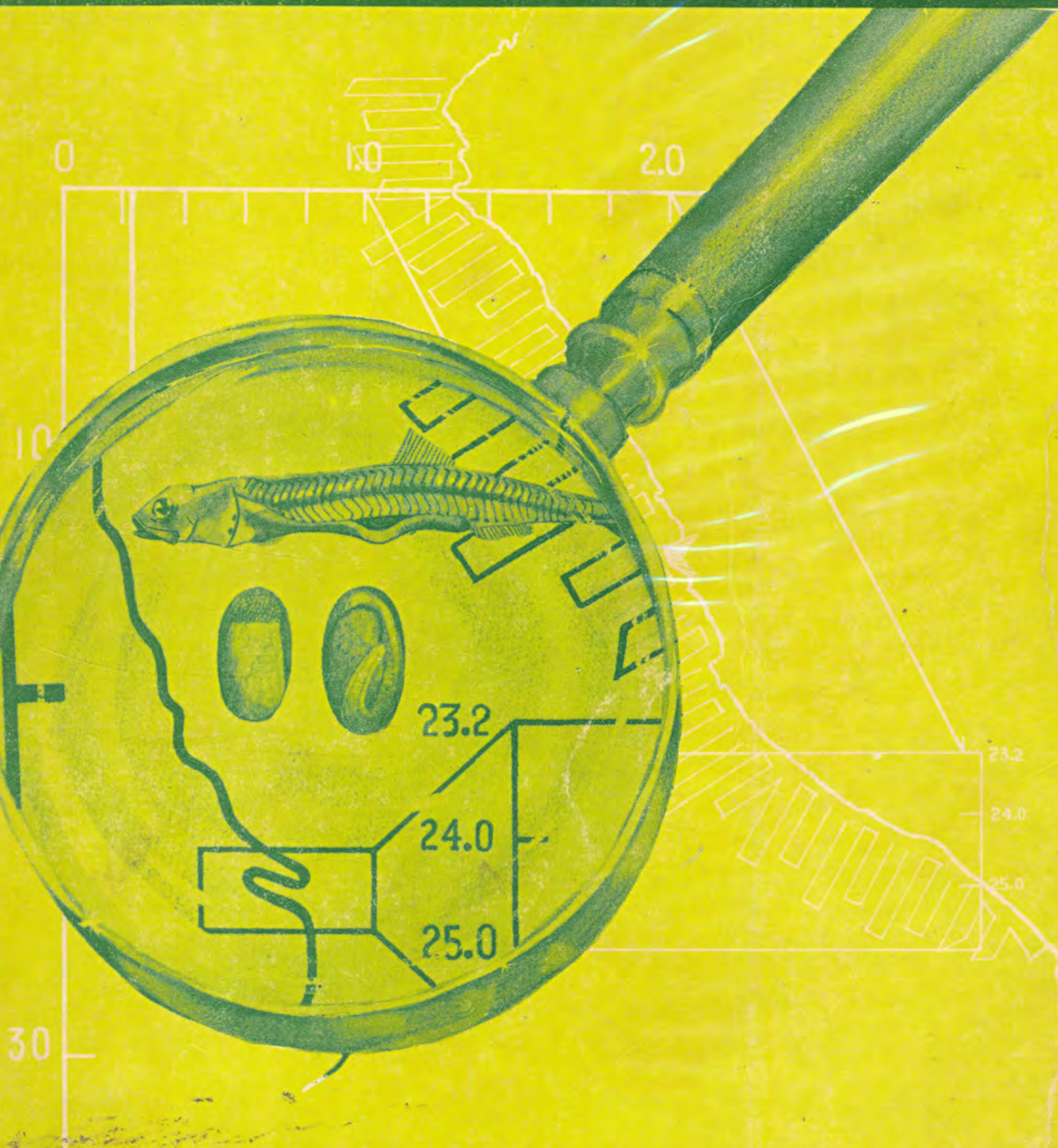




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**INVESTIGACION COOPERATIVA DE LA ANCHOVETA
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A POSSIBLE RECRUITMENT MODEL FOR THE PERUVIAN ANCHOVY

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ABSTRACT

Csirke's (1978) population model of the Peruvian anchovy is modified to include the relation between spawning stock biomass and winter egg production. IMARPE estimates of spawning intensity indicate that egg production per unit stock increased while the size of the population declined from 1969 to 1975. Analysis of the observed strengths of the 1969 to 1975 year-classes suggests that survival during the pre-recruit stage is strongly correlated with Csirke's index of stock concentration (Q).

