin, E. 1980. Fish stock changes and their description in terms of ecosystem modelling. IMARPE. MS.

Vilchez, R., P. Muck and A. Gonzales. 1988. Variaciones en la biomasa y en la distribución de los principales recursos pelágicos del Perú entre 1983 y 1987, p. 255-264. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento Peruano. Bol. Inst. Mar Perú-Callao, Volumen Extraordinario. 382 p.

Villavicencio, Z. y P. Muck. 1983a. Costos metabólicos de *Engraulis ringens* y *Sardinops sagax* en relación al peso, temperatura y nivel de actividad. Bol. Inst. Mar Perú-Callao 7(3):49-68.

Villavicencio, Z. y P. Muck. 1983b. La ración de mantenimiento, la densidad de mantenimiento y la eficiencia de crecimiento de *Engraulis ringens* y *Sardinops sagax* como una medida de su potentica ecológica. Bol. Inst. Mar Perú-Callao 7(4):69-108.

Weihs, D. 1974. Energetic advantages of burst swimming of fish. J. Theor. Biol. 48:215-229.

Interactions and Dynamics of the Peruvian Upwelling System: A Postscript*

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Abstract

The interrelationship of the various contributions in this volume are briefly reviewed as are some errors in this volume's predecessor. Some aspects of the modelling work presently underway on the Peruvian upwelling system are presented.

Resumen

Las inter-relaciones entre las diversas contribuciones en éste volumen son brevemente revisadas al iqual que algunos errores en el precesor a éste volumen. Se presentan además, algunos aspectos del trabajo de modelación actualmente en desarrollo acerca del sistema de afloramiento peruano.

Introduction

The book of which this is the last contribution represents the proceedings of the "International Workshop on Models for Yield Prediction in the Peruvian Upwelling Ecosystem", held at the Instituto del Mar del Perú, Callao, Perú, 24-28 August 1987, and the first contribution, by Csirke et al., presents the report of this workshop.

This book, however, includes more contributions than those which were prepared for presentation and formally presented at the said workshop. It also includes a paper that was conceived and essentially written during the workshop (Mendo et al., this vol.) in response to one of the formal presentations, as well as a number of papers that could be written only after the workshop was held. This applies particularly to the reestimation of anchoveta monthly biomasses from 1953 to the 1980s (Pauly and Palomares, this vol.) and of their reproductive output and egg mortality (Pauly and Soriano, this vol.). The former analysis could be performed only after the anchoveta consumption by hake had been estimated for that same period (Muck, this vol.), which itself could be estimated only after the available estimates of the biomass of hake of Northern/Central Peru had been extended from the last decades all the way back to 1953 (Espino and Wosnitza-Mendo, this vol.). In other words, this book presents a collection of closely integrated papers, of which the majority use time series data either derived or also considered in other contributions. Combined with the fact that the bulk of the contributions included here deals with *change,* this explains the subtitle of this book: "Dynamics and Interactions".

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*ICLARM Contribution No. 560.

The aim of the above-mentioned workshop was to examine whether sufficient information exists on the Peruvian upwelling system for a simulation model of that system to be developed which would be usable for purposes of fisheries management.

The answer was a guarded "Yes". Yes, because the predecessor of this volume (Pauly and Tsukayama 1987) considered a "formidable collection of papers" by one reviewer, indeed presented a vast amount of data in both raw and analyzed forms - enough to provide the basis for a serious modelling effort. This was a *guarded* "yes" however, because a large fraction of the variability of the physical components of the Peruvian upwelling system have the characteristics of an unpredictable "random walk" (Bohle-Carbonell, this vol.). Still, it is apparent that the anchoveta population off Peru is capable of stabilizing its biomass despite environmental variability. In fact, the consensus that emerged is that it is mainly the purse seine fishery which, in concert with predators such as the horse mackerel *Trachurus picturatus murphyi* (see Parrish, this vol.), nowadays prevents the anchoveta from reestablishing itself to the high levels prevailing,e.g., in the 1960s (see Muck's contribution on trends from the early 1950s to mid 1980s, this vol.).

Previous simulation models of the Peruvian ecosystem, notably that of Walsh (1975), emphasized primary and secondary production, and nutrient recycling, while giving scant attention to the species composition and biomass variability of the exploited fishes (anchoveta, sardine, mackerel, horse mackerel, bonito, etc.) of that system, not to speak of the guano birds and sea mammals (see also Walsh 1981).

Explicit consideration, in a simulation model of the Peruvian ecosystem, of the fishes and higher vertebrates requires that the various rates affecting their dynamics be precisely estimated; this pertains to growth and mortality rates, food consumption rates, etc. Hence, we have included contributions on some rates (e.g., the growth and food consumption rates of anchoveta) already considered in this book's predecessor, but reestimated them, using improved methods and/or new data (see e.g., contributions of Morales-Nin and of Pauly et al., this vol.).

We are well aware that none of the contributions included in this book and its predecessor, nor the planned modelling exercise, could make full use of all the information available from the Peruvian upwelling system (especially those on anchoveta, see Jarre et al., this vol.). For this reason, we document in Appendix I of this book a collection of fourteen 5 1/4" MSDOS diskettes (for IBM PC and compatible microcomputers) which contain all the time series and other data upon which the contributions in this book and its predecessor are based. Interested colleagues are invited to request copies of these diskettes from ICLARM, which is authorized to distribute them (for a small fee) throughout the world.

This form of data exchange is quite new; we hope it will contribute to the reestablishment of an important principle of science - now seriously endangered by massive databases analyzed with undocumented software - i.e., that the readers of a paper should be able to reproduce the results included in that paper *both in principle and in practice*.

We assume, obviously, that a wide dissemination of these data will encourage their further analysis, and hence will eventually benefit Peru, e.g., through elucidation of the mechanisms which determine the variable level of her fisheries resources. A recent contribution by Cury and Roy (1989), based on data presented in this book's predecessor, illustrates the process we have in mind here.

Another principle of science which is often neglected is the explicit correction of known errors in one's earlier publications. In this book, two chapters provide corrections for important errors in three earlier contributions (Table 1). I fear that while some will appreciate this information as an improvement to the book to which they refer, some others will feel that the existence of such errors - corrected or not - reduces the value of the previous book, and perhaps of this as well. Clearly, what we have here is a case of not being able to please all at the same time (see also Fig. 1).

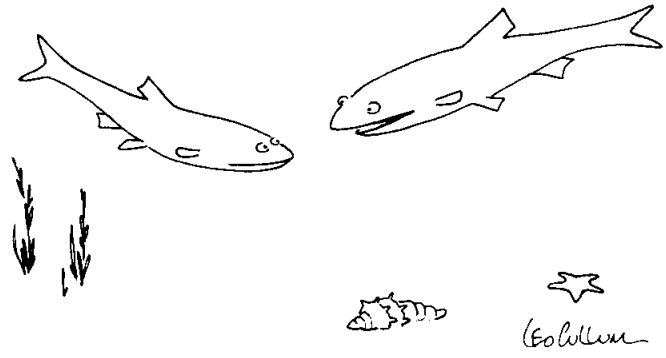
As suspected by Cushing (1988), the data in this volume and its predecessors are presently being used for multispecies modelling. This proceeds along two lines of inquiries:

- construction of a successive steady-state model covering relatively short periods during which the Peruvian upwelling system maintained identifiable states (e.g., early to mid-1960s or mid- to late 1970s).

Table 1. Some errors in contributions included in Pauly and Tsukayama (1987).[a]
Tabla 1. Algunos errores en las contribuciones en Pauly y Tsukayama (1987).

Error	Author, page and exhibit no.	Remedy
Programming error in estimating wind stress on sea surface	Bakun (1987, Figs. E, F and G)	See Bakun and Mendelssohn (this vol.)
Numerous erroneous values due to misalignment of entries	Santander (1987, Table 3)	Corrections included in Table 2 of Pauly and Soriano (this vol.)
Underestimation[b] of anchoveta egg mortality	Pauly (1987, p. 329-330, equation (4), Table 2 and Fig. 4)	See Pauly and Soriano (this vol.)

[a]This table does not cover the various misspellings and unimportant typographical and other errors that may be found upon close reading of this book.
[b]Interestingly, Cushing (1988) suggested that anchoveta egg mortality may be overestimated.



"Some will love you, son, and some will hate you. It's always been that way with anchovies."

Fig. 1. Drawing by Leo Cullum; © 1989. Reproduced by permission of the New Yorker Magazine, Inc.
Fig. 1. Algunos te amarán hijo, y otros te odiarán. Siempre ha sido asi con anchovetas.

- development of a simulation model of the Peruvian upwelling ecosystem, in which key processes are expressed through coupled differential equations, parameterized using the rate estimates time series and other data presented in this volume and its predecessor.

The first of these approaches, presently emphasized by Ms. A. Jarre, is intended to serve two major aims:

i) estimating, for various time periods the average biomass and/or production of elements of the system for which these characteristics are not available;
ii) linking up the studies conducted to date on the Peruvian upwelling system with the theory of ecosystem phenomenology developed by Ulanowicz (1986), as initiated in Pauly (1987, Table 1).

