

Diet diversity of jack and chub mackerels and ecosystem changes in the northern Humboldt Current system: A long-term study



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ABSTRACT

Jack mackerel *Trachurus murphyi* (JM) and chub mackerel *Scomber japonicus* (CM) are medium size pelagic fish predators and highly exploited resources. Here we investigated the spatiotemporal patterns of JM and CM diet composition using a large dataset of stomach samples collected from 1973 to 2013 along the Peruvian coast. In total 47,535 stomachs (18,377 CM and 29,158 JM) were analysed, of which 23,570 (12,476 CM and 11,094 JM) were non-empty. Results show that both species are opportunistic and present a trophic overlap. However, despite their smaller maximal size, CM consumed more fish than JM. Both diets presented high spatiotemporal variability. Spatially, the shelf break appears as a strong biogeographical barrier affecting prey species distribution and thus CM and JM diet. Opportunistic foragers are often considered as actual indicators of ecosystem changes; we show here that diet composition of CM and JM reveal ecosystem changes but is not always a good indicator of changes in prey biomass as prey accessibility and energy content can also play an important role. In addition we found that El Niño events have a surprisingly weak effect on stomach fullness and diet. Finally our results show that the classic paradigm of positive correlation between diversity and temperature is unlikely to occur in the Humboldt Current system where productivity seems to be the main driver. We show how energy content of forage species and the strength of the oxygen minimum zone most likely play an important role prey diversity and accessibility, and thus in fish foraging behaviour.

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1. Introduction

The diet of predatory fishes integrates many ecological components including feeding behaviour, habitat use over time and space, diversity and availability of forage fauna, energy intake and fish condition, inter- and intraspecific interactions, and environmental forcing. Food habits are therefore critical for understanding trophic functioning of marine ecosystems and then sustainability of exploited fish populations. In the Humboldt Current system, *Trachurus murphyi* (Jack mackerel, JM hereafter) and *Scomber japonicus* (Chub mackerel, CM hereafter) are important pelagic resources with high content of essential fatty acids (Celik, 2008). They are heavily exploited by artisanal and industrial fisheries (Arcos et al., 2001; Gerlotto et al., 2012).

JM occurs from the equator to the austral region of Chile and from the coast of South America to New Zealand and Tasmania (Grechina, 1998; Gerlotto et al., 2012). The JM fishery has been

one of the largest worldwide, with a maximum yearly yield of almost 5 million tonnes in 1995. Since the late 1990s, JM landings dropped off to reach ca. 0.5 million tonnes. This trend is attributed to both overfishing and climate variability (Gerlotto et al., 2012). Depicting the relative importance of natural and anthropogenic forcing is complex, making difficult the management of this transzonal resource, which is distributed in several EEZ and in international waters. JM has therefore become a concern for the South Pacific Region Fisheries Management Organization (SPRFMO: www.southpacificrfmo.org).

CM is an important commercial coastal-pelagic species with a worldwide distribution (Collette and Nauen, 1983; Castro and Santana, 2000). In the southeastern Pacific CM distribution extends from the Ecuador to Darwin Bay in Chile (45°S) (Konchina, 1982; Castro and Santana, 2000). In this region CM catches showed rises and falls during the last 40 years but a clear declining trend occurred after a maximum of ca. 0.7 million tonnes in 2003.

Variation in distribution and abundance of both species is related to a variety of abiotic (e.g. Ganoza, 1998; Arcos et al., 2001; Bertrand et al., 2006) and biotic factors (e.g. Quiñones

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et al., 1997; Grechina, 1998; Bertrand et al., 2004b, 2006). Both species exploit a large range of oceanographic conditions (Bertrand et al., 2004b) and are considered opportunistic predators (Konchina, 1981, 1982). Their distribution and abundance depend on a large extent on food availability (Konchina, 1981; Quiñones et al., 1997; Bertrand et al., 2004a, 2006). Investigating the dietary changes of JM and CM should allow us to better understand on the one hand their respective trophic niches, and on the other hand their resilience to climatic changes including El Niño Southern Oscillation (ENSO) events and decadal changes that strongly impact marine resources and affect the structure of the Humboldt Current system.

In this paper, we analysed an extensive dataset of more than 47,000 stomachs sampled over 40 years (1973–2013) and provided new insight in the variability in space and time of feeding habits and prey diversity of JM and CM in the northern Humboldt Current system (NHCS). We show that (i) both species are opportunistic and present a trophic overlap but surprisingly, JM does not seem more voracious than CM; (ii) fish diet presented high spatiotemporal variability, the shelf break being a main biogeographical frontier; (iii) fish diet composition is not necessarily a good indicator of changes in prey biomass as the diet can also be influenced by prey accessibility and energy content; (iv) unexpectedly, El Niño events have a weak effect on stomach fullness and on the diet of CM and JM; and (v) our results challenge the paradigm of positive correlation between diversity and temperature in the NHCS.

2. Materials and methods

2.1. Sample collection

JM and CM were collected between 1973 and 2013 along the Peruvian coast up to 470 km from the coast (Fig. 1), from scientific cruises carried out by the Peruvian Sea Institute (IMARPE), the industrial fishing fleet, and the Eureka program (quick synoptic surveys to collect biological and qualitative acoustic information aboard fishing vessels, see Gutiérrez et al., 2000, 2012). As far as

possible, three individuals of both species were randomly sampled by fishing set and by size classes of one centimetre covering the captured size range. In the laboratory, fork length (in cm; hereafter, fish size refers to fork length), total weight (in g) were measured and the sex and maturity stages (using the five-stage scale of Sánchez et al., 2013) were determined. Stomachs were fixed in 96% alcohol or in 10% formaldehyde. Samples were characterised according to year, season, latitude, zone (north 3°–6°S, centre-north 6°S–10°S, centre-south 10°–15°S, south 15°–18°S), distance to the shelf break (in km, negative to the continental shelf and positive towards offshore), sea surface temperature anomalies (SSTA, in °C) and depth of isotherm 15 °C ($Z_{15^\circ\text{C}}$, in m; see Flores et al., 2013). In addition, fish length and distance to the shelf break were classified in ordered categories: less than 20 cm, then by 10 cm bins above, for length; –100 to –10 km (i.e. continental shelf), –10 to 10 km (around shelf break), 10–40 km, 40–80 km and >80 km, for distance to the shelf break.

2.2. Stomach content analysis

Stomach contents were washed through a sieve mesh of 300 μm in order to retain prey remains and diagnostic hard parts (fish otoliths, cephalopod beaks, crustacean exoskeleton). The different items constituting a single taxon were sorted, counted and weighed to the nearest 0.01 g. Prey were determined using a binocular microscope to the lowest possible taxon using keys and descriptions for Teleostei (Fitch and Brownell, 1968; Chirichigno, 1998; Chirichigno and Cornejo, 2001; García-Godos, 2001), crustaceans (Newell, 1963; Méndez, 1981), zooplankton (Trégouboff and Rosse, 1957), cephalopods (Wolff, 1984) and other molluscs (Álamo and Valdivieso, 1987). A total of 90 and 102 prey taxa were identified for JM and CM, respectively. However the identification level varied over the 1973–2013 period. In particular crustaceans and especially zoea larvae were identified very precisely in 2009 because a specific investigation was performed on that taxonomic group during this year. We therefore homogenised the prey taxa for the whole sampling period, and obtained a total of 60 and 62 prey taxa mixing different taxonomic levels for JM and CM,

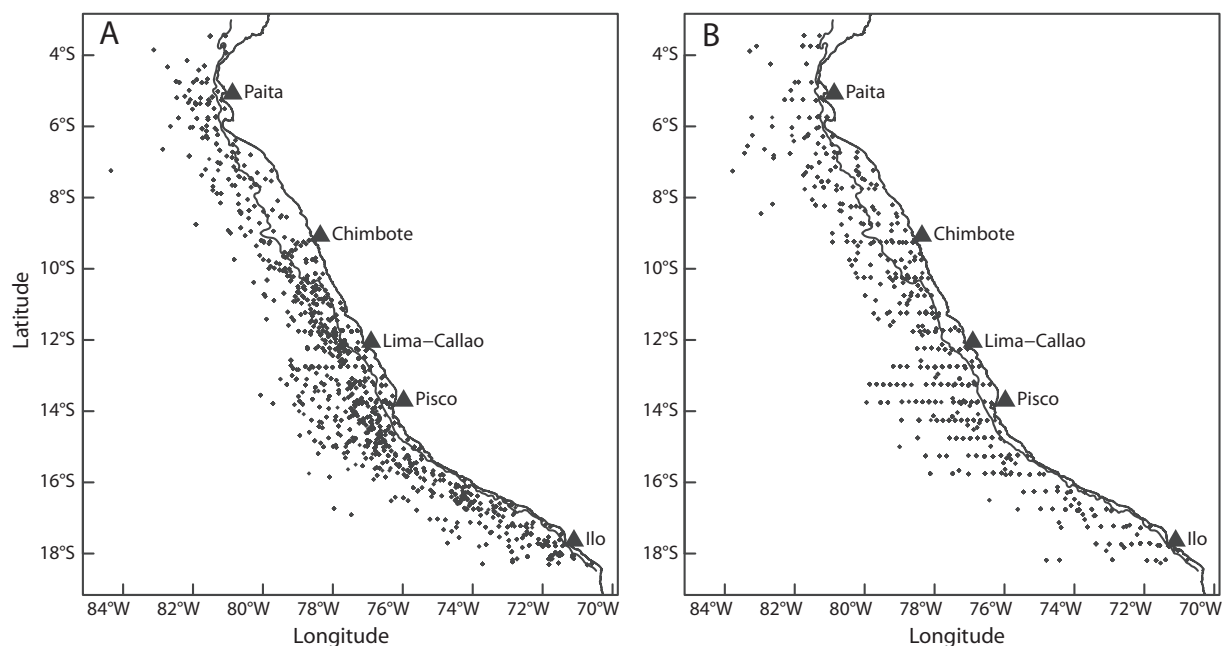


Fig. 1. Distribution of stomach samples (black dots) of (A) *Trachurus murphyi* and (B) *Scomber japonicus*. The black solid line indicates the 200 m isobath used as a proxy for shelf break position.

respectively (Table 1). In addition and for the sake of clarity of our quantitative assessments, we aggregated the prey taxa in 13 groups based on their consistency and their ecological importance in the NHCS (Table 2): tunicata, cephalopoda, copepoda, zoea larvae, euphausiidae, the squat lobster *Pleuroncodes monodon*, other crustacea, engraulidae, mesopelagic fishes, coastal fishes, other teleostei, eggs and larvae of teleostei, and other prey. Prey taxa were quantified by frequency of occurrence and by wet weight. Mean percentages by wet weight (%W) were computed by averaging the proportions of each prey taxa found in the individual stomachs (Chippis and Garvey, 2007). We thus treated individual as the sampling unit, allowing us to compute standard deviations.