These observations support the view that recruitment is the resultant of two population processes. A stock-dependent mechanism where egg production decreases at high population levels, and density-dependent process where pre-recruit survival is a function of the size of the year-class and environmental events. A model incorporating these factors accounted for 77% of the observed variance in recruitment from 1960-1975.

Although our interpretation of the reproductive success of anchovy requires independent confirmation of the actual mechanisms, the available data present an interesting picture. Thus we find that during unfavourable environmental conditions the stock tends to be more concentrated and, either as a direct response to crowding or poorer feeding opportunities, produces fewer eggs which have a poorer survival rate. Perhaps the "El Niño" phenomenon can therefore be viewed as eliciting the extreme response of a population, which is continuously adjusting its range and reproductive effort in relation to both intrinsic and large-scale oceanographic events.

SUMARIO

El modelo de población de anchoveta de Csirke (1978) ha sido modificado para incluir la relación entre la biomasa desovante y la producción invernal de huevos. Las estimaciones de intensidad de desove hechas por IMARPE indican que la producción de huevos por unidad de stock aumentó mientras el tamaño de la población disminuía de 1969 a 1975. El análisis de la fuerza de las clases anuales del 69 al 75 sugiere que la sobrevivencia durante el pre-reclutamiento se relaciona estrechamente con el índice de concentración de stock (Q) de Csirke.

Estas observaciones respaldan el punto de vista de que el reclutamiento es el resultado de dos procesos poblacionales. Un mecanismo dependiente del stock según el cual la producción de huevos disminuye a altos niveles de población, y un proceso dependiente de la densidad por el cual la sobrevivencia de pre-reclutas es una función del tamaño de la clase anual y de lo que sucede en el ambiente. Un modelo que incorpora estos factores explica el 77% de la variancia observada en el reclutamiento de 1960 a 1975.

Aunque nuestra interpretación del éxito reproductivo de la anchoveta requiere la confirmación independiente de los mecanismos reales, los datos disponibles ofrecen un cuadro interesante. Así vemos que cuando las condiciones ambientales no son favorables el stock tiende a concentrarse y, sea como respuesta directa al apiñamiento o debido a las pobres oportunidades de alimentación, produce menos huevos los cuales tienen una tasa menor de sobrevivencia. Por lo tanto, tal vez "El Niño" puede ser visto como un fenómeno que reclama una respuesta extrema a una población que continuamente ajusta su rango de ocupación y su esfuerzo reproductivo en relación tanto a factores intrínsecos como a sucesos oceanográficos de largo alcance.

INTRODUCTION

$$R = \alpha P \exp(-\beta PQ)$$

In an important paper Csirke (1978) found that much of the recruitment variability of the Peruvian anchovy over the last two decades can be described by a modified Ricker equation.

where in our notation R = recruitment index, P = stock biomass, Q = Csirke's coefficient of stock concentration or dispersion, and α and β are fitted constants. Csirke showed that for any given population size recruitment from the winter spawning

period was greatest when the stock was widely dispersed ($Q < 1$). For example, the recruitment index for the exceptionally good 1969 year-class was 553, and the stock concentration index was 0.55. By contrast, the recruitment index for the 1971 yearclass which experienced the 1972 El Niño was only 52, and the stock concentration index was the highest on record at 2.04.

Ware (1980) recently outlined an approach where recruitment is taken to be a function of two interacting population processes. A stock-dependent response where egg production per mature female declines non-linearly with stock size, and a density-dependent process where recruitment is an asymptotic function of the egg production of the parental stock. It was recognized that, in practice, both processes could be modified by environmental effects.

The purpose of this report is to determine if the recruitment dynamics of anchovy might be explained by a combined stock and density-dependent mechanism, modulated by large-scale oceanographic events. We caution from the outset that our interpretation should only be viewed as a working hypothesis, for it is based on limited data. Our scheme, however, is consistent with the observed variation in reproductive success and supports Csirke's findings, concerning the effect of spatial distribution of the spawning population on year-class strength.