The second modelling approach, emphasized by Dr. P. Muck, is both time- and space-structured: the Peruvian upwelling ecosystem has been divided up into nearly 200 squares, whose (SST-mediated) suitability for anchoveta, sardine, horse mackerel and other fishes is reassessed on a monthly basis and into which a purse seiner fleet can be deployed. The catch of

the fleet is then modelled, for each square fished, as a function of the biomass of various fish species which are themselves functions of the previous fishing and environmental regimes.

This approach, which is reminiscent of earlier work by Sharp (1979), is documented in Muck et al. (1989) and Jarre et al. (1989), where the abovementioned steady-state approach is also presented. Software and documentation for these models will become available in 1990, and readers may write to the author for information on this.

In conclusion, I wish to thank on my behalf and on behalf of my co-editors, the many colleagues and other friends who have made this book, and the workshop upon which it is based, possible, particularly:

In Peru, Messrs. Jaime Sobero and Rogelio Villanueva, present and former Executive Directors of IMARPE, respectively, for their support of PROCOPA and of cooperation with ICLARM; Ms. Blanca Rojas de Mendiola and A. Alamo, for contributing their valuable databases on anchoveta; to all PROCOPA and IMARPE staff, who may not be individually acknowledged in the various contributions of this book, but whose input is nevertheless appreciated.

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References

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46(4): 670-680.

Cushing, D.H. 1988. Review of: the Peruvian anchoveta and its upwelling ecosystem: three decades of change. J. Cons. CIEM 44: 297-300.

Jarre, A., P. Muck and D. Pauly. 1989. Interaction between fish stocks in the Peruvian upwelling system. Symposium on Multispecies Models Relevant to the Management of Living Resources. International Council for the Exploration of the Sea, 24 October 1979, The Hague, Netherlands. ICES, MSM Symp. Pap. No. 12.

Muck, P., A. Jarre and D. Pauly. 1989. Ecología del sistema de afloramiento peruano, con énfasis en el rol de la anchoveta. MS presented at the First Symposium on Ecology and Conservation in Peru, 24-29 July, Lima, Peru.

Pauly, D. 1987. Managing the Peruvian upwelling ecosystem: a synthesis, p. 325-342. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama, editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Santander, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru, 4-14°S, p. 179-207. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Sharp, G.D. 1979. Areas of potentially successful exploitation of tunas in the Indian Ocean with emphasis on surface methods. Indian Ocean Program, IOC/DEV/79/47, Rome, 54 p.

Ulanowicz, R.E. 1986. Growth and development: ecosystem phenomenology. Springer Verlag, New York.

Walsh, J.J. 1975. A spatial simulation model of the Peru upwelling ecosystem. Deep-Sea Res. 22: 201-236.

Walsh, J.J. 1981. A carbon budget for overfishing off Peru. Nature 290: 300-304.

Appendix I

Documentation of Available 5 1/4' MSDOS Data Diskettes on the Peruvian Upwelling Ecosystem[a]

The set of 14 diskettes presented below contains the bulk of the data used for or derived in the various contributions in the books "The Anchoveta and its Upwelling Ecosystem: Three Decades of Change" (Pauly and Tsukayama 1987) and its sequel, "The Peruvian Upwelling Ecosystem: Dynamics and Interactions" (this vol.). Diskettes 1-5 contain files created using the LOTUS 1-2-3 program. Diskettes 6-8 contain the egg maps presented in Santander (1987) and 9-10 contain monthly summaries of Santander's maps, documented in Senocak et al. (this vol.). Both sets of maps are presented in the form of DIASHOW picture files. The diskettes numbered 11-13 contain a DBASE III+ file combining the data compiled by Rojas de Mendiola (this vol.) and Alamo (this vol.). Finally, diskette 14 contains a preliminary bibliography of anchoveta *Engraulis ringens* created by Jarre et al. (this vol.) using the Microsoft WORD processor program. (Diskette 14 is not discussed further below.)

All files were created with IBM compatible (MSDOS) microcomputers. The worksheet files created in LOTUS 1-2-3 have the extension ".WK1". The picture files, created for the DIASHOW graphics software have the extension ".PIC"; the DBASE III+ file, on the other hand, has the ".DBF" as extension name, while the bibliography file has ".DOC" as its extension name. Brief descriptions of the contents of these files are presented in the following paragraphs.

Diskette 1: Abiotic Factors

Diskette 1 contains the file called ABIOTICS.WK1 with information on physicochemical parameters of the Peruvian upwelling ecosystem. These were assembled from data presented by several authors as time series covering various periods from 1948 to 1989, but generally from 1953 to 1982.

Information on sea surface temperatures (SST) are given from a total of 9 shore stations along the coast of Peru (4°34'S to 17°38'S), based on various sources (see Table 1). Of the data taken from Muck et al. (1989), only those which represented actual observations were included, i.e., values estimated by interpolation or regression (see Muck, this vol.) were omitted.

Further time series related to upwelling are provided on the following upwelling-related parameters: turbulence, wind velocity, turbulence indices, Lasker events (for definition see Mendelssohn and Mendo (1987, footnote to Table 1) and Pauly (1989), upwelling indices, thermocline depth, offshore transport velocity (i.e., the quotient of Ekman transport and thermocling depth), Southern Oscillation Index, solar radiation, cloud cover, Rossby radius and, finally, nitrate concentrations and primary production estimates derived from the models presented in this volume. Table 1 gives a list of the headings in the LOTUS worksheet ABIOTICS.WK1 with more details on the parameters presented above, their units as well as the references to the papers from which each parameter was taken.

Diskette 2: Anchoveta Catch and Related Data

This diskette contains only one file named ANCHOV1.WK1. The bulk of this file consists of a time series, covering the period 1953 to 1987, of percent length-frequency data per centimer length class, adapted from Tables 1-30 of Tsukayama and Palomares (1987) and Tables 1-5 of Pauly and Palomares (this vol.). Also included are data on the monthly total catch of the fishery in tonnes as well as anchoveta condition factors (c.f.) for those months in which they could be computed from catch samples (i.e., c.f. values estimated from SST are not included).

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[a]Prepared by M.L. Palomares, A. Jarre and V. Sambilay, Jr., International Center for Living Aquatic Resources Management, MC P.O. Box 1501, Makati, Metro Manila, Philippines.

Table 1. Contents of file ABIOTICS. WKI on the Peruvian upwelling system.
Tabla 1. Contenido del archivo ABIOTICS. WK1 en el sistema de afloramiento peruano.

Field	Unit	Source
Mean Peru SST	°C	Pauly and Tsukayama (1987, Table 2)
Callao SST	°C	Muck et al. (1989)
Chimbote SST	°C	Muck et al. (1989)
Talara SST	°C	Brainard and McLain (1987, Table 2)
Paita SST	°C	Muck et al. (1989)
Chicama SST	°C	Muck et al. (1989)
Don Martin SST	°C	Muck et al. (1989)
Pisco SST	°C	Muck et al. (1989)
San Juan SST	°C	Muck et al. (1989)
Ilo SST	°C	Muck et al. (1989)
Mean SST for Central Area	°C	Brainard and Maclain (1987, Table 6)
Mean SST	°C	Bakun (1987, Table 2)
Turbulence	m^3/sec^3	Bakun (1987, Table 7)
Wind velocity (Trujillo)	m/sec	Mendo (unpub. data)[a]
Turbulence index (Trujillo)	m^3/sec^3	Mendo et al. (1987, Table 4)
Turbulence index (Callao)	m^3/sec^3	Mendo et al. (1987, Table 5)
Lasker events		Mendelssohn and Mendo (1987, Table 1)
Ocean. upwelling	m^3/sec per	Bakun and Mendelssohn (this vol., Table 1)
Upwelling (Trujillo)	m of coast	Mendo et al. (1987, Table 2)
Upwelling (Callao)		Mendo et al. (1987, Table 3)
Thermocline depth	m	Brainard and McLain (1987, Table 7)
Velocity	m/sec	Upwelling/thermocline
SOI	mbar	Brainard and McLain (1987, Table 1)
Solar radiation	watt/m^2	Bakun (1987, Table 8)
Cloud cover	-	Bakun (1987, Table 3)
Rossby radius	km	Mendo et al. (this vol., Fig. 2)
NO_3-Concentration at thermocline	mM/m^3[b]	Mendo et al. (this vol., Fig. 3)
NO_3-Concentration < = 60 km offshore	mM/m^3	Mendo et al. (this vol., Fig. 3)
Coastal NO_3-Flux (CDM) for Trujillo	mM/m/day	Mendo et al. (this vol., Fig. 4)
Coastal NO_3-Flux (CDM)	mM/m^2/day	Mendo et al. (this vol., Fig. 4)
Coastal NO_3-Flux (VDM) for Trujillo	mM/m/day	Mendo et al. (this vol., Fig. 4)
Coastal NO_3-Flux (VDM)	mM/m^2/day	Mendo et al. (this vol., Fig. 4)
Coastal primary production (CDM)	gC/m^2/day	Mendo et al. (this vol., Table 2)
Coastal primary production (VDM)	gC/m^2/day	Mendo et al. (this vol., Table 3)
NO_3-Concentration > 60 km offshore	mM/m^3	Mendo et al. (this vol., Fig. 3)
Oceanic NO_3-Flux (CDM) for Bakun's upwelling	mM/m/day	Mendo et al. (this vol., Fig. 4)
Oceanic NO_3-Flux (CDM)	mM/m^2/day	Mendo et al. (this vol., Fig. 4)
Oceanic NO_3-Flux (VDM) for Bakun's upwelling	mM/m/day	Mendo et al. (this vol., Fig. 4)
Oceanic NO_3-Flux (VDM)	mM/m^2/day	Mendo et al. (this vol., Fig. 4)
Oceanic primary production (CDM)	gC/m^2/day	Mendo et al. (this vol., Table 4)
Oceanic primary production (VDM)	gC/m^2/day	Mendo et al. (this vol., Table 5)
Primary production	gC/m^2/day	Chavez et al. (this vol., Table 2)