A stomach fullness weight index (FWI, in%) was calculated as:

$$FWI = \frac{W_{st} \times 100}{W - W_{st}}$$

where W_{st} is the wet weight of the stomach content (in g) and W the body wet weight of the individual (in g).

2.3. Index of condition

Variation in the condition of the two fish species was investigated using the relative condition factor K_n (Le Cren, 1951) computed for each weighed (We , observed eviscerated weight) and measured (FL , length in cm) individual:

$$K_n = We/We'$$

where We' is the predicted weight of an individual of a given length FL ($We' = 10^z \cdot FL^\beta$).

The following parameters were estimated for CM: $\alpha = -2.233 \pm 0.0098$, $\beta = 3.243 \pm 0.0067$ and for JM: $\alpha = -1.786 \pm 0.0046$, $\beta = 2.906 \pm 0.0031$.

2.4. Data analyses

The proportions of empty stomachs per fishing set were computed for both species, using sets with at least 8 individuals of the same species. The effect of several covariates (fish length, sex, maturity, latitude and distance to the shelf break) was tested on the diet composition of CM and JM, using log-likelihood G tests for independence and the Williams' correction (Sokal and Rohlf, 1995). In addition, covariates were assessed on stomach fullness index FWI and on condition factor K_n using Kruskal–Wallis and Wilcoxon rank sum tests. To investigate potential impact of ENSO events, we selected the periods encompassing the strongest El Niño (October 1982 to May 1983 and October 1997 to May 1998) and La Niña (January 1975 to March 1976; July 1988–April 1989; all 1999 and 2000; August 2010–May 2011) events. Other periods are considered as 'Neutral'. As very few CM sample were available during El Niño events in our database (only 39 stomachs), ENSO impact was investigated for JM data only. But large JM (size >40 cm) were then removed because they were mainly captured during the very first years of the survey period. The diel effect on JM and CM trophic ecology could not be fully assessed in this study due to a lack of information on the time in most (>90%) of the data base. We however tested for diel effect on FWI on a subsample for which time was available and did not observed any robust pattern.

To explore cross-shore patterns, the density of stomachs according to distance to the shelf break (km) was estimated for the whole data set of non empty stomachs with known distance to shelf break and for the subsets containing euphausiidae, *P. monodon* or engraulidae. A Gaussian kernel was used for modelling density with a bandwidth selected according to Venables and Ripley (2002).

To take into account potential dependence and interactions between explanatory variables, we performed classification and

regression tree (CART) analyses proposed by Breiman et al. (1984) and adapted to diet data by Kuhnert et al. (2011). Classification tree allows identifying the relationships between explanatory variables and the distribution of prey groupings. This non-parametric method uses a partitioning algorithm to estimate a series of binary decision rules that divide the data into smaller homogeneous subgroups in an optimal way. The whole dataset is represented by a single node at the top of the tree. Then the tree is built by repeatedly splitting the data. Each split is defined by a simple rule based on a single explanatory variable. Diet data were transformed following Kuhnert et al. (2011). Each row represents a unique predator–prey combination, where the proportion by wet weight of one of the thirteen prey taxa potentially present in the stomach is used as a case weight for the classification tree. As the splitting procedure grows an overlarge tree, we applied a prune back procedure. Each terminal node (or leaf) of the final tree is characterised by a predicted probability distribution of prey composition (proportion by weight of groups), given explanatory continuous and categorical variables. We first performed a CART analysis on the stomachs of JM (1973–2013) using four explanatory continuous variables (fish length, year, SSTA, $Z_{15^\circ C}$) and two categorical variables (zones: north, centre-north, centre-south, south; distance to the shelf break: –100 to –10 km, –10 to 10 km, 10 to 40 km, 40 to 80 km and >80 km). This analysis allowed us to account for the temporal variation (year effect) that could not be considered with CM data due to the absence of data for eight years (see Fig. 4E). We then implemented a new CART analysis with diet data of both species using the same exploratory variables and species (CM and JM) as well, but without year.

JM and CM were also used as biological samplers for documenting the diversity of the forage fauna. Diet composition can indeed provide valuable information on diversity changes over time and space. Datasets based on occurrences of the 60 and 62 prey taxa identified in the stomachs of JM and CM respectively were used to compute average tables of occurrences of prey taxa per year, per zone and per category of distance to the shelf break. A correspondence analysis performed on the average table per year for JM (analysis not performed on CM due to the absence of data for eight years) showed that the first axis was a good proxy of the temporal evolution of the composition of prey taxa. The first axis was thus used to order year and taxa in the graphical representation of this average table. A hierarchical clustering of the years according to their coordinates in the correspondence analysis was used to perform a typology of the main groups of years based on their prey taxa composition. In addition we estimated the richness of forage fauna of CM and JM by computing the species richness indexes S_{obs} on the 60 and 62 prey taxa and for all the modalities of the factors of interest (year, zone and categories of distance to the shelf break). But sample size (i.e., number of stomachs) strongly influences species richness. To deal with this bias, we applied a bootstrap procedure and randomly took with replacement m stomachs from the n recovered in a modality of a given factor. This procedure was repeated 500 times and a $(S_{boot})_i$ was calculated for all the samples $i = 1, \dots, 500$. We chose $m = 100$ for year and $m = 500$ for zone and distance to the shelf break, according to the corresponding sampling effort by modality. Years with less than 100 stomachs were discarded. Finally, for both species, we computed the mean and standard deviation of the bootstrap samples $(S_{boot})_i$ for each modality and for all the factors of interest.

The Sørensen index was used to compare the similarity of El Niño vs. La Niña periods and before/after 1996 periods in terms of presence/absence of taxa.

Analyses were conducted using the R software (R Core Team, 2015), with the *rpart* package for the classification tree (Venables and Ripley, 2002).

Table 1
Overall description of the prey taxa observed in jack mackerel (*T. murphyi*) and chub (*S. japonicus*) mackerel stomach sampled off Peru during 1973–2013. Are indicated, the taxonomic information, the dietary group, the mean value (\pm standard deviation) of the proportion by weight (%W), and the frequency of occurrence (%O).