SKETCH OF THE THEORY

Reproductive Effort and Surplus Energy

It is well known that the reproductive effort of fishes (ΔR , mass/time) in year, t , is an allometric function of body weight,

$$\Delta R(t) = c \theta f w(t)^\phi \quad (1)$$

where the parameters are either measured, e.g. θ = mean egg mass (g), f = factor to account for higher energy content of gonadal tissue ~ 1.2 (dimensionless); or fitted constant: c = eggs/gram time, ϕ (dimensionless). Similarly, there is ample experimental evidence to show that the maximum physiological rate at which a fish can store surplus "energy", ΔS (the total energy either added as body substance or released as reproductive products during year t) is also a power function of body size:

$$\Delta S(t) = \delta w(t)^\xi \quad (2)$$

Substituting Eq. (2) into (1) for $w(t)$ we can describe reproductive effort in relation to surplus energy as

$$\Delta R(t) = \xi \Delta S(t)^\eta \quad (3)$$

where $\xi = c\theta f \delta^{-\eta}$. Note that to simplify the calcu-

lations surplus energy has been given the dimensions of mass/time.

Stock-dependent Egg Production

Harris (1975) made a useful distinction between stock-dependent and density-dependent population processes. In a broader context, his definitions identify a stock-dependent process as one in which a selected response or rate varies with the abundance of the parent stock. By contrast, a density-dependent process is some function of the size of a year-class at any moment. According to this interpretation, Ware (1980) suggested that egg production is probably a stock-dependent variable. The rationale for this view is that in addition to the effect of body size, fish often acquire surplus energy in a fashion that depends on the size of the competing population.

Ware (1980) found that the contribution of both factors can be described satisfactorily by the equation.

$$\Delta S(t) = \delta W(t)^\zeta \exp[-aN(t)], \quad (4)$$

where $N(t)$ = number of immature fish in a specified year-class in year, t . If the process characterized by Eq. (4) holds throughout the immature phase of the life cycle, the average body weight at maturity, W_m , will be a complex function of the particular growth and mortality history of the year-class. After examining several possibilities, Ware (1980) showed that $W_m(t)$ tends to be a non-linear decreasing function of year-class size. Though the exact relationship cannot be definitively established, $W_m(t)$ can be approximated by the expression.

$$W_m(t) = W_\sigma \exp[-a'P(t)]. \quad (5)$$

Here, for convenience, a' is taken to be proportional to a , i.e. $a' = \kappa a$, W_σ = maximum possible body weight at the age of first maturity, m , and $P(t)$ is the number of mature fish in age-group, m , in year, t .

Since reproductive effort depends on the availability of surplus energy, both of these functions can be expected to vary according to the particular life-history features of the population. For the case where sexual maturity occurs at a constant age, and $\Delta S(t)$ is a function of body weight and year-class size, we can substitute $P(t)$ for $N(t)$ and $W_m(t)$ for $W(t)$ in Eq. (4) to obtain

$$\Delta S(t) = \delta W_\sigma^\zeta \exp\{-a[1 + \kappa \zeta]P(t)\} \quad (6)$$

Similarly, using Eq. (6) and (3), we find that individual reproductive effort is given by

$$\Delta R(t) = c\theta f W_\sigma^\phi \exp\{-a\eta[1 + \kappa \zeta]P(t)\} \quad (7)$$

The total number of eggs produced in year, t , then is

$$N_0(t) = \Delta R(t) P(t) / 2 \theta f, \tag{8}$$

where the factor 2 in the denominator implies an equal sex ratio. Using Eq. (7) we can rewrite Eq. (8) as

$$N_0(t) = \alpha P(t) \exp [-\beta P(t)] \tag{9}$$

where

$$\alpha = 1/2 cW \frac{\psi}{\sigma} \text{ and } \beta = a\eta [1 - \kappa\zeta].$$

Since we are considering a single year-class at maturity, it is reasonable to assume that the various coefficients in Eq. (1) to (9) are constant. If the concept is extended to a multi-age stock, however, some parameters like a , κ , ζ , and δ might vary with age. In this event, total egg production can be calculated by summing the contribution of each mature age-group.