[a]These monthly mean wind velocity data are means of daily means, themselves based on 8 observations per day. These original observations are available, along with their associated directions (in degree), also for Callao, for the years 1953 to 1982 in the form of ASCII files on twelve 360 K 5 1/4" diskettes for MSDOS computers, from Mr. Jaime Mendo, c/o IMARPE, P.O. Box 22, Callao, Perú.

[b]mM = millimole.

Diskette 3: VPA Estimates of Anchoveta Biomass

This diskette consists of two files, ANCHOV2.WK1 and ANCHOV3.WK1. The former, ANCHOV2.WK1, contains monthly biomass estimates, by cm length class, for the Peruvian coast from 4-14°S, as obtained through the VPA III routine of the Compleat ELEFAN program package, and which were presented, for the years 1953 to 1982,

in Tables 5 to 33 of Pauly et al. (1987). This file also includes information on the total anchoveta biomass per month and the number of 3-month old fish recruited to the fishery. The estimated biomass of the parent stock, the estimated biomass of the mature females in the population and the number of eggs produced per month by the mature individuals in the population are also included, as estimated by Pauly and Soriano (1987). All biomass estimates are expressed in metric tonnes while recruitment and egg output are both expressed as number x 10^9 (i.e., in billions).

ANCHOV3.WK1 contains similar information except that this pertains to the reestimation of the total biomasses and of mature anchoveta presented in Pauly and Palomares (this vol.), and Pauly and Soriano (this vol.), respectively. Also, the catch and catch composition time series were updated to July 1987 based on more recent data (see Pauly and Palomares, this vol., and description of contents of diskette 2).

Diskette 4: Data on Predators and Predation

This diskette contains the file called PREDAT.WK1 which consists of time series data covering the period 1953-1982 on monthly abundance and/or biomasses of the major predators and their consumption of anchoveta. The major predators included are bonito, hake, mackerel and horse mackerel, three species of guano birds and two species of pinnipeds. Also included in the file are time series data from 1953 to 1985 on monthly anchoveta biomass as estimated from VPA III by Pauly and Palomares (this vol.). The time series of monthly nominal catch data in 1953-1982 from Tsukayama and Palomares (1987) and in 1983-1987 from Pauly and Palomares (this vol.) were included in this file such that any colleague interested in computing mortality caused by each predator does not need to use any other diskette. Three estimates of natural mortality, i.e., total (M), baseline (M_o) from Pauly et al. (1987) and baseline (M_o) from Pauly and Palomares (this vol.) are also included here (see Table 2 for details).

Table 2. Contents of file PREDAT.WK1 on the Peruvian upwelling system.[a]
Tabla 2. Contenido del archivo PREDAT. WK1 en el sistema de afloramiento peruano.

Headings	Units	Source
Date	month-year	
Anchoveta biomass	t	Pauly and Palomares (1989, Table 8)
Bonito biomass	t	Pauly et al. (1987, Table 6)
Anchoveta consumption by bonito	t/month	Pauly et al. (1987, Table 13)
Cormorant numbers	N x 10^6	Tovar et al. (1987, Table 3)
Cormorant biomass	10^3 t	Muck and Fuentes (unpub. data)
Anchoveta consumption by cormorants	t/month	Muck and Pauly (1987, Table 6)
Boobies numbers	N x 10^6	Tovar et al. (1987, Table 4)
Boobies biomass	10^3 t	Muck and Fuentes (unpub. data)
Anchoveta consumption by boobies	t/month	Muck and Pauly (1987, Table 7)
Pelican numbers	N x 10^6	Tovar et al. (1987, Table 5)
Pelican biomass	10^3 t	Muck and Fuentes (unpub. data)
Anchoveta consumption by pelicans	t/month	Muck and Pauly (1987, Table 8)
Sea lion biomass	t	Muck and Fuentes (1987, Table 7)
Total food consumption by sea lions	t/month	
Anchoveta consumption by sea lions	t/month	Muck and Fuentes (1987, Table 7)
Fur seal biomass	t	Muck and Fuentes (1987, Table 8)
Total food consumption by fur seals	t/month	
Anchoveta consumption by fur seals	t/month	Muck and Fuentes (1987, Table 8)
Mackerel abundance in MAR	t	Muck (1989, and unpub. data)
Anchoveta consumption by mackerels	t/month	Muck and Sánchez (1987, Table 13)
Horse mackerel abundance in MAR		Muck (1989, and unpub. data)
Anchoveta consumption by horse mackerel	t/month	Muck and Sánchez (1987, Table 14)
Hake abundance	N x 10^3	Espino and Wosnitza-Mendo (this vol., Table 3); Muck (1989: seasonal values, interpolated by month)
Anchoveta consumption by hake	t/month	Muck (1989, Table 4)
Anchoveta nominal catch	t/month	Tsukayama and Palomares (1987, Tables 1-30)
Anchoveta total natural mortality (M)	year	Pauly and Palomares (1989, Fig. 7)
Anchoveta baseline natural mortality (M_o)	year	Pauly et al. (1987, Table 3)
Anchoveta baseline natural mortality (M_o)	year	Pauly and Palomares (1989, Table 7, with interpolations)

[a]This file also contains the fishing effort data in Table 3 of Csirke (this vol.).

Diskette 5: Information on Egg Maps and Egg Mortality

This diskette consists of four files, namely: EGGNUM.WK1 and EGGMAPS.WK1. The first file, EGGNUM.WK1, summarizes the data on anchoveta egg surveys presented in Santander (1987) for the period 1964-1985. This file also includes derived statistics from Table 2 of Pauly and Soriano (this vol.) such as the daily reproductive output expressed as number of eggs ($Nx10^{12}$), the biomass (in $tx10^6$) of the anchoveta parent stock and of the sardine population, the anchoveta egg development time (in days) and observed and predicted total egg mortality (Z, day). Note that the column in the spreadsheet labeled "midmonth" represents the month on which the center of the sampling survey period fell.

The second file, EGGMAPS.WK1, contains a detailed analysis, per half degree square of the egg standing stocks off Peru obtained from Santander's (1987) egg survey maps as performed by Senocak et al. (this vol.). The file is organized such that the column headings indicate the dates of each survey (from start to finish) with their corresponding "midmonths" (the same as the "midmonths" in EGGNUM.WK1, see above) and the map numbers (in Santander 1987). The rows refer to the different half degree squares (see Fig. 1 in Senocak et al., this vol.); the cells give the egg standing stock estimates of each half degree square. Note that the coordinates of each square are expressed both in terms of degrees (longitude and latitude) and as vertical and horizontal code numbers (i.e., X-axis and Y-axis codes, see Fig. 1 in Senocak et al., this vol.). The following two conventions were used throughout the spreadsheet: (1) 0.00 means that the half degree square in question was sampled but that no eggs were found; and (2) -9 means that the half degree square containing this value was not sampled at all.

Diskettes 6-10: Picture Files of Egg Maps

These diskettes contain a program called DIASHOW.EXE and picture files which allow for a graphics display of Santander's egg survey maps. Diskettes 6-8 contain the picture files of the original 90 egg survey maps as presented in Figs. 3 to 25 of Santander (1987), while diskettes 9-10 contain the picture files of the mean monthly anchoveta egg distributions presented in Fig. 6 of Senocak et al. (this vol.) as derived from the original 90 egg survey maps. Please note that the DIASHOW.EXE program runs only on a HERCULES or compatible graphics card.

It should also be noted that, in order to access the graphics from diskettes 6-8, the contents of all three diskettes must first be copied onto a hard disk sub-directory. Then go into this subdirectory and view the maps by typing DIASHOW LIST at the C> prompt. The program will ask for the user to press either the spacebar to continue viewing or "e" to exit.