Phylum	Class	Order	Family	Species	Dietary group	<i>T. murphyi</i>		<i>S. japonicus</i>	
						%W	%O	%W	%O
Algae				Algae n/i	Other	0.08 (2.8)	0.08	0.0001 (0.01)	0.01
Rhizaria	Radiolaria			Radiolaria n/i	Other	0.00	0.00	0.00003 (0.002)	0.003
Cnidaria				Cnidaria n/i	Other	0.02 (1.4)	0.03	0.04 (2.00)	0.04
Chaetognatha				Chaetognatha n/i	Other	0.00	0.00	0.0001 (0.01)	0.002
Annelida	Polychaeta	Phyllodocida	Alciopidae	Polychaeta n/i	Other	0.05 (1.8)	0.05	0.21 (3.58)	0.29
				Alciopidae n/i	Other	0.03 (1.6)	0.03	0.01 (0.36)	0.12
Mollusca				Mollusca n/i	Other	0.00	0.00	0.00003 (0.003)	0.01
	Gastropoda			Gastropoda n/i	Other	0.11 (3.1)	0.21	0.10 (2.60)	0.25
		Thecosomata		Thecosomata n/i	Other	0.17 (4.2)	0.18	0.08 (2.82)	0.09
			Cavoliniidae	<i>Diacria</i> spp.	Other	0.30 (5.4)	0.28	0.06 (2.41)	0.06
		Littorinimorpha	Atlantidae	<i>Atlanta</i> spp.	Other	0.00	0.00	0.02 (1.27)	0.02
			Naticidae	<i>Natica</i> spp.	Other	0.09 (2.7)	0.15	0.23 (4.21)	0.62
	Bivalvia			Bivalvia n/i	Other	0.01 (0.6)	0.02	0.03 (1.44)	0.07
		Veneroida	Semelidae	<i>Semele</i> spp.	Other	0.10 (3.1)	0.06	0.00	0.00
	Cephalopoda			Cephalopoda n/i	Cephalopoda	0.29 (5.2)	0.27	1.76 (12.83)	1.77
				Cephalopoda paralarvae	Cephalopoda	0.00	0.00	0.03 (1.55)	0.03
		Myopsida	Loliginidae	Loliginidae n/i	Cephalopoda	0.15 (3.6)	0.14	0.16 (3.83)	0.15
		Octopoda	Argonautidae	<i>Argonauta</i> spp.	Cephalopoda	0.00	0.00	0.08 (2.84)	0.08
		Oegopsida		Oegopsida n/i	Cephalopoda	0.00	0.00	0.04 (1.71)	0.02
			Enoploteuthidae	<i>Abraliopsis affinis</i>	Cephalopoda	0.09 (3.0)	0.09	0.13 (3.37)	0.14
			Ommastrephidae	<i>Dosidicus gigas</i>	Cephalopoda	0.03 (1.5)	0.03	0.15 (3.35)	0.13
			Pyroteuthidae	<i>Pterygioteuthis giardi</i>	Cephalopoda	0.02 (1.3)	0.02	0.00	0.00
Arthropoda				Crustacea n/i	Other Crustacea	0.32 (5.4)	0.29	0.16 (3.57)	0.14
				Crustacea eggs	Other Crustacea	0.06 (2.5)	0.06	0.02 (0.83)	0.04
				Crustacea larvae	Other Crustacea	0.00	0.00	0.11 (2.40)	0.1
	Maxillopoda			Cirripedia n/i	Other Crustacea	0.02 (1.4)	0.03	0.00	0.00
				Copepoda n/i	Copepoda	7.10 (25.1)	7.26	14.29 (31.98)	15.44
	Ostracoda			Ostracoda n/i	Other Crustacea	0.07 (2.1)	0.09	0.20 (4.12)	0.12
		Podocopida	Cyprididae	Cypris larvae	Other Crustacea	0.0002 (0.02)	0.01	0.02 (0.94)	0.07
	Malacostraca	Amphipoda		Amphipoda n/i	Other Crustacea	0.29 (5.2)	0.33	0.57 (6.39)	0.86
			Gammaridae	Gammaridae n/i	Other Crustacea	0.05 (2.1)	0.07	0.05 (1.80)	0.1
			Hyperiididae	Hyperiididae n/i	Other Crustacea	0.02 (1.4)	0.04	0.25 (3.42)	0.77
			Caprellidae	Caprellidae n/i	Other Crustacea	0.05 (2.2)	0.05	0.001 (0.09)	0.03
		Decapoda		Decapoda n/i	Other Crustacea	0.78 (8.6)	0.78	0.50 (6.40)	0.54
				Decapoda eggs	Other Crustacea	0.00	0.00	0.01 (0.88)	0.004
				Zoea larvae	Zoea larvae	12.29 (32.4)	12.49	13.35 (31.87)	13.05
				Megalopa larvae	Other Crustacea	1.09 (9.9)	1.12	1.58 (11.32)	1.54
			Hippidae	<i>Emerita analoga</i>	Other Crustacea	0.14 (3.4)	0.17	0.23 (4.65)	0.13
			Munididae	<i>Pleuroncodes monodon</i>	<i>P. monodon</i>	7.66 (26.3)	7.6	5.39 (1.99)	5.24
		Euphausiacea	Euphausiidae	Euphausiidae n/i	Euphausiidae	49.31 (49.3)	49.08	27.45 (42.68)	26.51
		Stomatopoda		Stomatopoda n/i	Other Crustacea	0.21 (4.4)	0.26	0.28 (4.86)	0.31
			Squillidae	<i>Squilla</i> spp.	Other Crustacea	0.04 (1.9)	0.04	0.04 (1.59)	0.06
Echinodermata				Echinodermata n/i	Other	0.00	0.00	0.003 (0.24)	0.01
Chordata				Tunicata n/i	Tunicata	0.09 (3.0)	0.09	0.30 (5.16)	0.34
	Thaliacea			Thaliacea n/i	Tunicata	0.00	0.00	3.46 (17.52)	2.99
	Actinopterygii			Teleostei n/i	Other Teleostei	6.88 (24.9)	6.87	12.55 (32.25)	11.99
				Teleostei eggs	Eggs larvae	1.06 (9.9)	0.94	0.96 (8.98)	1.2
				Teleostei larvae	Teleostei	0.60 (7.3)	0.63	2.69 (15.32)	2.66
				Teleostei larvae	Teleostei	0.60 (7.3)	0.63	2.69 (15.32)	2.66
			Atherinopsidae	<i>Odontesthes regia</i>	Coastal fishes	0.40 (6.2)	0.4	0.39 (6.18)	0.36
		Aulopiformes	Paralepididae	Paralepididae n/i	Mesopelagics	0.00	0.00	0.02 (1.12)	0.02
		Clupeiformes		<i>Sardinops sagax</i>	Other Teleostei	0.03 (1.5)	0.03	0.03 (1.63)	0.03
			Engraulidae	Engraulidae n/i	Engraulidae	0.39 (6.1)	0.36	2.39 (15.05)	2.3
				<i>Anchoa</i> spp.	Engraulidae	0.14 (3.7)	0.14	0.25 (4.92)	0.25
				<i>Engraulis ringens</i>	Engraulidae	4.44 (20.4)	4.33	5.99 (23.50)	5.76
		Gadiformes	Bregmacerotidae	<i>Bregmaceros</i> spp.	Other Teleostei	0.02 (1.3)	0.02	0.00	0.00
			Merlucciidae	<i>Merluccius gayi peruanus</i>	Other Teleostei	0.83 (9.0)	0.84	0.00	0.00
		Myctophiformes	Myctophidae	Myctophidae n/i	Mesopelagics	1.48 (11.7)	1.42	0.43 (6.23)	0.42
		Osmeriformes	Bathylagidae	Bathylagidae n/i	Mesopelagics	0.01 (1.0)	0.01	0.05 (2.26)	0.05
			Osmeridae	Osmeridae n/i	Mesopelagics	0.00	0.00	0.002 (0.27)	0.002

Table 1 (continued)

Phylum	Class	Order	Family	Species	Dietary group	<i>T. murphyi</i>		<i>S. japonicus</i>	
						%W	%O	%W	%O
		Perciformes	Blenniidae	Blenniidae n/i	Coastal fishes	0.01 (0.7)	0.003	0.00	0.00
			Carangidae	Carangidae n/i	Other Teleostei	0.09 (2.8)	0.08	0.30 (5.44)	0.3
			Centrolophidae	Centrolophidae n/i	Other Teleostei	0.01 (1.0)	0.01	0.05 (2.13)	0.05
			Labrisomidae	Labrisomidae n/i	Coastal fishes	0.01 (0.6)	0.01	0.00	0.00
			Sciaenidae	<i>Sciaena deliciosa</i>	Coastal fishes	0.01 (1.0)	0.01	0.00	0.00
			Sphyraenidae	<i>Sphyraena</i> spp.	Coastal fishes	0.00	0.00	0.02 (1.27)	0.02
			Trichiuridae	<i>Lepidopus</i> spp.	Coastal fishes	0.01 (1.0)	0.01	0.00	0.00
				<i>Trichiurus lepturus</i>	Coastal fishes	0.01 (1.0)	0.01	0.00	0.00
		Pleuronectiformes	Cynoglossidae	Cynoglossidae n/i	Coastal fishes	0.01 (0.4)	0.01	0.00	0.00
		Scorpaeniformes	Normanichthyidae	<i>Normanichthys crockeri</i>	Coastal fishes	0.70 (8.2)	0.65	0.93 (9.46)	0.91
		Stomiiformes		Stomiiformes n/i	Mesopelagics	0.00	0.00	0.01 (0.91)	0.01
			Phosichthyidae	Phosichthyidae n/i	Mesopelagics	0.00	0.00	0.0004 (0.04)	0.003
				<i>Vinciguerria lucetia</i>	Mesopelagics	1.56 (12.0)	1.48	1.22 (10.59)	1.11
			Sternoptychidae	Maurolicinae n/i	Mesopelagics	0.15 (3.4)	0.13	0.18 (3.69)	0.15
		Syngnathiformes	Syngnathidae	Syngnathidae n/i	Coastal fishes	0.00	0.00	0.06 (2.44)	0.06
				<i>Leptonotus blainvillanus</i>	Coastal fishes	0.07 (2.5)	0.07	0.13 (3.27)	0.08

Table 2

Distribution of the thirteen dietary groups recovered from jack and chub mackerels stomach contents off Peru during 1973–2013. Are indicated, the dietary group, the prey code, the number of stomachs with presence, the mean value (±standard deviation) of the proportion by weight (%W), and the frequency of occurrence (%O).

	Prey code	<i>Trachurus murphyi</i>			<i>Scomber japonicus</i>		
		N° stomachs	%W	%O	N° stomachs	%W	%O
Tunicata	Tunic	11	0.09 (3.01)	0.1	568	3.76 (18.21)	3.33
Cephalopoda	Cepha	79	0.57 (7.27)	0.56	366	2.34 (14.6)	2.33
Copepoda	Copep	936	7.10 (25.09)	7.26	2993	14.29 (31.98)	15.49
Zoea larvae	Zoea	1539	12.29 (32.38)	12.51	2412	13.35 (31.87)	13.08
Euphausiidae	Eupha	5732	49.31 (49.27)	49.09	4120	27.45 (42.68)	26.54
Pleuroncodes monodon	Pleur	907	7.66 (26.27)	7.61	778	5.39 (21.99)	5.24
Other Crustacea	Crust	496	3.15 (16.84)	3.35	1127	4.01 (17.48)	4.71
Engraulidae	Engra	575	4.96 (21.47)	4.83	1126	8.64 (27.77)	8.3
Mesopelagics	Mesop	413	3.20 (17.02)	3.03	297	1.90 (13.13)	1.75
Coastal fishes	Coast	148	1.21 (10.68)	1.16	208	1.52 (12.03)	1.43
Other Teleostei	Teleo	941	7.85 (26.49)	7.85	1847	12.93 (32.67)	12.37
Eggs and larvae Teleostei	EgLa	231	1.66 (12.29)	1.58	733	3.65 (17.61)	3.86
Other	Other	171	0.95 (9.37)	1.09	433	0.78 (7.67)	1.58

3. Results

3.1. Overall diet description

In total 47,535 stomachs (18,377 CM and 29,158 JM) were analysed, of which 23,570 (12,476 CM and 11,094 JM) were non-empty. The proportion of empty stomachs was much higher for JM (62%) than for CM (32%). This proportion was lower for samples collected by research vessels (36% and 22% for JM and CM, respectively) than by commercial vessels (64% and 33% for JM and CM, respectively). In addition, considering all samples the distribution of the proportion of empty stomachs per fishing set was different for CM and JM (Fig. 2). For CM, 39% of the fishing sets had less than 10% of empty stomachs and only 6% had more than 90% of empty stomachs. In contrast, empty stomachs of JM were concentrated in some fishing sets: 21% of the fishing sets had more than 90% of empty stomachs.