Pre-Recruit Mortality

During the pre-recruit phase of the life history, the instantaneous death rate is believed to be density-dependent. Beverton and Holt (1957) developed the case where the natural mortality rate was a linear function of the current size of the year-class. They found that the number of survivors which eventually recruit to the population is given by the difference equation

$$N(t+r) = \{ [\psi/N_0(t)] + \gamma \}^{-1} \tag{10}$$

where r = age at recruitment, ψ and γ are mortality coefficients.

The abundance of each generation, therefore, can be related to the parent stock by substituting Eq. (9) into (10)

$$N(t+r) = \left[\frac{\lambda \exp [\beta P(t)] + \gamma}{P(t)} \right]^{-1} \tag{11}$$

where $\lambda = \psi/\alpha$. This curve increases to a maximum of

$$N_{max}(t+r) = \frac{1}{\gamma + 2.7 \lambda \beta},$$

when

$$P(t) = 1/\beta.$$

Equation (11) has the properties we seek. It contains a combined stock and density-dependent component (Eq. 9) which is identical in form to the Ricker equation. However, the mechanism envisaged here is different since the parents are no longer directly implicated in the deaths of their offspring. Another important characteristic of Eq. (11) is that for any increasing series of values of $\beta > 0$ the recruitment curves become increasingly dome-shaped. By contrast, when $\beta = 0$, Eq. (11) reduces to a

simple asymptotic curve of the type proposed by Beverton and Holt (1957).

APPLICATION

Egg Production and Anchovy Stock Biomass

Table 1 shows the number of anchovy eggs produced during the winter spawning season (July to December) along the north-central region of the Peruvian coast, calculated from the Eureka surveys conducted by IMARPE, and the corresponding biomass of the parent stock for the years in which these data were available. Notice that because of the nature of the estimates, for our analysis the parent stock is expressed in units of mass rather than numbers. If Equation (9) describes the egg production of anchovy then the relative production rate $\log_e \{ N_0(t)/P(t) \}$ ought to decrease linearly with stock size. The observations in Table 1 support the view that egg production is indeed stock-dependent:

$$\log_e \left\{ \frac{N_0(t)}{P(t)} \right\} = 21.753 - 1.675 \times 10^{-7} P(t) \tag{11}$$

where the correlation coefficient $r = -0.91$.

Pre-Recruit Survival and the Index of Stock Concentration

Noting that Eq. (10) can be rearranged so that

$$\psi = (1 - R(t+r)\gamma) N_0(t)/R(t+r) \tag{12}$$

where $R(t+r)$ is assumed to be proportional to $N(t+r)$. The value of ψ was estimated for each year-class from 1969 to 1975 by substituting the corresponding egg production and recruitment values in Table 1 into Eq. (12). Examination of the complete recruitment record suggested that $R_{max} \sim 600$, so we assume $\gamma = 1/600 = 0.00167$. A review of various possibilities indicated that the most appropriate hypothesis (which resulted in the highest correlation coefficient) was that ψ increased expo-

Table 1. Relation between estimated winter egg production, $N_0(t)$, and stock biomass $P(t)$. G strike's coefficient of stock concentration $Q(t)$, the observed recruitment index $R(t+r)$, and the calculated recruitment coefficient, ψ , are also indicated. Egg production values in parentheses were calculated from the empirical regression: $N_0(t) = 9.982 \times 10^{12} N_2(t)$, where $N_2(t)$ = mean number eggs/m² in September.

YEAR-CLASS (t)	$N_0(t)$ ($\times 10^{13}$ eggs)	$P(t)$ ($\times 10^6$ kg)	$\log_e \left[\frac{N_0(t)}{P(t)} \right]$	$Q(t)$	$R(t+r)$	ψ ($\times 10^{-12}$)
1969	(499.1)	12.7	19.7893	0.55	553	0.6903
1970	(399.3)	14.2	19.4546	0.81	539	0.7399
1971	(299.5)	10.0	19.5176	2.04	52	52.595
1972	259.4	1.5	21.2710	1.76	160	11.881
1973	444.7	4.2	20.7094	1.23	190	17.279
1974	833.8	4.5	21.3400	1.47	160	38.188
1975	972.8	4.9	21.4090	0.47	392	8.571
1976	481.8	?	?	?	?	?
1977	713.4	?	?	?	?	?