The monthly egg maps in diskettes 9 and 10 were arranged into two groups of 12 each, one for the period 1964-1971 (diskette 9) and the other for 1972-1986 (diskette 10). Thus, in order to view the egg maps for 1964-1971, type DIASHOW LIST1 at the A> prompt with diskette 6 in drive A; to view the maps for 1972-1986, type DIASHOW LIST2 with diskette 7 in drive A.

DIASHOW will then require that the user presses the spacebar to continue or to press "e" to exit the program. The next screen shows a title page in German which is here translated as:

Simulation
of the egg distribution of *Engraulis ringens*
off Peru
in two year groups (1964-1971, 1972-1986)

then, press the spacebar to go to the next screen which shows

1.
Year group
(1964-1971)

Pressing the spacebar again gives on screen the "climatological" average map for the month of January and so on until the last map for the month of December. Typing DIASHOW LIST2 with diskette 7 in drive A will put on screen the maps for each month of the second year group. Note that pressing "e" at any time while the DIASHOW program runs will abort its execution and bring the user back to the A> prompt.

Diskettes 11-13: The Anchoveta Database

The information available on the food and feeding and reproduction of anchoveta in the raw data sheets of Rojas de Mendiola (this vol.) and Alamo (this vol.) were used to create one DBASE III Plus database, consisting of 28 fields and 9,735 records in total. Each record represents one single specimen of anchoveta.

A detailed description of the fields is given in Table 3. For the coding system of the available information see Rojas de Mendiola (this vol.), Alamo (this vol.) and Pauly et al. (this vol.). Missing information in the raw data sheets were generally coded with -9 in the database, except for the fields describing the food items of anchoveta: empty records for the latter (six) fields were coded as "0". If only qualitative information on anchoveta eggs in the stomach was available, this information was coded as "-9" in the "ancheggs" field. In this case, "0" refers to observation of zero anchoveta eggs in the stomach.

Table 3. Definition of data fields in the Rojas/Alamo anchoveta database.
Tabla 3. Definición de campos de datos en la base de datos para anchoveta Rojas/Alamo.

Field no.	Name	Field description	Value Minimum	Value Maximum	Number of values > 0[a]	Remarks
Information on sampling location						
1	SAMPLENO	Sample number as stated in raw data sheets	1	9,260	9,735	
2	S-DAY	Day of sampling	1	31	9,678	
3	S-MONTH	Month of sampling	1	12	9,725	
4	S-YEAR	Year of sampling	1,953	1,982	9,725	
5	S-TIME	Time of sampling	9	2,400	7,665	Midnight = 2,400
6	DEG-S	Latitude position of sample (in degrees)	4.5	19.4	9,527	Generally: central points of Marsden squares
7	DEG-W	Longitude position of sample (in degrees)	70.5	82.5	9,258	
8	TEMP	Sea surface temperature (in °C)	12.5	25.6	7,471	
Biological information on fish sampled						
9	LENGTHMM	Total body length (in mm)	30	201	9,782	SL converted to TL if necessary (Tsukayama and Palomares 1987)
10	WEIGHTGR	Total body wet/weight (in g)	1.1	57.9	6,630	
11	GUTMM	Length of the digestive tract (in mm)	13	460	2,396	
12	STOMCONTGR	Weight of the stomach content (in g)	0	5.7	6,966	
13	EVISWTGR	Body weight of gutted fish (in g)	0.9	44.2	2,055	
14	GONADWTGR	Weight of the gonads (in g)	0.01	1.29	1,166	
15	VISCERFAT	Amount of fat surrounding the intestines	0	3	4,604	See Alamo (this vol.) for scale
16	DIGESTAGE	Stage of digestion of the stomach content	0	1	3,678	
17	FULLNESSGA	Fullness index of the gastric part of the stomach	0	1	4,905	See Rojas de Mendiola (this vol.) for scale
18	FULLNESSPY	Fullness index of the pyloric part of the stomach	0	1	3,576	
19	GONADSTAGE	Maturity stage of the gonads	I	VII	6,115	
20	SEX	Sex of fish	0	1	7,003	Females 0 - 3,361 records; Males 1 - 3,642 records
Information on ingested food[a]						
21	ZF	"Zooplankton Fraction": percent of zooplankton in diet	0	100	6,416	
22	ANCHEGGS	Number of anchoveta egg in the stomach	1	319	1,178[b]	
23	FOOD-1	Food items in the stomach	1	14	6,530	
24	FOOD-2	Food items in the stomach	1	14	5,711	
25	FOOD-3	Food items in the stomach	1	14	4,872	
26	FOOD-4	Food items in the stomach	1	14	2,092	
27	FOOD-5	Food items in the stomach	1	14	336	
28	FOOD-6	Food items in the stomach	1	14	31	

[a]For fields no. 22-28, the numbers refer to values > 0.
[b]In this field, "-9" means some eggs were present, but their number is not known.

For coding of the sampling positions, the center of the squares used for locating samples in the raw data sheets (see Fig. 1 in Rojas de Mendiola, this vol., and Fig. 2 in Alamo, this vol.) was taken as representative of the whole square and re-expressed in degrees latitude (S) and longitude (W). Erroneous entries for the sampling location were adjusted longitudinally when they resulted in sampling "on land".

Single stomach fullness observations in the raw data sheet were taken as referring to the gastric part of the stomach; when two entries for stomach fullness occurred, the first was recorded as pertaining to the gastric part, and the second, to the pyloric part. Maturity stage "VII" (recuperating), as given in the original data sheets, was set to stage "II", which thus represent either (smaller) "immature" or (larger) "recuperating" specimens. Missing entries in the sea surface temperature field ("temp") were completed using temperature values of the same sampling month, year and at the same sampling position when available. For inshore data, filling of gaps was performed based on monthly means SST values in Rojas de Mendiola (1958), Zuta and Urquizo (1972), Zuta et al. (1983), Zuta et al. (1984), Brainard and McLain (1987), Senocak et al. (this vol.), Tsukayama (this vol.), or based on three-month means (Urquizo et al. 1987). For offshore data, filling of gaps was achieved by extrapolation of inshore temperatures according to the inshore-offshore temperature gradient off Chimbote.

A number of "logic-checks" were then performed on the database in order to detect biologically inconsistent entries. Details are provided in Table 4. First of all, range checks were performed for each field. Then, obvious relationships between two fields were checked (e.g., if the weight of the stomach content is "0", the digestion stage of the stomach content must be "-9"). Finally, some numerical relations between two or more fields were examined: their ratio (e.g. the gonadosomatic index) was calculated, their frequency distribution examined for outliers, and these were set to "-9" in the database.

Table 4. Details on quality and logic checks of entries in the Rojas/Alamo anchoveta database.
Tabla 4. Detalles acerca de la calidad y verificaciones lógicas en la base de datos de Rojas/Alamo sobre anchoveta.

No.	Condition	Changes if conditions not met
1	LENGTHMM < 210	Whole record excluded
2	WEIGHTGR > 60	WEIGHTGR set to -9
3	STOMCONTGR = 0 --> FULLNESSGA = 0 or FULLNESSGA = -4	FULLNESSGA set to -9
4	STOMCONTGR = 0 --> FULLNESSPY = 0 or FULLNESSPY = -9	FULLNESSPY set to -9
5	STOMCONTGR = 0 and FULLNESSGA = 0 --> FULLNESSPY = 0	FULLNESSPY set to 0
6	STOMCONTGR = 0 --> DIGESTAGE = -4	DIGESTAGE set to -9
7	STOMCONTGR = 0 --> ANCHEGGS = 0	STOMCONTGR set to -9
8	ZF = 100 --> FOOD-1 . . . FOOD-6 ≠ 2 . . . 8	ZF set to -9
9	ZF = 0 --> FOOD-1 . . . FOOD-6 = 2 . . . 8 or FOOD-1 . . . FOOD-6 = -9	ZF set to -9
10	If WEIGHTGR ≠ -9: STOMCONTGR + GONADWTGR + EVISWTGR ≤ WEIGHTGR	Values checked separately, erroneous values set to -9 (missing values set to 0)
11	If EVISWTGR ≠ -9: STOMCONTGR + GONADWTGR ≤ EVISWTGR	Values checked separately, erroneous values set to -9 (missing values set to 0)
12	$0.3 \leq$ WEIGHTGR * 100 / (LENGTHMM 10)$^3 \leq 1.2$	WEIGHTGR set to -9
13	20 ≤ GUTMM * 100 / LENGTHMM ≤ 250	GUTMM set to -9
14	50 ≤ EVISWTGR * 100 / WEIGHTGR < 100	EVISWTGR set to -9
15	0 ≤ GONADWTGR * 100 / EVISWTGR < 9	GONADWTGR set to -9
16	0 ≤ STOMCONTGR * 100 / WEIGHTGR < 10	STOMCONTGR set to -9

If the weight of the stomach content was "0", but non-zero entries had been made under the "food items" fields, it was assumed that the food composition had been derived based on examination of other parts of the intestines; also, the "zooplankton fraction" (ZF) was accepted, but not the entries on the digestion stage of the food, as the latter was assumed to pertain exclusively to the condition of food in the stomach.