Despite some disparity, the overall diet composition in wet weight (Fig. 3) was not significantly different between JM and CM ($G = 14.6, p = 0.265$). Euphausiidae was the dominant prey for both species and contributed to 49.3% and 27.4% for JM and CM, respectively. Zoea larvae (12.3%), *P. monodon* (7.7%), copepods (7.1%) and other teleostei (7.0%) were the additional main prey groups for JM, while copepods (14.3%), zoea larvae (13.3%), other

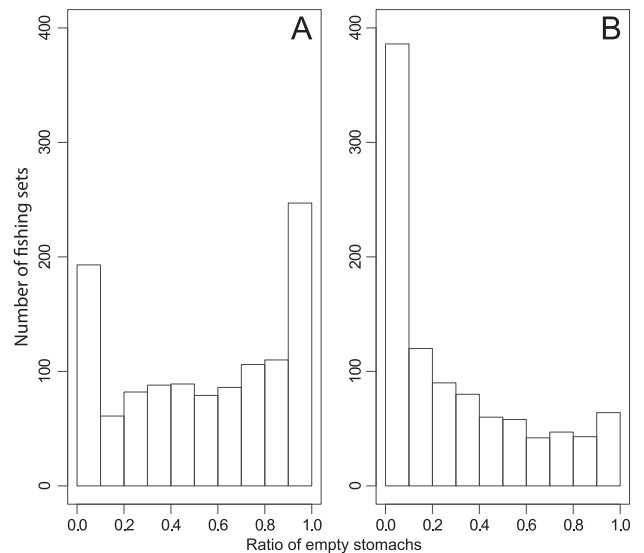


Fig. 2. Distribution of the ratio of empty stomachs per fishing set for (A) *Trachurus murphyi* and (B) *Scomber japonicus*.

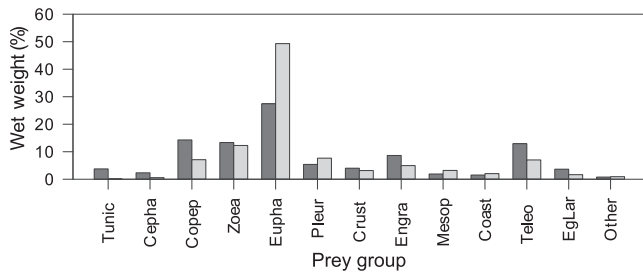


Fig. 3. *Trachurus murphyi* (light grey bars – 11,094 stomachs) and *Scomber japonicus* (dark grey bars – 12,476 stomachs) diet composition in wet weight (%) by prey group.

teleostei (12.9%) and engraulidae (8.6%) were the extra main prey groups for CM (Fig. 3). Overall diets of both species were dominated by zooplankton (74% and 82% and for CM and JM, respectively), and contribution of fish was higher in CM diet (25% and 17% for CM and JM, respectively).

The diet composition of JM varied significantly ($G = 277.7$; $p < 0.0001$) according to size (Fig. 4A). Euphausiidae contribution by wet weight increased with size until 40 cm (41.8% for JM less than 21 cm and 56.5% for fish size ranging 31–41 cm), but decreased to 6% for individuals larger than 51 cm. Fish contribution was low for JM < 41 cm (maximum contribution 16.2%) but this pattern reversed for larger sizes. Engraulidae dominated indeed the fish diet composition of JM larger than 41 cm, and the largest JM (>51 cm) foraged mainly on engraulidae (55.5%) and other teleostei (25.3%). CM did not exceed 40 cm and its diet composition (Fig. 4A) did not vary significantly with size ($G = 29.8$; $p = 0.19$). Euphausiidae contribution however increased from 12.7% for CM < 21 cm to 28.3% for CM larger than 31 cm. Diet composition according to maturity stages had similar trends to those observed for fish size, and neither diet composition of JM and CM varies with sex ($G = 2.51$, $p = 0.99$ and $G = 0.72$, $p = 1$, respectively). Sex and maturity stages were therefore not taken into account in further analyses.

3.2. Spatial patterns

JM and CM diet composition had similar trends according to latitudinal zones (Fig. 4B). The contribution of species associated to the coastal upwelling (e.g. engraulidae, coastal fishes, *P. monodon*, zoea larvae) increased in the centre-south zone (10–15°S) while other species (e.g. euphausiidae and copepod) showed an opposite trend. Diet composition according to the distance to the shelf break (Fig. 4C) illustrates the higher contribution of coastal species over the shelf (distance ≤ 10 km). The density distribution of the occurrence in the stomachs of two 'coastal' prey taxa (engraulidae and *P. monodon*) and of one 'oceanic' one (euphausiidae), showed that the highest density for *P. monodon* was located before the shelf break for both JM and CM (Fig. 5). The distribution of engraulidae was similar to the one of *P. monodon* for CM, but more widely extended for JM. Finally, euphausiidae were clearly distributed after the shelf break, with a wide distribution for both CM and JM. Note that these cross-shore patterns were not related to changes in fish size except for CM that presented slightly smaller sizes inshore.

3.3. Temporal patterns

Seasonal variations in JM and CM diet composition were slight and rather inconsistent between species (Fig. 4D). We can note, however, a lesser importance of zoea larvae in fall and an opposite pattern for engraulidae. Yearly changes between 1973 and 2013 highlight the fact that euphausiidae clearly dominated by wet

weight the diet of JM before year 2000 ($67.7 \pm 46.2\%$) whereas contribution was reduced by half after 2000 ($31.9 \pm 45.6\%$) (Fig. 4E). Proportion of zoea larvae showed an opposite trend ($0.3 \pm 4.7\%$ before year 2000 and then $23.8 \pm 42.0\%$), such as *P. monodon* ($1.3 \pm 11.0\%$ before year 2000 and then $13.8 \pm 34.1\%$). Fish consumption by JM (especially engraulidae) was rather modest except in 1975–1977. Temporal patterns were blurred for CM because of a lack of data for several years, in particular during El Niño years. However, as for JM but to a lesser extent, euphausiidae contribution by wet weight was higher until year 2000 ($41.0 \pm 47.1\%$ vs. $22.0 \pm 39.5\%$ after 2000). Once more, proportions of zoea larvae and *P. monodon* exhibited an opposite trend ($1.4 \pm 10.7\%$ before 2000 vs. $18.2 \pm 36.0\%$ after for zoea larvae; $1.0 \pm 9.7\%$ before 2000 vs. $7.2 \pm 25.1\%$ after for *P. monodon*). In addition, the mean condition factor of JM computed for the period 1973–1999 was significantly lower than the mean computed after 1999: $K_n = 0.96 \pm 0.11$ before year 2000 and $K_n = 1.05 \pm 0.10$ for the period 2000–2013 ($p < 0.0001$; Fig. 6A). The condition factor of CM exhibited the same significant pattern despite the missing years: $K_n = 0.94 \pm 0.15$ vs. 1.04 ± 0.10 ($p < 0.0001$; Fig. 6B). On the contrary, the fullness of non-empty stomachs for both species was significantly higher for the period 1973–1999 than for the period 2000–2013 (JM: FWI = 0.94 ± 1.51 vs. 0.77 ± 1.22 , $p < 0.000$; CM: FWI = 1.62 ± 2.01 vs. 1.22 ± 1.51 , $p < 0.0001$; Fig. 7).

3.4. El Niño and La Niña

For JM less than 40 cm, the percentage of non-empty stomachs was identical during El Niño and La Niña periods (24.3%). However the fullness of non-empty stomachs was significantly higher during El Niño than during La Niña periods (1.55 ± 1.56 vs. 0.71 ± 1.00 , $p < 0.0001$), whereas the condition factor K_n was significantly lower during El Niño than during La Niña periods (0.92 ± 0.12 vs. 1.02 ± 0.10 , $p < 0.0001$). Diet composition did not differ between El Niño, La Niña (and 'Neutral') periods (Fig. 8) despite higher contributions by wet weight of teleostei (17.8% vs. 3.9%) and of eggs and larvae of teleostei (8.6% vs. 0.2%), a lower proportion of zoea larvae (<1% vs. 7.3%) and an absence of *P. monodon* during El Niño period (10.4% during La Niña). The contribution of euphausiidae did not vary between El Niño and La Niña periods (52.0% vs. 53.9%).

3.5. Multivariate approach

Fig. 9 shows the pruned classification tree performed on JM diet data. The first split separated stomachs according to time. Before 2000, JM diet was dominated by Euphausiidae. Among this group, the main node (Node #4; $n = 5031$) encompassed individuals smaller than 40 cm with a predicted diet dominated by euphausiidae (predicted probability = 0.74). The predicted diet of JM larger than 40 cm showed the dominance of copepoda (Node #1; $n = 125$) and euphausiidae (Node #2; $n = 198$) for individuals collected from 1978 to 1999 (predicted probability = 0.77 and 0.60, respectively) and of engraulidae for fish collected before 1978 (Node #3; $n = 459$; predicted probability = 0.51). From 2000, a second temporal split occurred in 2002. In 2000 and 2001 the predicted diet was dominated by *P. monodon* when $Z_{15^\circ\text{C}}$ was deeper than 85 m (Node #6; $n = 143$; predicted probability = 0.85) and by other teleostei and euphausiidae when $Z_{15^\circ\text{C}}$ was shallower than 85 m (Node #5; $n = 804$; predicted probability = 0.30 and 0.27, respectively). From 2002 the predicted diet composition was more diverse. Zoea larvae (Node #9; $n = 1662$; predicted probability = 0.45) and euphausiidae (main predicted prey in Nodes 7 and 8 with probability of 0.37 and 0.36, respectively) were the dominant prey but other prey taxa such as *P. monodon* contributed significantly (e.g. predicted probability = 0.24 in Node #8 and 0.10 in Nodes #7 and #9).