$$(i) \log_e \left[\frac{N_0(t)}{P(t)} \right] = 21.753 - 1.675 \times 10^{-7} P(t) \quad (r = -0.91)$$

$$\frac{\psi}{\gamma} = 1/R_{max} = 0.00167$$

$$\psi = (1 - R(t+r)\gamma) N_0(t)/R(t+r)$$

$$\psi_1 = 6.102 \times 10^{11} \exp [2.145Q(t)] \quad (r = 0.74)$$

$$(ii) \log_e \left[\frac{N_0(t)}{P(t)} \right] = 22.546 - 1.907 \times 10^{-7} P(t) - 0.522 Q(t) \quad (R = -0.97)$$

TABLE 2: Estimation of egg production, α and β for the years 1960-68:

Assuming $\gamma = 0.00167$
 $\psi_1 = 6.102 \times 10^{11} \exp [2.145Q(t)]$
 $N_0(t) = \frac{\psi_1 R(t+r)}{1-\gamma R(t+r)}$

YEAR-CLASS (t)	STOCK (Px10 ⁻⁶ Mg)	Q(t)	ψ_1 (x10 ⁻¹³)	R(t+r)	$N_0(t)$ (x10 ⁻¹³ eggs)	$\log_e \left[\frac{N_0(t)}{P(t)} \right]$
1960	20.1	1.0	0.521	332	388.2	19.0789
1961	25.8	1.0	0.521	237	204.4	18.1876
1962	24.4	1.0	0.521	183	137.3	17.8457
1963	11.9	1.01	0.533	403	656.9	20.7291
1964	12.0	1.51	1.556	193	443.1	19.7271
1965	17.4	0.62	0.231	439	380.0	19.2018
1966	15.7	0.98	0.499	383	530.3	19.6379
1967	21.6	0.84	0.370	338	287.1	18.7054
1968	14.5	1.04	0.568	377	578.1	19.8037

$$\log_e \left[\frac{N_0(t)}{P(t)} \right] = 21.7803 - 1.4508 \times 10^{-7} P(t) \quad (r = 0.96)$$

Hence the geometric mean regression is,

$$N_0(t) = 3.2215 \times 10^9 P(t) \exp (-1.513 \times 10^{-7} P(t))$$

nentially in relation to Csirke's index of stock concentration, Q (t) (Table 1):

$$\psi_1 = 6.10 \times 10^{11} \exp (2.145 Q(t)) \quad (13)$$

Eq. (13) was then used to predict ψ for the 1960-68 period, and the corresponding annual winter egg production calculated from the equation

$$N_0(t) = \psi R(t+r) / [1 - \gamma R(t+r)].$$

The resulting estimates (Table 2) were normalized by dividing by stock size to determine the geometric mean regression (Ricker, 1973) of $\log_e [N_0(t)/P(t)]$ on $P(t)$, thus giving α and β . The result

TABLE 3. Second estimate of ψ and its relation to the coefficient of stock concentration Q(t), assuming $\gamma = 0.00167$. Table also includes estimates of recruitment $\hat{R}(t+r)$, relative survival $R(t+r)/N_0(t)$, and the average maximum range in the monthly temperature anomalies off Chimbote and Don Martin during January to June in the year following spawning $T_R(t+1)$.

YEAR-CLASS (t)	STOCK (Px10 ⁻⁶ Mg)	$N_0(t)$ (x10 ⁻¹³)	R(t+r)	ψ (x10 ⁻¹²)	Q(t)	ψ_2 (x10 ⁻¹²)	$\hat{R}(t+r)$	$R(t+r)/N_0(t)$ (x10 ⁻¹³)	$T_R(t+1)$ (°C)
1960	20.1	309.4	332	4.152	1.0	5.622	287	1.07	1.5
1961	25.8	167.6	237	4.273	1.0	5.622	199	1.41	1.8
1962	24.4	196.0	183	7.437	1.0	5.622	220	0.93	2.0
1963	11.9	633.4	403	5.139	1.01	5.770	387	0.64	2.5
1964	12.0	629.1	193	22.090	1.51	21.162	199	0.31	3.8
1965	17.4	403.0	439	2.450	0.62	2.094	457	1.09	1.8
1966	15.7	470.3	383	4.425	0.98	5.337	357	0.81	1.0
1967	21.6	265.0	338	3.415	0.84	3.709	326	1.28	1.9
1968	14.5	520.8	377	5.117	1.04	6.238	349	0.72	2.5
1969	12.7	598.9	553	0.828	0.55	1.746	510	0.92	2.4
1970	14.2	533.7	539	0.989	0.81	3.431	432	1.01	2.3
1971	10.0	709.5	52	124.594	2.04	83.905	74	0.07	4.5
1972	1.5	385.1	160	17.638	1.76	40.527	82	0.42	5.0
1973	4.2	716.7	180	27.848	1.23	10.222	323	0.25	2.6
1974	4.5	733.8	160	33.608	1.47	19.073	234	0.22	2.5
1975	4.9	752.1	392	6.626	0.47	1.418	538	0.52	2.2