Table 5 is a facsimile of a sample printout of the database, pertaining to entries nos. 3271 to 3321.

Note that the Rojas/Mendiola database, as described above, can only be run on a hard disk, using the DBASE III+ program (not included here). Run RESTORE (of DOS 3.2) to access the file using the path C:\DBASE\ANCHOVET\ANCHOVET.DBF.

Table 5. Facsimile of a sample printout of the Rojas/Alamo anchoveta database, for entries No. 3271 to 3321 (see also Table 4).

Tabla 5. Facsimil de una impresión de muestra de la base de datos de Rojas/Alamo sobre anchoveta para entradas del No. 3271 a 3321 (ver además Tabla 4).

SAMPLE No.	DAY	MONTH	YEAR	TIME	DEG_S	DEG_W	TEMP	LENGTH (mm)	WEIGHT (gr)	GUT (mm)	STOMCONT (gr)	EVISWT (gr)	GONADWT	FAT	DIGESTAGE	FULLNESS GASTRIC	FULLNESS PYLORIC	GONAD-STAGE	SEX	IF	ANCHEGGS	FOOD_1	FOOD_2	FOOD_3	FOOD_4	FOOD_5	FOOD_6
3271	19	9	1974	400	11.5	77.5	14.7	195	-9.0	460	0.52	-9.0	-9.00	-9	0.50	1.00	0.60	V	1	1	42	2	6	5	14	0	0
3272	6	8	1975	721	10.5	77.5	14.9	151	26.0	185	0.04	-9.0	-9.00	0	0.50	0.00	0.40	V	1	0	0	6	6	5	0	0	0
3273	6	8	1975	721	10.5	77.5	14.9	156	26.5	250	0.04	-9.0	-9.00	1	0.50	0.00	0.40	V	1	0	0	6	6	5	0	0	0
3274	6	8	1975	721	10.5	77.5	14.9	148	23.7	190	0.03	-9.0	-9.00	1	0.50	0.00	0.40	V	1	20	0	6	6	5	0	0	0
3275	6	8	1975	721	10.5	77.5	14.9	165	32.0	220	0.05	-9.0	-9.00	1	0.50	0.40	0.60	VI	1	5	2	6	6	12	0	0	0
3276	6	8	1975	721	10.5	77.5	14.9	154	27.0	215	0.02	-9.0	-9.00	1	0.50	0.00	0.40	V	1	15	0	6	6	12	0	0	0
3277	6	8	1975	721	10.5	77.5	14.9	160	30.0	215	0.02	-9.0	-9.00	-9	0.50	0.00	0.40	VI	1	30	0	6	6	12	0	0	0
3278	6	8	1975	721	10.5	77.5	14.9	162	29.5	180	0.04	-9.0	-9.00	2	0.50	0.00	0.40	VI	1	15	0	6	6	12	0	0	0
3279	6	8	1975	721	10.5	77.5	14.9	158	26.5	205	0.04	-9.0	-9.00	2	0.50	0.00	0.40	VI	1	20	0	6	6	12	0	0	0
3280	6	8	1975	721	10.5	77.5	14.9	163	29.0	190	0.02	-9.0	-9.00	2	0.50	0.00	0.40	VI	1	20	0	6	6	12	0	0	0
3281	6	8	1975	721	10.5	77.5	14.9	160	29.0	205	0.04	-9.0	-9.00	2	0.00	0.00	0.40	VI	1	-9	0	0	0	0	0	0	0
3282	6	8	1975	800	17.5	71.5	16.0	150	38.6	200	0.06	-9.0	-9.00	2	0.50	0.00	0.60	V	0	2	0	6	6	6	14	0	0
3283	6	8	1975	800	17.5	71.5	16.0	135	-9.0	160	0.03	-9.0	-9.00	2	0.50	0.00	0.60	V	1	2	0	6	6	6	0	0	0
3284	6	8	1975	800	17.5	71.5	16.0	170	33.5	150	0.05	-9.0	-9.00	2	0.50	0.00	0.60	V	0	1	0	6	6	6	0	0	0
3285	6	8	1975	800	17.5	71.5	16.0	157	31.0	180	0.07	-9.0	-9.00	-9	0.50	0.00	0.60	V	1	2	0	6	6	6	0	0	0
3286	6	8	1975	800	17.5	71.5	16.0	150	21.2	180	0.17	-9.0	-9.00	1	0.50	0.60	1.00	V	1	1	6	6	6	6	0	0	0
3287	6	8	1975	800	17.5	71.5	16.0	158	28.0	160	0.12	-9.0	-9.00	-9	0.50	0.60	1.00	V	1	0	1	6	6	6	0	0	0
3288	6	8	1975	800	17.5	71.5	16.0	149	23.5	155	0.18	-9.0	-9.00	-9	0.50	0.40	1.00	V	1	1	0	6	6	6	0	0	0
3289	6	8	1975	800	17.5	71.5	16.0	162	28.5	221	0.10	-9.0	-9.00	-9	0.50	0.40	0.60	V	1	0	4	6	6	6	0	0	0
3290	6	8	1975	800	17.5	71.5	16.0	165	31.5	180	0.15	-9.0	-9.00	-9	0.50	0.00	1.00	V	1	0	4	6	6	6	0	0	0
3291	6	8	1975	800	17.5	71.5	16.0	158	26.6	185	0.50	-9.0	-9.00	-9	0.50	1.00	1.00	V	1	1	1	6	6	6	0	0	0
3292	6	8	1975	930	17.5	71.5	14.9	155	29.1	160	0.03	-9.0	-9.00	-9	0.50	0.40	0.40	V	0	10	1	9	6	1	0	0	0
3293	6	8	1975	930	17.5	71.5	14.9	158	25.8	220	0.07	-9.0	-9.00	-9	0.50	0.40	1.00	V	0	10	0	9	6	1	0	0	0
3294	6	8	1975	930	17.5	71.5	14.9	156	27.5	185	0.06	-9.0	-9.00	-9	0.50	0.40	1.00	V	1	5	8	9	6	1	0	0	0
3295	6	8	1975	930	17.5	71.5	14.9	156	24.5	182	0.06	-9.0	-9.00	-9	0.50	0.40	0.40	V	1	10	1	9	6	1	0	0	0
3296	6	8	1975	930	17.5	71.5	14.9	158	25.3	197	-9.00	-9.0	-9.00	-9	-9.00	0.00	0.00	V	1	-9	0	0	0	0	0	0	0
3297	6	8	1975	930	17.5	71.5	14.9	153	25.8	190	0.04	-9.0	-9.00	-9	0.50	0.00	0.40	V	1	15	0	9	6	1	0	0	0
3298	6	8	1975	930	17.5	71.5	14.9	156	25.4	242	0.05	-9.0	-9.00	-9	0.50	0.00	0.40	V	1	10	0	9	6	1	0	0	0
3299	6	8	1975	930	17.5	71.5	14.9	162	35.7	190	0.14	-9.0	-9.00	-9	0.50	0.00	1.00	V	1	15	0	9	6	1	0	0	0
3300	6	8	1975	930	17.5	71.5	14.9	168	31.0	165	0.09	-9.0	-9.00	-9	0.50	0.00	1.00	V	0	10	0	9	6	1	0	0	0
3301	6	8	1975	930	17.5	71.5	14.9	169	40.6	220	0.10	-9.0	-9.00	-9	0.50	0.00	0.40	V	1	15	0	9	6	1	0	0	0
3302	6	8	1975	1040	8.5	79.5	16.1	188	44.8	235	0.06	-9.0	-9.00	-9	0.50	1.00	0.60	V	0	10	0	6	6	6	0	0	0
3303	6	8	1975	1040	8.5	79.5	16.1	182	38.3	192	0.14	-9.0	-9.00	-9	0.50	0.00	1.00	V	1	5	0	6	6	6	0	0	0
3304	6	8	1975	1040	8.5	79.5	16.1	188	43.7	263	0.09	-9.0	-9.00	-9	0.50	0.00	1.00	V	0	10	0	6	6	14	0	0	0
3305	6	8	1975	1040	8.5	79.5	16.1	163	29.7	200	0.22	-9.0	-9.00	1	0.50	0.00	1.00	V	0	15	0	6	6	2	14	0	0
3306	6	8	1975	1040	8.5	79.5	16.1	190	45.5	295	0.06	-9.0	-9.00	1	0.50	0.00	0.60	V	0	15	0	6	0	0	0	0	0
3307	6	8	1975	1040	8.5	79.5	16.1	140	17.8	130	0.04	-9.0	-9.00	1	0.50	0.00	1.00	V	1	20	0	6	6	2	14	0	0
3308	6	8	1975	1040	8.5	79.5	16.1	140	17.7	120	0.06	-9.0	-9.00	1	0.25	0.40	1.00	V	1	15	0	6	14	0	0	0	0
3309	6	8	1975	1040	8.5	79.5	16.1	168	30.3	230	0.07	-9.0	-9.00	1	0.50	1.00	1.00	V	0	30	0	6	6	2	14	0	0
3310	6	8	1975	1040	8.5	79.5	16.1	166	29.6	205	0.14	-9.0	-9.00	1	0.50	1.00	1.00	V	1	10	2	6	6	2	14	0	0
3311	6	8	1975	1040	8.5	79.5	16.1	160	27.2	202	0.07	-9.0	-9.00	1	0.50	0.00	1.00	V	1	15	0	6	6	2	0	0	0
3312	6	8	1975	1040	17.5	71.5	15.2	162	39.0	195	0.03	-9.0	-9.00	2	0.50	0.40	0.40	V	0	60	9	12	6	3	0	0	0
3313	6	8	1975	1040	17.5	71.5	15.2	157	33.0	220	0.04	-9.0	-9.00	3	0.50	0.00	0.40	V	1	30	2	6	3	9	12	0	0
3314	6	8	1975	1040	17.5	71.5	15.2	155	30.5	205	-9.00	-9.0	-9.00	2	-9.00	0.00	1.00	V	1	-9	0	0	0	0	0	0	0
3315	6	8	1975	1040	17.5	71.5	15.2	160	46.5	253	0.03	-9.0	-9.00	3	0.25	0.00	0.40	V	1	-9	0	12	6	3	0	0	0
3316	6	8	1975	1040	17.5	71.5	15.2	172	30.0	235	0.02	-9.0	-9.00	2	0.00	0.00	0.40	V	0	-9	0	0	0	0	0	0	0
3317	6	8	1975	1040	17.5	71.5	15.2	152	31.0	130	0.03	-9.0	-9.00	1	0.50	0.00	0.40	V	1	60	0	12	6	9	0	0	0
3318	6	8	1975	1040	17.5	71.5	15.2	157	28.3	176	0.01	-9.0	-9.00	1	0.00	0.00	0.40	V	1	-9	0	0	0	0	0	0	0
3319	6	8	1975	1040	17.5	71.5	15.2	173	40.5	195	0.05	-9.0	-9.00	2	0.50	0.40	0.60	V	0	50	72	12	6	3	0	0	0
3320	6	8	1975	1040	17.5	71.5	15.2	161	35.0	245	0.07	-9.0	-9.00	2	0.50	0.40	0.60	V	1	100	0	12	0	0	0	0	0
3321	6	8	1975	1040	17.5	71.5	15.2	159	31.0	195	0.05	-9.0	-9.00	3	0.50	0.00	0.60	V	0	90	0	12	6	0	0	0	0