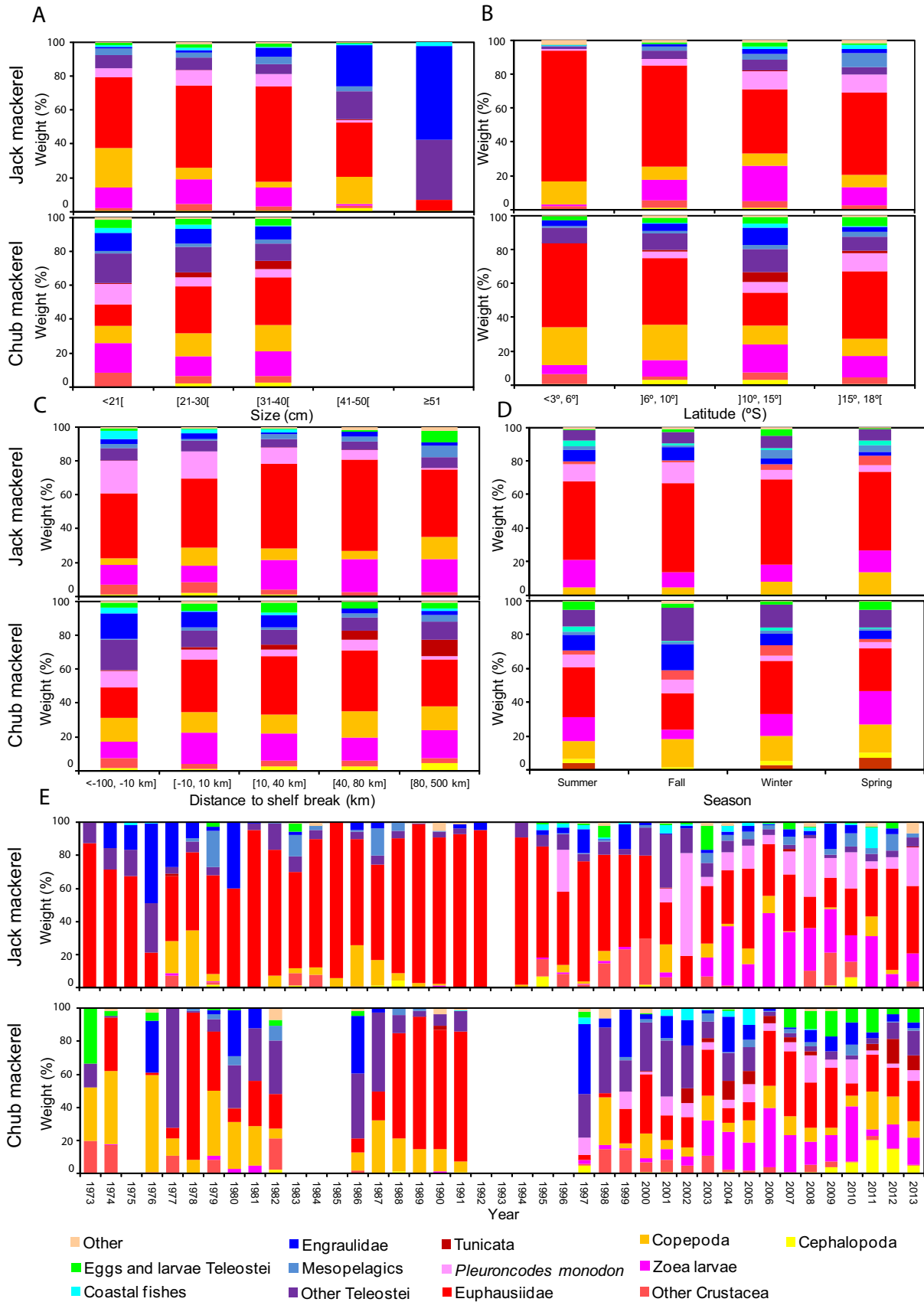


Fig. 4. (A) Diet composition of *Trachurus murphyi* (JM) and *Scomber japonicus* (CM) in mean weight percentage (%W) according to the individual fork length (in cm). (B) Diet composition of JM and CM in%W according to the latitudinal zone. (C) Diet composition of JM and CM in%W according to the distance to the shelf break (in km, negative inshore and positive offshore). (D) Diet composition of JM and CM in%W per season. (E) Diet composition of JM and CM in%W per year from 1973 to 2013.

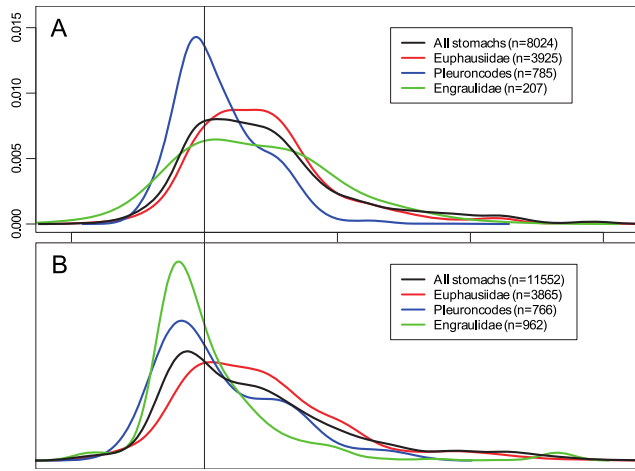


Fig. 5. Kernel density estimates of stomach numbers for the whole datasets and for the subsets containing euphausiidae, *P. monodon* and engraulidae according to distance to the shelf break (in km, negative inshore and positive offshore) for (A) *Trachurus murphyi* and (B) *Scomber japonicus*; the numbers in parenthesis indicate the number of stomachs.

The second classification tree was performed on both JM and CM diet, without taking into account the year effect (Fig. 10). The pruned classification tree showed seven nodes and the first split discriminated the two species. The predicted diet of JM smaller than 43 cm was dominated by euphausiidae (Node #7; $n = 11,447$; predicted probability = 0.51). The diet of larger JM distributed in waters with $Z_{15^\circ\text{C}} < 89$ m was dominated by copepods (Node #4; $n = 79$; predicted probability = 0.97) and by euphausiidae (Node #5; $n = 395$; predicted probability = 0.36), while those distributed in waters with $Z_{15^\circ\text{C}} \geq 89$ m fed mainly on engraulidae (Node #6; $n = 258$; predicted probability = 0.65). The predicted diet of CM in the north, centre-north and south zones was dominated by euphausiidae (Node #1; $n = 5937$; predicted probability = 0.43). In the centre-south zone, the predicted diet composition of CM distributed around and off the shelf was mainly distributed between euphausiidae, zoea larvae, copepoda and other teleostei (Node #3; $n = 8143$; predicted probability = 0.24, 0.17, 0.14, and 0.12,

respectively). The predicted diet of CM distributed over the shelf was dominated by teleostei, engraulidae, *P. monodon* and zoea larvae (Node #2; $n = 2928$; predicted probability = 0.24, 0.18, 0.12, and 0.12, respectively).

3.6. Diversity of the prey taxa

The average occurrence of the 60 prey taxa of JM per year showed a clear temporal pattern (Fig. 11), summarised by the first axis of the Correspondence Analysis. Years were classified into two groups, before and after 1996. The classification satisfied temporal contiguity except year 1997 grouped in the first period (note that in 1997 most of samples were collected before the rise of El Niño). The first period was characterised by low diversity (mainly 15 prey taxa); the main prey were euphausiidae, other teleostei, copepoda and engraulidae. Some other taxa such as the hake *Merluccius gayi peruanus*, were also reported (in 1975 and 1976). On the opposite, a larger number of taxa were observed from 1996. Among them, Zoea larvae and *P. monodon* were largely dominant, but other taxa such as *Vinciguerria lucetia*, teleostei larvae and stomatopoda were also frequently observed in the JM stomach content. Finally, euphausiidae, copepoda, other teleostei, occurred throughout the whole study and composed the stable part of the prey taxa community.

For both species, the estimated richness index S_{boot} per year for 100 stomachs (Fig. 12A) was significantly ($p < 0.0001$) higher since 1996 (11.3 ± 2.9 for JM; 15.1 ± 3.1 for CM) than before (6.2 ± 3.4 for JM; 6.9 ± 3 for CM). This is confirmed by the Sørensen index of similarity calculated between both periods (before and after 1996). The index value was 0.68, with 31 prey taxa common to both periods but 6 versus 23 unique prey taxa before and after 1996, respectively.

Regarding the estimated richness index for 500 stomachs per latitudinal zone (Fig. 12B), the highest values were observed in the Centre-South zone (10° – 15°S) for both species (28.7 ± 2.4 for JM and 38.5 ± 2.4 for CM). The Centre-North (6° – 10°S) and the Southern (15° – 18°S) zones presented similar estimated richness with 24.5 ± 1.8 and 24.5 ± 2.0 for JM, and 34.7 ± 1.8 and 30.5 ± 2.1 for CM; while the Northern zone ($<3^\circ$ – 6°S) presented the lowest richness (20.4 ± 1 for JM and 19.5 ± 2 for CM). Finally, the

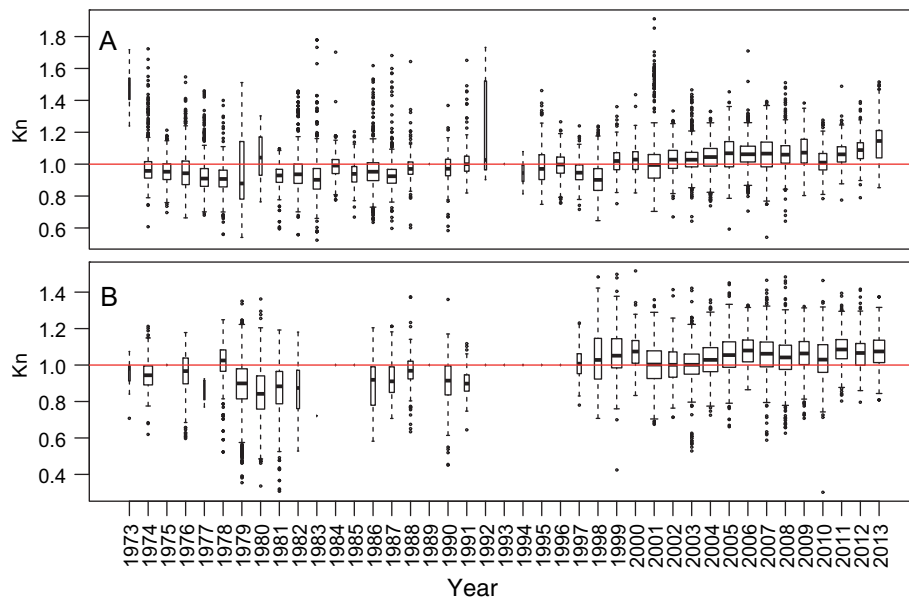


Fig. 6. Year evolution of the relative condition factor (K_n) of (A) *Trachurus murphyi* and (B) *Scomber japonicus*. Box width is proportional to square root of the number of stomachs sampled for a given year. The red line corresponds to a theoretical value of $K_n = 1$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