$$N_0(t) = 3.22 \times 10^9 P(t) \exp (-1.513 \times 10^{-7} P(t))$$

$$\psi_2 = 4.18 \times 10^{11} \exp (2.599Q(t)); \quad r = 0.85$$

$$N_0(t) = 3.22 \times 10^9 P(t) \exp [-1.513 \times 10^{-7} P(t)] \quad (14)$$

is consistent with our earlier finding that egg production is strongly stock-dependent (Fig. 1).

Prediction of Recruitment

Having obtained an acceptable estimate of α and β , we recalculated ψ by solving Eq. (12) for the entire record (1960-74), in order to find the best fitting relation between ψ and Q(t) (Table 3):

$$\psi_2 = 4.18 \times 10^{11} \exp (2.599 Q(t)). \quad (15)$$

Recruitment can therefore be found by substituting Eq. (14) and (15) into Eq. (10). The results are summarized in Table 3.

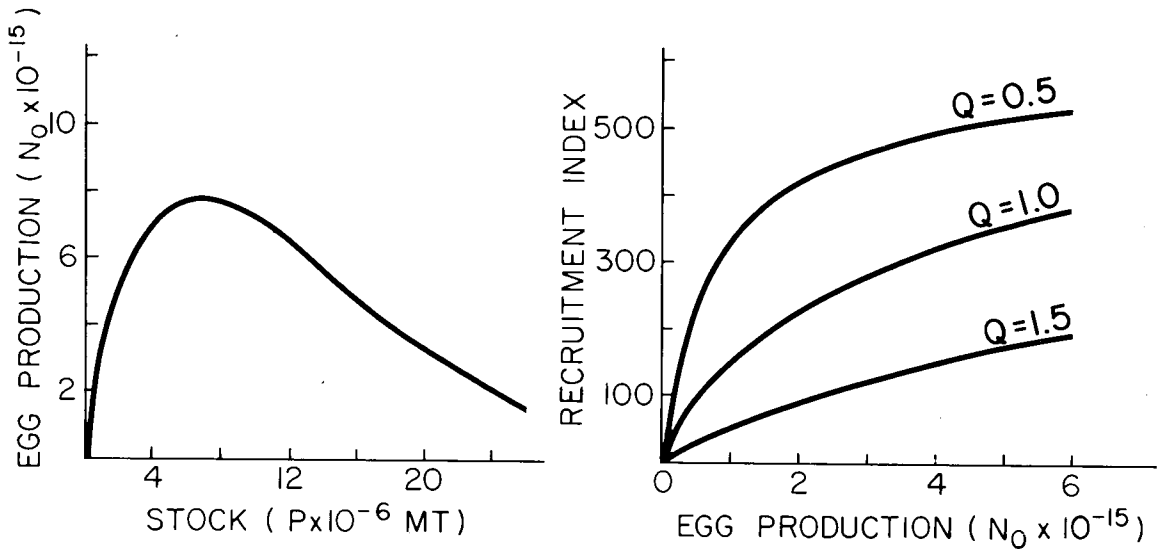
Although Csirke's (1978) model gives a slightly better estimate of $R(t+r)$ than ours, for all practical purposes, both methods have the same accuracy (Table 4). The scheme we propose, however, makes some very explicit predictions about the way in which egg production and pre-recruit survival ought to change in relation to stock size, and the coefficient of stock concentration (Figs. 1 and 2).