References

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1972 to 1984, p. 14-45. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.). The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Mendo, J., L. Pizarro and S. Castillob. 1987. Monthly turbulence and Ekman transport indexes, 1953 to 1985, based on local wind records from Trujillo and Callao, Perú, p. 75-88. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and G. Sanchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P., I. Tsukayama and E. Ferrandis. 1989. Temperaturas superficiales del mar a lo largo de la costa peruana para el período 1950-1988. Inf. Inst. Mar Perú-Callao 95: 1-26.

Pauly, D. 1989. An eponym for Reuben Lasker. U.S. Fish. Bull. 87(3): 383-384.

Pauly, D. and M. Soriano. 1987. Monthly spawning stock and egg production of Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1982, p. 167-178. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. and I. Tsukayama, editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., M.L. Palomares and F.C. Gayanilo. 1987. VPA estimates of the monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Rojas de Mendiola, B., 1958. Breve estudio sobre la variación cualitativa anual del plancton superficial de la bahia de Chimbote. Cia. Admin. Guano, Suplemento Científico 34(12): 7-17.

Santander, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru, 4-14°S, p. 179-207. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Tovar, H., V. Guillen and M.E. Nakama. 1987. Monthly population size of three guano bird species off Peru, 1953 to 1982, p. 208-218. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Tsukayama, I. and M.L. Palomares. 1987. Monthly catch and catch composition of Peruvian anchoveta *(Engraulis ringens)* (northern-central stock, 4-14°S), 1953-1982, p. 89-108. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Urquizo, W., C. Wosnitza-Mendo, E. Valdivia and C. Moreno, 1987. Catalogo de datos oceanograficos (T,S,Y,O_2 por estaciones del año en diferentes profundidades frente a la costa peruana, período 1970-1985. Bol. Inst. Mar Perú-Callao, Volumen Extraordinario. 445 p.

Zuta, S. and Urquizo, W. 1972. Temperatura promedio de la superficie del mar frente a la costa peruana, período 1928-1969. Bol. Inst. Mar Perú-Callao 2(8): 462-519.

Zuta, S., I. Tsukayama and R. Villanueva. 1983. El ambiente marino y las fluctuaciones de las principales poblaciones pelágicas de la costa peruana. *In* Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. No. 291. Vol. 2.

Zuta, S., M. Farfán and O. Morón. 1984. Características principales del mar frente al Perú durante la evolución del evento El Niño 1982-1983, p.141-177. *In* Rev. Com. Perm. Pacífico Sur No. 15, Comisión Permanente del Pacífico Sur, Quito, Ecuador.

Appendix II

Publications of the Programa Cooperativo Peruano-Aleman de Investigación Pesquera (PROCOPA) 1982-1989

No.	References*
1	Santander, H., P.E. Smith and J. Alheit. 1982. Determination of sampling effort required for estimating egg production of anchoveta, *Engraulis ringens*, off Peru. Bol. Inst. Mar Perú-Callao 7(1): 1-18.
2	Rosenberg, R., W.E. Arntz, E. Chumán de Flores, G. Carbajal, I. Finger and J. Tarazona. 1983. Benthos biomass and oxygen deficiency in the upwelling system of Peru. J. Mar. Res. 41: 263-279.
3	Smith, P.E., H. Santander and J. Alheit. 1983. Technical detail of a cruise plan for the anchoveta spawning biomass estimate. Bol. Inst. Mar Perú-Callao 7(2): 19-48.
4	Villavicencio, Z. and P. Muck. 1983. Costos metabólicos de *Engraulis ringens* y *Sardinops sagax* en relación al peso, temperatura y nivel de actividad. Bol. Inst. Mar Perú-Callao 7(3): 49-68.
5	Villavicencio, Z. and P. Muck. 1983. La ración de mantenimiento, la densidad de mantenimiento y la eficiencia de crecimiento de *Engraulis ringens* y *Sardinops sagax* como una medida de su potencia ecológica. Bol. Inst. Mar Perú-Callao 7(4): 69-108.
6	Samamé, M., M. Espino, J. Castillo, A. Mendieta and U. Damm. 1983. Evaluación de la población de merluza y otras especies demersales en el área Pto. Pizarro-Chimbote (Cr. Bic Humboldt 8103-04, Marzo-Abril 1981). Bol. Inst. Mar Perú-Callao 7(5): 111-191.
7	Alheit, J., B. Alegre, V.H. Alarcón and B.J. Macewicz. 1983. Batch fecundity and spawning frequency of various anchovy (Genus: *Engraulis*) populations from upwelling areas and their use for spawning biomass estimates. FAO Fish. Rep. 291(3): 977-985.
8	Santander, H., J. Alheit, A.D. MacCall and A. Alamo. 1983. Egg mortality of the Peruvian anchovy *(Engraulis ringens)* caused by cannibalism and predation by sardines *(Sardinops sagax)*. FAO Fish. Rep. 291(3): 1011-1025.
9	Smith, P.E., H. Santander and J. Alheit. 1983. Comparison of egg sample probability distributions of the anchovy *(Engraulis ringens)* off Peru and the anchovy *(E. mordax)* and the sardine *(Sardinops caerulea)* off California. FAO Fish. Rep. 291(3): 1027-1038.
10	Wolff, M. and R. Wolff. 1983. Observations on the utilization and growth of the pectinid *Argopecten purpuratus* (L.) in the fishing area of Pisco, Peru. Bol. Inst. Mar. Perú-Callao 7(6): 192-235.
11	Goldberg, S.R., V.H. Alarcón and J. Alheit. 1984. Postovulatory follicle histology of the Pacific sardine, *Sardinops sagax*, from Peru. U.S. Fish. Bull. 82: 443-445.
12	Santander, H., J. Alheit and P.E. Smith. 1984. Estimación de la biomasa de la población desovante de anchoveta peruana *Engraulis ringens* en 1981 por aplicación del "Método de Producción de Huevos". Bol. Inst. Mar Perú-Callao 8(6): 209-250.

Editors' note: Most of the documents listed as "unpublished MS" will be submitted or published in 1990.

13 Alarcón, V.H., S.R. Goldberg and J. Alheit. 1984. Histología de folículos post-ovulatorios de la sardina *(Sardinops sagax)* del Perú. Bol. Inst. Mar Perú-Callao 8(1): 1-15.

14 Pauly, D. and I. Tsukayama. 1983. On the seasonal growth, monthly recruitment and monthly biomass of Peruvian anchoveta *(Engraulis ringens)* from 1961 to 1979. FAO Fish. Rep. 291(3): 987-1004.