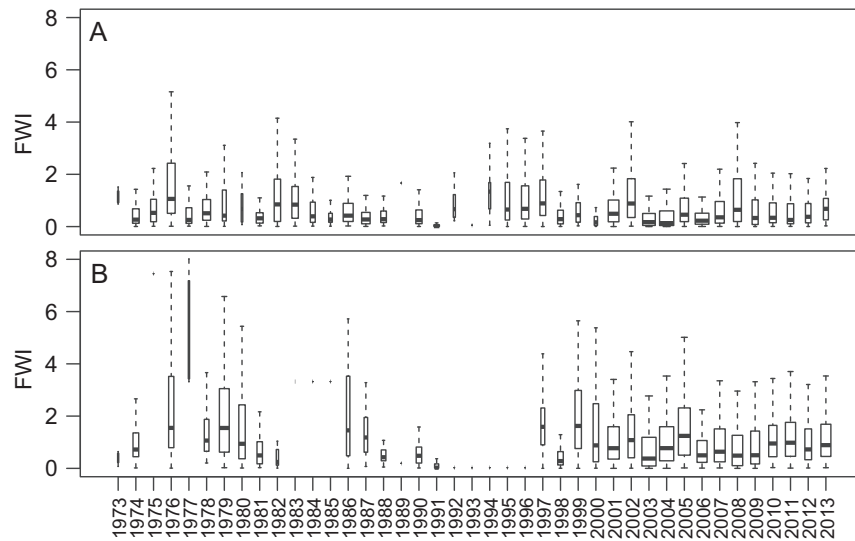


Fig. 7. Year evolution of the Fullness Weight Index (FWI) for non empty stomachs of (A) *Trachurus murphyi* and (B) *Scomber japonicus*. Box width is proportional to square root of the number of stomachs sampled for a given year. Outliers are not printed.

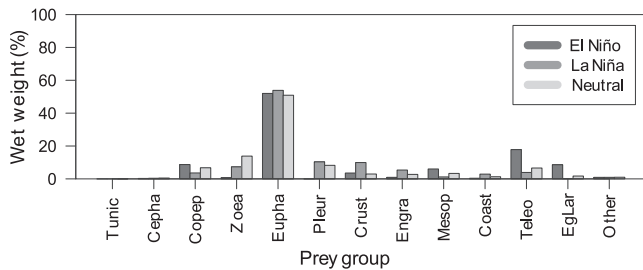


Fig. 8. *Trachurus murphyi* diet composition in wet weight (%) by prey group during El Niño (dark grey bars), La Niña (grey bars) and Neutral (light grey bars) periods.

estimated richness for 500 stomachs per categories of distance to the shelf break (Fig. 12C) varied between 24 and 28 taxa for JM and between 30 and 36 taxa for CM. All differences between categories of distance to the shelf break were significant, except for CM between (–10 to 10 km) and (40 to 80 km), but no trend was clearly identified.

We also tested the impact of El Niño and La Niña periods on JM prey diversity. The diversity was significantly ($p < 0.001$ in all cases) lower during El Niño (11.5 ± 1.6) than neutral (15.7 ± 2.3) and La Niña (16.2 ± 2.0) periods. The Sørensen index of similarity strengthens these findings. The index value was 0.57 between El Niño and La Niña periods, with 12 common prey taxa, but 5 versus 13 unique prey taxa for El Niño and La Niña periods, respectively.

4. Discussion

This work is based on a wide dataset on JM and CM diet encompassing a large range of spatiotemporal location and sizes. Beyond the usual diet description, our results provide new knowledge on the comparative trophic behaviour of these species, in particular the role of geographical features and how interannual and decadal climatic variability impact ecosystem structure and fish trophic ecology.

4.1. Overall diet, size effect and comparative trophic ecology

JM and CM distribute over an area larger than the Peruvian EEZ (Bertrand et al., 2004a) and are considered as opportunistic foragers adapting their trophic behaviour to prey accessibility

(Konchina, 1981, 1982; Muck and Sánchez, 1987; Alegre et al., 2013). Our results confirm such opportunistic trophic behaviour since both species foraged over a large variety of taxa (60 and 62 for JM and CM, respectively); but the picture of the diet combining all data (Fig. 3) hides high spatiotemporal variability. The global diet of both species was widely dominated by zooplankton (82% and 74% for JM and CM, respectively). Such results are in accordance with most published studies (e.g. Konchina, 1982; Konchina et al., 1996; Castro and Santana, 2000; Antezana, 2010). The diet of JM varied with size (Figs. 4A and 8). Individuals less than 40 cm consumed mainly zooplankton, in particular euphausiids, zoea larvae, *P. monodon* and, for the smallest (<21 cm), copepoda. Over ~40 cm the diet shifted towards a dominance of fish with an important contribution of engraulidae that exceeded 50% for JM larger than 50 cm. Such shift has already been reported (Muck and Sánchez, 1987; Ermolovich and Gardina, 1994). This change in diet composition with fish size can be attributed to the predator's ability to capture and handle the prey (Crowder, 1985; Christensen, 1996; Lundvall et al., 1999). Large JM have access to highly energetic prey such as the Peruvian anchovy *Engraulis ringens*. However overfishing removed these large JM from the system (Gerlotto et al., 2012). This could explain why high fish proportion in the diet was only observed in the first years of our time series before the JM commercial fishing development (Fig. 4E). On the opposite, CM, which has a lower size-range than JM, did not present clear ontogenetic trend towards larger prey. Such pattern was already mentioned by Konchina (1982). Indeed in her and our studies (but not in the one of Muck and Sánchez, 1987) CM foraged on small zooplankton (copepoda) at all size classes and its contribution was even greater in CM > 30 cm while small CM could paradoxically consume more fishes than large CM (Figs. 4A and 9).

The proportion of non-empty stomach was low (38%) for JM, in accordance with other studies (Medina and Arancibia, 2002). This proportion reached 68% for CM; such high proportion was also reported by Konchina (1982, 1990) off Peru. This specific difference could be due to higher food regurgitation during capture for JM or to a difference in feeding behaviour (see Konchina, 1990). In our dataset, the distribution of proportion of empty or non empty JM stomachs per fishing set (Fig. 2) was not homogeneous, indicating that the behavioural hypothesis with JM foraging actively only at given periods/places is the most likely.

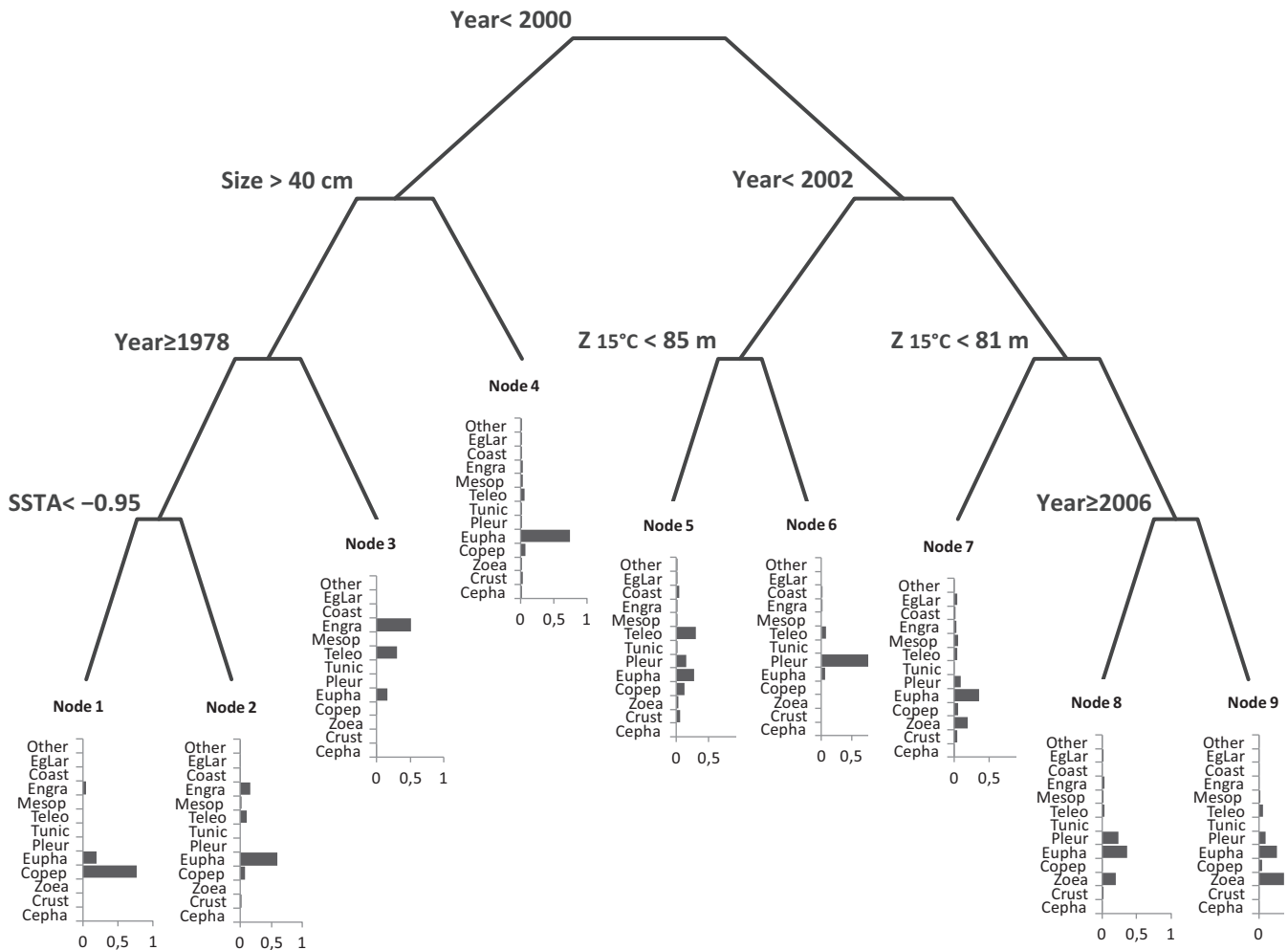


Fig. 9. Classification tree of *Trachurus murphyi* diet (prey groups) according to the year, $Z_{15^\circ\text{C}}$ (in m), the size (in cm), the SSTA (in $^\circ\text{C}$), the distance to the shelf break (in km, negative inshore and positive offshore) and the zone (North, Centre, South). For each final node, the predicted probabilities of occurrence of the 13 prey groups is detailed (histograms). See Table 2 for prey codes.