DISCUSSION

Contrary to current theory, it is important to note that the observed variation in winter spawning intensity indicates that the relative egg production

$$\hat{R}(t+r) = \frac{1}{\frac{\psi_2}{N_0(t)} + 0.00167}$$

Fig. 1 Apparent change in egg production with stock-size (Eq. 14), and recruitment with egg production at different levels of stock concentration (Q).



of anchovy $N_0(t)/P(t)$, declines more or less exponentially with an increase in the biomass of the mature stock. Thus, the generally lower recruitment from a large stock seems to be due in part to a reduction in individual reproductive effort.

Measurements of anchovy gonad weights in 1962 and 1974 confirm that fertility varies with stock size. In the winter of 1962 the anchovy population was of the order of 24 million metric tons. According to Miñano (1968, Fig. 5), the gonad weight of a 21 gram anchovy at that time averaged 1.1 grams. By 1974 the stock declined to 4.5 million metric tons and the corresponding gonad weight of a 21 gram anchovy was 1.7 grams. This finding clearly contradicts the long standing assumption of classical theory that fecundity of marine

fish is not affected by fluctuations in population size (Harris, 1975).

The most important contribution in recent years concerning the dynamics of the Peruvian anchovy was Csirke's discovery that recruitment seems to be linked to the coefficient of stock concentration. In fact, this parameter, when incorporated in either the Ricker recruitment equation or Eq. (11), explains most of the observed variation in year-class strength. There are a number of possible ways in which the degree of aggregation of the spawning stock might be affecting recruitment:

(1) Analysis of the data in Table 1 (Eq. ii) indi-

Fig. 2 Possible recruitment function for the Peruvian anchovy at different levels of stock concentration (Q).

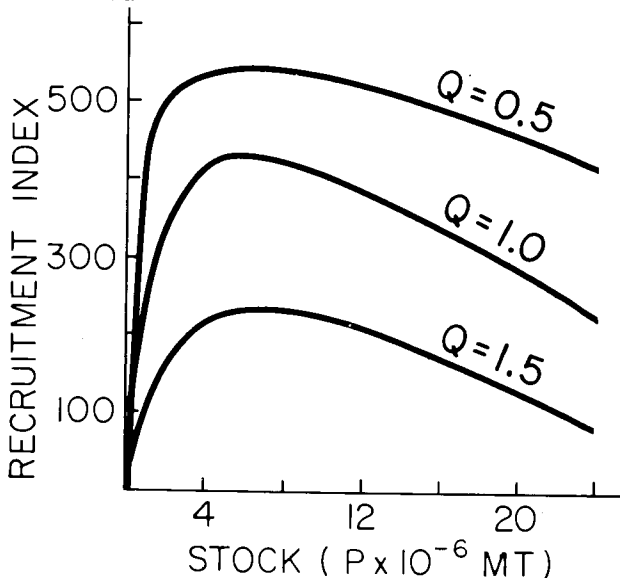
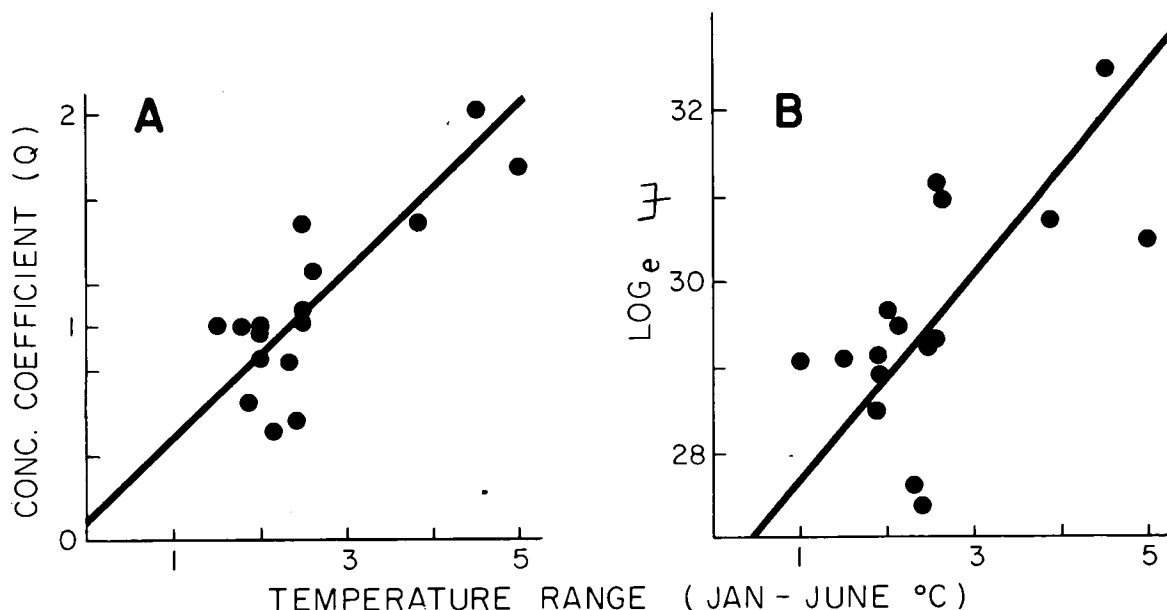