15 Alheit, J., V.H. Alarcón and B.J. Macewicz. 1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. Calif. Coop. Oceanic Fish. Invest. Rep. 25: 43-52.

16 Espino, M. and C. Wosnitza-Mendo. 1984. Manuales de evaluación de peces. N° 1. Area Barrida. Informe Inst. Mar Perú-Callao (86): 1-31.

17 Espino, M., C. Wosnitza-Mendo and U. Damm. 1984. Análisis de la pesquería de la merluza peruana *(Merluccius gayi peruanus)*. Bol. Inst. Mar Perú-Callao 8(2): 17-68.

18 Espino, M. and C. Wosnitza-Mendo. 1984. Manuales de evaluación de peces. N° 2. Análisis de cohortes. Informe Inst. Mar Perú-Callao 87. 23 p.

19 Villavicencio, Z. and P. Muck. 1984. Estudio de otolitos de *Odonthestes regia r.*, pejerrey: determinación de edad. Bol. Inst. Mar Perú-Callao 8(3): 69-100.

20 Mendo, J. 1984. Edad, crecimiento y algunos aspectos reproductivos y alimentarios de la caballa *(Scomber japonicus peruanus)*. Bol. Inst. Mar Perú-Callao 8(4): 101-156.

21a Espino, M., C. Wosnitza-Mendo and R. Castillo. 1984. La pesca de arrastre de la flota costera de Paita entre 1970-1982. Bol. Inst. Mar Perú-Callao 8(5): 159-178.

21b Espino, M. and C. Wosnitza-Mendo. 1984. La relación entre stock y reclutamiento de la merluza peruana *(Merluccius gayi peruanus)*. Bol. Inst. Mar Perú-Callao 8(5): 179-189.

21c Espino, M. and C. Wosnitza-Mendo. 1984. El uso del modelo de Csirke-Caddy para la merluza peruana *(Merluccius gayi peruanus)*. Bol. Inst. Mar Perú-Callao 8(5): 191-205.

22 Wosnitza-Mendo, C. and M. Espino. 1986. The impact of "El Niño" on recruitment in the Peruvian hake *(Merluccius gayi peruanus)* Meeresforsch. 31(1): 47-51.

23 Muck, P., B. Rojas de Mendiola and E. Antonietti. 1989. Comparative studies on feeding in larval anchoveta *(Engraulis ringens)* and sardine *(Sardinops sagax)*, p. 86-96. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

24 Arntz, W., A. Landa and J. Tarazona, editors. 1985. El Niño: su impacto en la fauna marina. Bol. Inst. Mar. Perú-Callao. Volumen Extraordinario. 222 p.

25 Espino, M. and C. Wosnitza-Mendo. 1986. Peruvian hake fisheries from 1971 to 1982. Calif. Coop. Oceanic Fish. Invest. Rep. 27: 113-120.

26 Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15.

27 Wosnitza-Mendo, C., M. Espino, T. Dioses, E. Sánchez and A. Pereda. 1985. Rendimiento de equilibrio de la merluza peruana *(Merluccius gayi peruanus)* y propuestas para su manejo. Bol. Inst. Mar Perú-Callao. 9(2): 67-92.

28 Lo, N.C.H., J. Alheit and B. Alegre. 1986. Fecundidad parcial de la sardina peruana *(Sardinops sagax)*. Bol. Inst. Mar Perú-Callao. 10(2): 45-60.

29 Alegre, B. and J. Alheit. 1986. Un nuevo método para la determinación de la fecundidad de la sardina peruana *(Sardinops sagax)*. Bol. Inst. Mar Perú-Callao. 10(3): 61-90.

30 Smith, P.E., H. Santander and J. Alheit. Comparison of the mortality and dispersal of sardine *(Sardinops sagax)* and anchovy *(Engraulis ringens)* eggs off Peru. (In press).

31 Alheit, J. 1985. Egg production method for spawning biomass estimates of anchovies and sardines. ICES C.M. 1985/H: 41, 10 p.

32 Peña, N., J. Alheit and M.E. Nakama. 1986. Fecundidad parcial de la caballa del Perú *(Scomber japonicus peruanus)*. Bol. Inst. Mar Perú-Callao 10(4): 91-104.

33 Benites, C. and V. Valdivieso. 1986. Resultados de la pesca exploratoria de 1979/80 y desembarque de cefalópodos pelágicos en el litoral peruano. Bol. Inst. Mar Perú-Callao. 10(5): 105-139.

34 Mendo, J. and J. Vélez. 1986. Contribución a la identificación de los especies de cachema, *Cynoscion analis* y *Cynoscion altipinnis* (Pisces: Sciaenidae) de la costa norte del Perú. Bol. Inst. Mar Perú-Callao 10(6): 140-164.

35 Cardenas, G. and J. Mendo. 1985. Preliminary length-based growth parameter estimates of Peruvian sardine *(Sardinops sagax sagax)*. Fishbyte 3(3): 10-12.

36 Castillo, S. and J. Mendo. 1987. Estimation of unregistered Peruvian anchoveta *(Engraulis ringens)* in official catch statistics, 1951 to 1982, p. 109-116. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15.

37 Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15.

38 Espino, M., J. Castillo, F. Fernández, A. Mendieta, C. Wosnitza-Mendo and J. Zeballos. 1986. El stock de merluza y otros demersales en Abril de 1985. Crucero Bic Humboldt (23 de Marzo al 5 de Abril, 1985). Informe Inst. Mar Perú-Callao, Nº 89. 57 p.

39 Wosnitza-Mendo, C. and M. Espino. 1986. La construcción de curvas de rendimiento sostenible (Shepherd 1982) para la merluza peruana. Bol. Inst. Mar Perú-Callao 10(7): 165-183.

40 Mendo, J. 1987. Edad y crecimiento de una especie de cachema *Cynoscion analis* de la zona frente a Paita, Perú. Bol. Inst. Mar Perú-Callao 11(1): 1-39.

41 Mendo, J., L. Pizarro and S. Castillo. 1987. Monthly turbulence and Ekman transport indices, 1953 to 1985, based on local wind records from Trujillo and Callao, Peru, p. 75-88. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15.

42 Mendo, J., L. Pizarro and A. Huaytalla. 1987. Reporte de datos sobre índices de afloramiento y turbulencia diarios para Trujillo y Callao, Perú, 1953-1985. Bol. Inst. Mar Perú-Callao 11(2): 40-117.

43 Muck, P. and G. Sanchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly

and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15.

44 Espino, M. and C. Wosnitza-Mendo. 1988. Efecto de la concentración en la mortalidad natural y su aplicación en el análisis de cohortes, p. 235-252. *In* T. Wyatt and M.G. Larrañeta (eds.) Long-term changes in marine fish population. A symposium held in Vigo, Spain, 18-21 November 1986, Vigo.

45 Pauly, D., I. Tsukayama and H. Tovar. 1986. Some preliminary results from an international multidisciplinary project aimed at reconstructing monthly time series on the Peruvian ecosystem for the years 1953-1982. *In* Chapman Conference on El Niño: an International Symposium, 27-31 October 1986, Guayaquil, Ecuador. Vol. of Abstracts, 45 p.

46 Pauly, D. and I. Tsukayama, editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

47 Mendo, J., L. Pizarro and S. Castillo. 1987. Daily upwelling and turbulence indices off the Peruvian coast at Callao and Trujillo during the period 1953-1983. Tropical Ocean-Atmosphere Newsletter 42: 4-7.

48 Cárdenas, G. 1987. Estudios de la edad y crecimiento de la sardina *Sardinops sagax sagax* de la región central del Perú. Bol. Inst. Mar Perú-Callao 11(3): 118-145.

49 Salzwedel, H., L.A. Flores, G. Carbajal, E. Canahuire, A. Zafra and C. Aranda. 1987. Información básica sobre muestras de bentos, sedimentos y factores abióticos en la plataforma continental del Peru entre 1976 y 1987. Informe Inst. Mar Perú-Callao 90: 1-41.

50 Sanchez de Benites, G. and P. Muck. 1987. La situación alimentaria del jurel *Trachurus murphyi* Nichols en un año normal (1979) y el El Niño 1982/83. Bol. Inst. Mar Callao-Perú 11(4): 146-177.

51 Tarazona, J., H. Salzwedel and W. Arntz. 1988. Oscillations of macrobenthos in shallow waters of the Peruvian central coast induced by El Niño 1982-83. J. Mar. Res. 46(3): 593-611.

52 Palomares, M.L., P. Muck, J. Mendo, E. Chumán de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta *(Engraulis ringens)*, 1953 to 1982, p. 117-141. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15.

53 Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. Studies and Reviews 15.

54 Muck, P., O. Sandoval de Castillo and S. Carrasco. 1987. Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Peru, p. 268-275. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15.