Even if there is a trophic overlap between JM and CM as observed by Konchina (1992) and Medina and Arancibia (1998), their diet exhibited various differences. Surprisingly, despite their smaller maximal size, CM consumed more fish than JM (25% vs. 17%). This contradicts the idea of JM being more voracious than CM (Medina and Arancibia, 1998). Actually CM diet was more diverse (Table 1) and it consumed a larger amount of large prey (fish) but also of small prey (copepoda and eggs and larvae of teleostei).

4.2. Spatial patterns

JM and CM diet varied according to the along-shore (latitude) and cross-shore (distance to the shelf break) ranges with related patterns. The contribution of euphausiidae and other oceanic components (e.g. mesopelagic fishes) was greater off the shelf break but also in northern (north of $\sim 10^\circ\text{S}$) and southern (south of $\sim 15^\circ\text{S}$) Peru. On the opposite the contribution of coastal taxa (e.g. *P. monodon*, engraulidae and coastal fishes) was higher in central Peru (from $\sim 10^\circ\text{S}$ – 15°S). The latitudinal pattern can be related to genuine latitudinal effects on plankton distribution (Ayón et al., 2008) and to the geography of the Peruvian coast than. Indeed the shelf offshore extension is much larger in central Peru than in the north and south boundaries (see Fig. 1 for the shelf

break position as illustrated by the 200 m isobath). The shelf break appears thus as an important biogeographical barrier affecting species distribution (e.g. Ballón et al., 2011) and therefore the fish diet.

4.3. Long term trend and the euphausiidae paradox

Euphausiids were strongly dominant in JM diet before 2000, while after 2000 *P. monodon* and zoea larvae took much more importance. The increase of *P. monodon* in fish diet is consistent with the dramatic increase in *P. monodon* observed off Peru since the late 1990s (Gutiérrez et al., 2008). Similarly, the population of coastal sand crab *Emerita analoga*, which makes the bulk of zoea larvae (Blaskovic' et al., 2009), was likely favoured by the increase in productivity observed off Peru during the last decades (Sifeddine et al., 2008; Gutiérrez et al., 2009). The case for euphausiidae is more paradoxical. Indeed euphausiidae contribution to JM diet was very high from the late 1970 to the late 1990s and dropped then after. This trend is contradictory with the actual trend in euphausiids abundance off Peru (Ayón et al., 2011) that presented lower biomasses in the late 1970–1990s when the NHCS was less productive and more oxygenated than before and since the late 1990s (Ayón et al., 2011; Bertrand et al., 2011).

Let us consider JM and CM be opportunistic foragers as indicated in Konchina (1981, 1982) and Muck and Sánchez (1987)

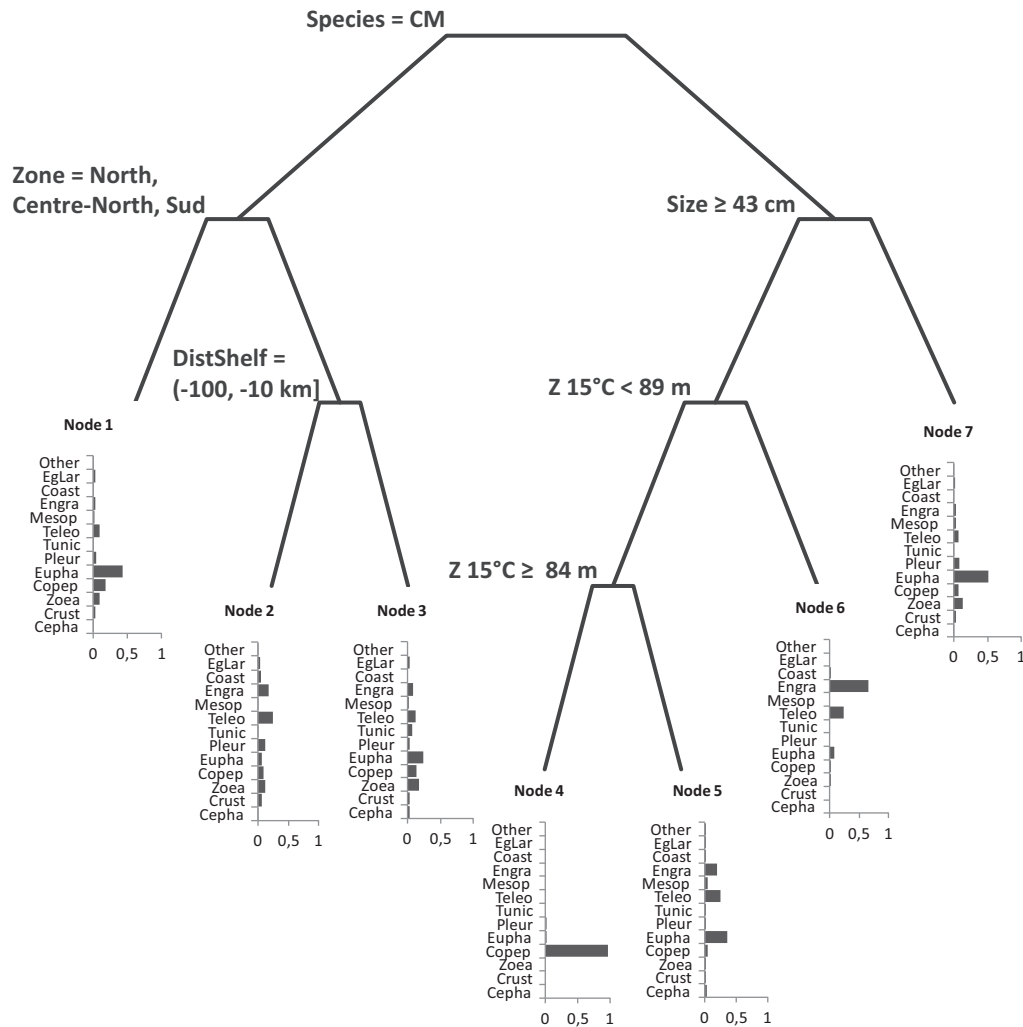


Fig. 10. Classification tree of *Trachurus murphyi* and *Scomber japonicus* diet (prey groups) according to the species, $Z_{15^\circ\text{C}}$ (in m), the size (in cm), the SSTA (in $^\circ\text{C}$), the distance to the shelf break (in km, negative inshore and positive offshore) and the zone. For each final node, the predicted probabilities of occurrence of the 13 prey groups is detailed (histograms). See Table 2 for prey codes.

and in the present work; changes in their diet should then indicate changes in the ecosystem. Indeed JM abundance and biology is known to be affected by climatic regime (Csirke, 2013). Here we showed that changes in prey contribution actually corresponded to observed changes in the ecosystem in the case of *P. monodon* but not for euphausiidae. This paradox can be explained by the fact that *P. monodon* and zoea larvae are prey easy to handle and, as part of the epipelagic community, they are concentrated in dense patches within a thin surface layer above the oxycline (Bertrand et al., 2011, 2014). Additionally, they are accessible during the complete diel cycle when most euphausiidae perform diel vertical migration and are inaccessible during the day (Ballón et al., 2011). Furthermore, *P. monodon* energy content is high. Aurióles-Gamboia et al. (2004) showed that the fatty acid composition of a close species, *Pleuroncodes planipes*, directly depended of the available food quality. In the highly productive NHCS, *P. monodon* has high protein and fatty acid content (Gutiérrez, 2002) and is exploited to produce seafood oil, and protein concentrates. JM thus responded and adapted to the increased abundance increased availability, accessibility and biomass of *P. monodon* and zoea larvae. The temporal shift in diet composition was accompanied by a shift in fish condition: the condition factor of JM was significantly lower before than after 2000. Such difference can be due to a change towards

better food quality but also to density dependence processes. Indeed JM has been over-exploited in the southeastern Pacific (www.southpacificrfmo.org) and was more abundant during the late 1970–mid 1990s when macrozooplankton (in particular euphausiidae) abundance was lower (Ayón et al., 2011). On the opposite, in recent year, when JM was less abundant, macrozooplankton biomass was high (Ayón et al., 2011; Ballón et al., 2011) and prey were concentrated over a thin surface layer (Bertrand et al., 2011).

The incomplete time series for CM diet blurs the conclusion that could be drawn on decadal patterns. However as for JM, CM foraged on a high proportion of *P. monodon* and zoea larvae since the early 2000s, when they were abundant in the system. Its condition factor was also higher after 2000 than before.

Our findings show that diet composition of CM and JM reveal ecosystem changes but is not always a good indicator of specific changes in prey biomass as illustrated in the euphausiids case. Indeed the decadal changes in JM diet point out that it target the most abundant prey, and within these prey would prefer those that are the most accessible (e.g. along the whole diel cycle and concentrated in dense layer), demand less energy to grab or catch and provide a higher energy intake per energy invested. Foraging behaviour does matter in our long-term feeding study!