TABLE 4: Comparison of Csirke's (1978) recruitment estimates and those predicted by Eq. 10 $\hat{R}(t+r)$, with the observed value $R(t+r)$

YEAR-CLASS	R (t+r)	$\hat{R}(t+r)$ CSIRKE	$\hat{R}(t+r)$
1960	332	249	287
1961	237	182	199
1962	183	197	220
1963	403	338	387
1964	193	184	199
1965	439	558	457
1966	383	318	357
1967	338	329	326
1968	377	304	349
1969	553	600	510
1970	539	427	432
1971	52	122	74
1972	160	110	82
1973	180	240	323
1974	160	221	234
1975	392	373	538

Correlation Coefficient (r^2)	0.80	0.77
Chi-Square	243.4	263.9

Fig. 3 A. Relation between coefficient of stock concentration (Q) and the average, maximum range in water temperature anomalies (T_R , °C) off Chimbote and Don Martin during Jan to June following spawning: GM regression, $Q = 0.063 + 0.405T_R$, $r = 0.77$, $p < 0.001$.
 B. Relation between recruitment coefficient ($\log_e \psi$) and T_R : GM regression, $\psi = 3.08 \times 10^{11} \exp(1.24 T_R)$, $r = 0.62$, $P \sim 0.01$.



cates that egg production per unit stock tends to vary inversely with $Q(t)$. In other words, when the spawning stock is more concentrated egg production tends to be reduced. This might occur if there were a deterioration in feeding conditions for the spawners, either as a direct result of crowding or a change in the abundance or quality of their food supply. We did not include this effect in our analysis, but the possibility should be re-examined in the future when more data are available.

(2) The recruitment parameter ψ , which may be taken to reflect conditions during the pre-recruit stage, increases roughly exponentially with the range in monthly temperature anomalies in the summer following spawning. In other words, the survival of anchovy larvae and juveniles tends to be poorer when the variation in water temperature along the coast is especially large (Fig. 3B).

As a working hypothesis, we suggest that, in addition to the possible effect of Q on egg production, the strong correlation we have found between the concentration of the stock and ψ might reflect the fact that the circumstances which cause the spawning population to restrict its range are also less suited to support a large year-class; perhaps because of limited feeding opportunities for the young larvae and juveniles, or higher mortality rates associated with the increased aggregation of both the spawning stock and their progeny.

(3) There is a tendency for Q to be related to thermal conditions along the coast. Fig. 3A, which was constructed from Enfield's (1979) data, suggests that anchovy are more concentrated when the maximum range in the temperature anomalies during

the summer and fall after spawning is large. This correlation is difficult to explain, assuming it is not completely fortuitous because the stock concentration coefficient was measured during the winter and spring of the preceding calendar year. What is even more puzzling is that the correlation between either the range in temperature anomalies or mean temperature during July to December, and Q , when all of these indices were measured, was much weaker than that of Fig. 3A, indicating that the dispersion of the spawning stock was less strongly linked to the thermal conditions prevailing along the coast during the reproductive season.

Although the nature of a possible relation between temperature and Q is unclear at this time, and, if the concentration of the stock reflects the amount of suitable habitat containing adequate feeding opportunities and physical conditions for anchovy, there is a tendency for the amount of this space (or perhaps it would be more appropriate to think in terms of a volume) to diminish in anomalously cold or warm waters.

To critically test these hypotheses, special studies are needed to clarify the causal links between large-scale oceanographic conditions in the north, the distribution and egg production of the spawning stock, and subsequent survival of anchovy during the pre-recruit stage.

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