55 Tarazona, J., H. Salzwedel and W. Arntz. 1988. Positive effects of "El Niño" on macrozoobenthos inhabiting hypoxic areas of the Peruvian upwelling system. Oecologia (Berl.) 76: 184-190.

56 Delgado, C., G. Reidner, H. Salzwedel, L.A. Flores and G. Carbajal. 1987. Sedimentos superficiales del margen continental peruano: un mapa textural. [Surface sediments of the Peruvian continental margin: a textural map]. Bol. Inst. Mar. Perú-Callao 11(5): 178-190.

57 Fernandez, F. 1987. Edad y crecimiento de la merluza peruana *(Merluccius gayi peruanus)*. Bol. Inst. Mar Perú-Callao 11(6): 191-220.

58 Alamo, V. and V. Valdivieso. 1987. Lista sistemática de moluscos marinos del Perú. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 205 p.

59 Arntz, W., E. Valdivia and J. Zeballos. 1988. Impact of El Niño 1982-83 on the commercially exploited invertebrates (mariscos) of the Peruvian shore. Meeresforsch. 32(1): 3-22.

60 Urquizo, W., C. Wosnitza-Mendo, E. Valdivia and C. Moreno. 1987. Catálogo de datos oceanográficos (T, S y O_2) por estaciones del años en diferentes profundidades frente a la costa peruana 1970-1985. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 445 p.

61 Kameya, A. and J. Zeballos. 1988. Distribución y densidad de percebes *Pollicipes elegans* (Crustacea: Cirripedia) en el mediolitoral peruano (Yasila, Paita, Chilca, Lima). Bol. Inst. Mar Perú-Callao 12(1): 1-22.

62 Wosnitza-Mendo, C. and M. Espino. A review of the Peruvian trawl fisheries. (Unpublished MS)

63 Arntz, W., P. Muck and H. Salzwedel. 1988. Marine Ökosystemforschung in Perú: Grundlage für eine rationelle Bewirtschaftung der fischereilichen Ressourcen, p. 71-82. *In* Beispiele deutscher Agrarforschung in den Tropen und Subtropen. Bundesministerium für Wirtschaftlische Zusammenarbeit, Bonn, Federal Republic of Germany.

64. Ferrandis, E., J.A. Posadas, M. Espino and C. Wosnitza-Mendo. A multivariate version of the separable model for the evaluation of marine resources by means of virtual population analysis. Unpublished MS.

65 Salzwedel, H. and A. Landa, editors. 1988. Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

66 Sánchez, S., J. Tarazona, R. Flores, M. Maldonado and G. Carbajal. 1988. Características del fitoplancton de invierno en Bahía Independencia, Perú, p. 59-66. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

67 Salzwedel, H., L.A. Flores, E. Ch. De Flores, A. Zafra and G. Carbajal. 1988. Macrozoobentos del sublitoral peruano, antes, durante y después del fenómeno El Niño 1982-1983, p. 77-98. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

68 Zafra, A., H. Salzwedel and L.A. Flores. 1988. Distribución y biomasa de bacterias filamentosas (*Thioploca* spp.) en la costa norte del Perú durante 1976 a 1985, p. 99-106. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

69 Tarazona, J., W. Arntz and L. Hoyos. 1988. Repartición de recursos alimenticios entre algunos peces bentófagos frente al Perú antes, durante y después de El Niño 1982-83, p. 107-144. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

70 Tarazona, J., E. Canahuire, H. Salzwedel, G. Carbajal, R.A. Flores and T. Jeri. 1988. El macrozoobentos en dos áreas con diferente productividad del ecosistema de afloramiento peruano. Unpublished MS.

71 Ferrandis, E., M. Espino and C. Wosnitza-Mendo. 1988. Análisis comparativo de cohortes, p. 217-230. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

72 Espino, M., C. Wosnitza-Mendo and F. Fernandez. 1988. Ajuste del análisis de cohortes con información de cruceros de evaluación, p. 239-244. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

73 Muck, P., M. Espino, H. Fuentes, C. Wosnitza-Mendo and M. Esquerre. 1988. Predación de la merluza peruano *(Merluccius gayi peruanus)* sobre la anchoveta *(Engraulis ringens)*, p. 249-254. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

74 Vilchez, R., P. Muck and A. Gonzales. 1988. Variaciones en la biomasa y en la distribución de los principales recursos pelágicos del Perú entre 1983 y 1987, p. 255-264. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

75 Moreno, C., M. Veliz, M. Espino and C. Wosnitza-Mendo. 1988. Análisis preliminar de la pesquería artesanal del Callao, Perú, p. 321-328. *In* H. Salzwedel and A. Landa (eds.) Recursos y dinámica del ecosistema de afloramiento peruano. Bol. Inst. Mar Perú-Callao. Volumen Extraordinario. 382 p.

76 Véliz, M., M. Chavez and C. Wosnitza-Mendo. Algunas características de la pesquería artesanal en dos diferentes puntos del litoral peruano. Presentado al Simposio sobre Recursos Vivos y Pesquerias en el Pacifico Sudeste del 9-13 Mayo 1988. Viña del Mar, Chile. Unpublished MS.

77 Wosnitza-Mendo, C. Una base de datos para la investigación y manejo pesquero artesanal: problemas y opciones en el caso del Perú. Presented at the 46th International Congress of Americanists, 4-8 July 1988, Amsterdam, the Netherlands. Unpublished MS.

78 Mendo, J., M. Samamé, C. Wosnitza-Mendo, A. Mendieta and J. Castillo. 1988. Análisis biológico-pesquero y poblacional de la cachema *Cynoscion analis* del área de Paita, Perú. Bol. Inst. Mar Perú-Callao 12(2): 23-57.

79 Salzwedel, H. 1988. Estado actual de la investigación cuantitativa del macrozoobentos en el Perú. Unpublished MS.

80 Mendo, J. and D. Pauly. 1988. Indirect estimation of oxygen and food consumption in bonito *Sarda chiliensis* (Scombridae). J. Fish Biol. 33(5): 815-818.

81 Mendo, J. and C. Wosnitza-Mendo. Resumen de las investigaciones sobre la dinámica poblacional de la cachema *(Cynoscion analis)* de la costa peruana. Unpublished MS.

82 Pellón, J., N. Peña and J. Mendo. 1988. Reporte de datos de madurez sexual de la anchoveta *(Engraulis ringens)*, 1961-1987. Informe Inst. Mar Perú-Callao 92: 1-77.

83 Wosnitza-Mendo, C., M. Espino and M. Véliz, editors. 1988. La pesquería artesanal en el Perú durante Junio de 1986 a Junio de 1988. Informe Inst. Mar Perú-Callao 93. 144 p. (extra: Anexo de 64 paginas).

84 Landa, A. 1989. Un nuevo método de análisis de distribuciones polimodales de Biología Pesquera. Bol. Inst. Mar Perú-Callao 13(1): 1-37.

85 Mendo, J. 1989. Análisis poblacional de la cachema (Cynoscion analis) de la costa peruana: un ejemplo de como enforcar una investigación pesquera. Fishbyte 7(1): 6-7.

86 Csirke, J., J. Mendo, J. Zuzunaga, G. Cardenas, P. Muck and F. Chávez. 1989. Informe del taller de trabajo sobre modelos para la predicción del rendimiento en el sistema de afloramiento Peruano, IMARPE, Callao, 24-28 Agosto 1987, p. 1-13. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

87 Espino, M. and C. Wosnitza-Mendo. 1989. Biomass of hake *(Merluccius gayi)* off Peru, 1953-1987, p. 297-305. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

88 Mendo, J., M. Bohle-Carbonell and R. Calienes. 1989. Time series of upwelling nitrate and primary production off Peru derived from wind and ancillary data, 1953-1982, p. 64-76. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

89 Muck, P. 1989. Anchoveta consumption of Peruvian hake: a distribution and feeding model, p. 306-320. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

90 Muck, P. 1989. Major trends in the pelagic ecosystem off Peru and their implications for management, p. 386-403. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

91 Muck, P., A. Zafra de Moreno and C. Aranda. 1989. The seasonal dynamics of sea surface temperature and its impact on anchoveta distribution off Peru, p. 33-44. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

92 Pauly, D., P. Muck, J. Mendo and I. Tsukayama, editors. 1989. The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

93 Peña, N., J. Mendo and J. Pellón. 1989. Sexual maturity of Peruvian anchoveta *(Engraulis ringens)*, 1961-1987, p. 132-142. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

94 Sandoval de Castillo, O., C. Wosnitza-Mendo, P. Muck and S. Carrasco. 1989. Abundance of hake larvae and its relationship to hake and anchoveta biomass off Peru, p. 280-296. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

95 Tsukayama, I. 1989. Dynamics of the fat content of Peruvian anchoveta *(Engraulis ringens)*, p. 125-131. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18.

Author Index*

*The names of persons that are parts of eponyms (e.g., *von Bertalanffy* growth function, *Lasker* event) are not included.

Geographic Index

Species Index*

*This index excludes, for obvious reasons, references to the Peruvian anchoveta *Engraulis ringens*.