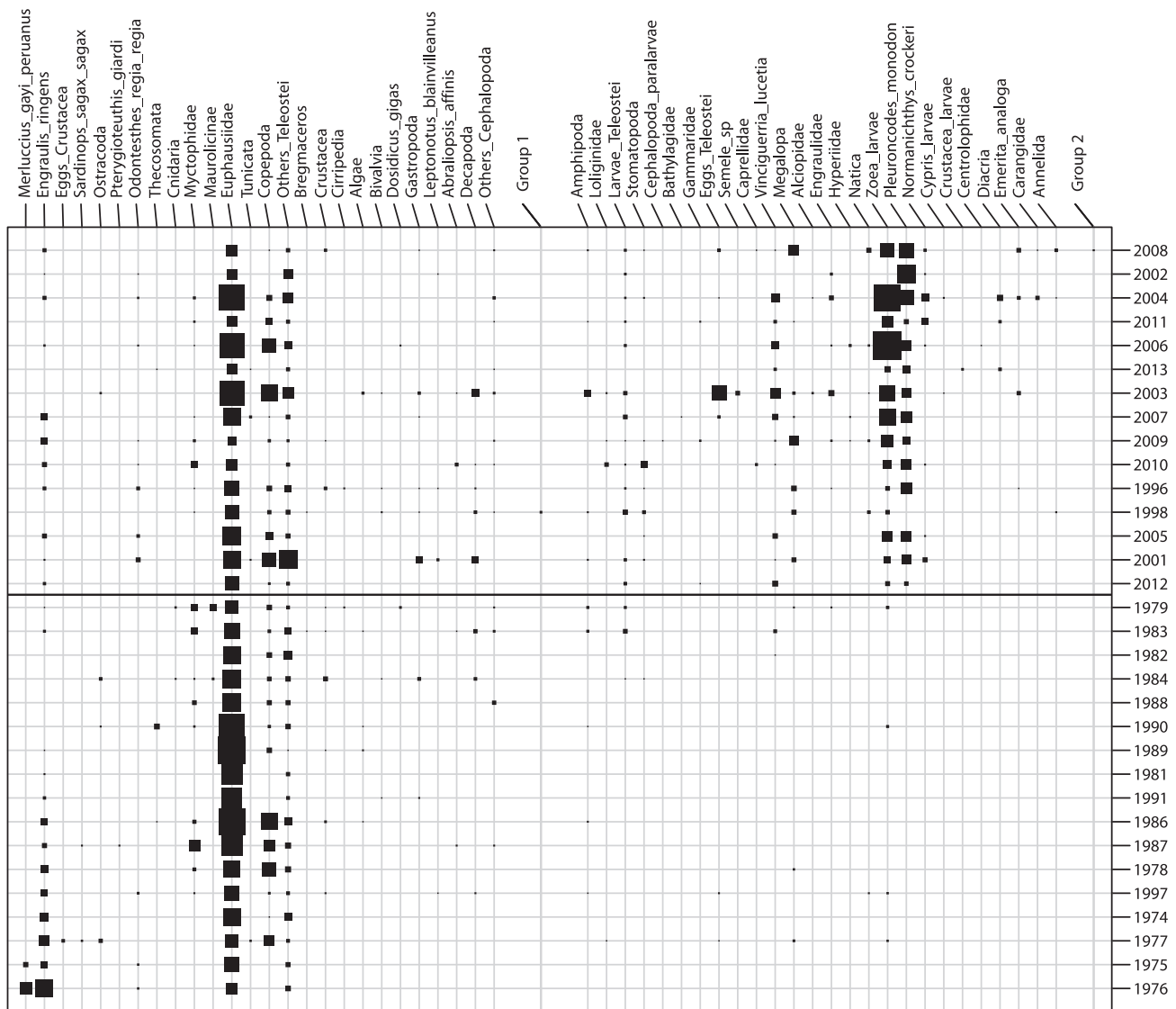


Fig. 11. Mean occurrence of *Trachurus murphyi* prey taxa per year. Group 1: *Anchoa* sp., *Lepidopus* sp., *Squilla* sp. and *Trichiurus lepturus*; Group 2: Blenniidae, Cynoglossidae, Labrisomidae. Prey taxa and years are ordered after their position on the first axis of the correspondence analysis of the table which expresses a temporal gradient in the prey distribution. The solid horizontal line discriminates between the two clusters obtained by the hierarchical clustering.

4.4. El Niño and La Niña events: do they matter?

The NHCS is a region notably affected by El Niño southern oscillation (Chavez et al., 2008). Exceptional El Niño events, such as those that occurred in 1982–83 and 1997–98, affect all marine ecosystems components (e.g. Barber and Chavez, 1983; Arntz and Tarazona, 1990; Fiedler, 2002) including JM and CM populations (Arcos et al., 2001; Bertrand et al., 2004b; Gerlotto et al., 2012). Actually, the condition factor was lower during El Niño than La Niña periods. Surprisingly we observed an opposite pattern in terms of fullness since the percentage of non-empty stomach was identical during El Niño and La Niña periods (24.3%) but the fullness of non-empty stomachs was significantly higher during El Niño than La Niña periods. This counterintuitive result also observed by Diones (1985) could be due to a higher metabolic requirement during warmer El Niño condition. However, specific bioenergetic studies need to be conducted to propose a robust interpretation.

Prey diversity was significantly lower during El Niño (see next section) but contrary to previous studies (Sánchez de Benites and

Muck, 1987; Muck and Sánchez, 1987) we did not observed strong differences in diet composition between El Niño, La Niña and neutral periods (Fig. 8). Comparable results were observed on anchovy diet with no clear changes in diet composition and stomach fullness related to El Niño or La Niña events (Espinoza and Bertrand, 2008). The difference between our studies and those reporting an ENSO effect (e.g. Sánchez de Benites and Muck, 1987) is most likely due to samples' size. Comparing two years (e.g. an El Niño versus a La Niña year) can lead to misleading conclusion when number of samples is low. Indeed our findings demonstrated a high spatiotemporal variability in diet composition of CM and JM. Over-interpretation could have been resulting from data collected in narrower spatial and/or temporal ranges.

The reason for such a weak effect of ENSO events on pelagic fish trophic ecology is puzzling. In this system, euphausiidae are the main prey group for pelagic fishes (this study, Espinoza and Bertrand, 2008, 2014; Espinoza et al., 2009), and their occurrence and abundance seem highly resilient to El Niño events (Brinton, 1967; Arones et al., 2009; Ballón et al., 2011). Other pelagic components with a wide range of distribution may also be little affected

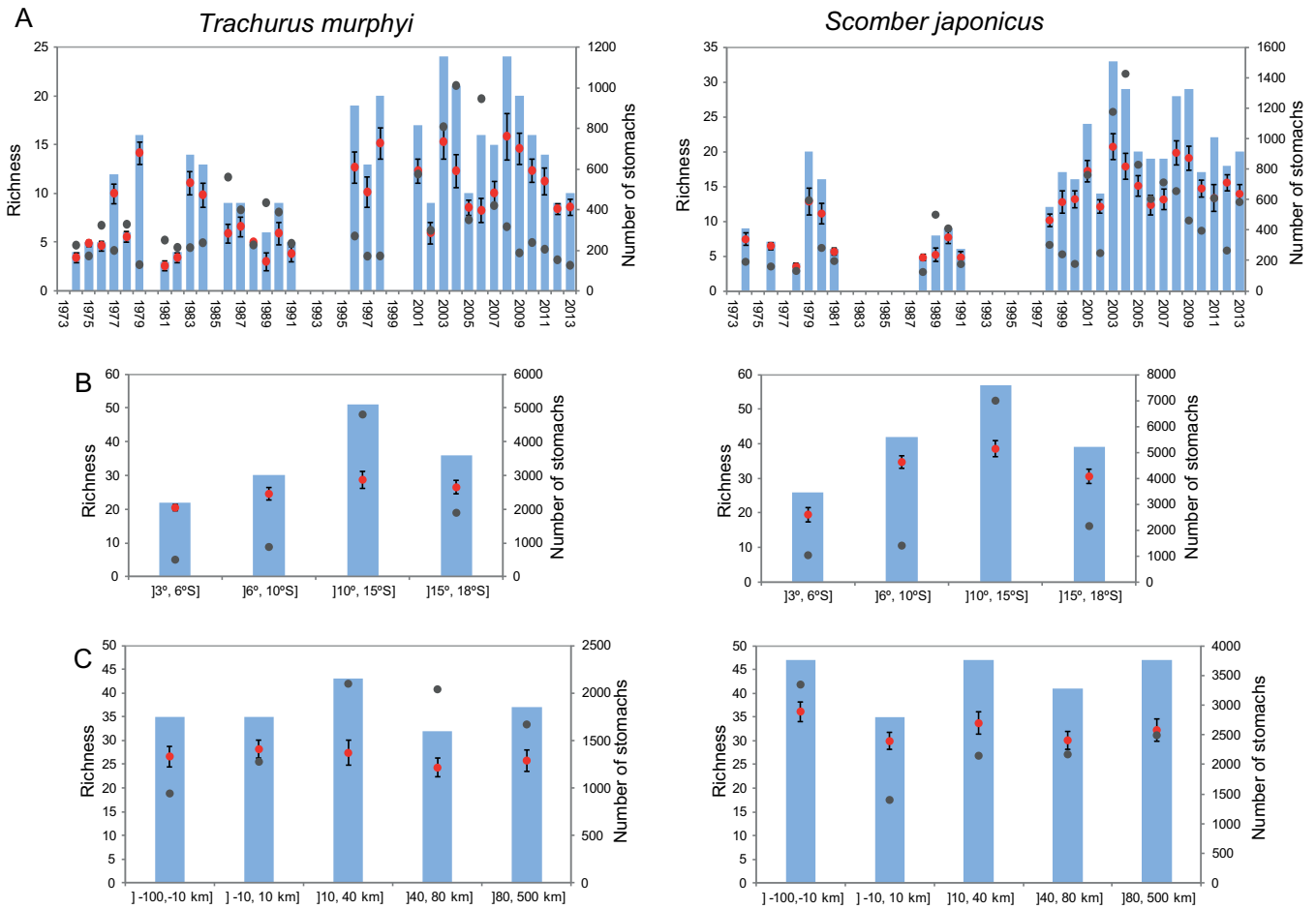


Fig. 12. Observed and estimated (see text) index of prey taxa richness for *Trachurus murphyi* (left panels) and *Scomber japonicus* (right panels) computed according to (A) the year; (B) the latitudinal zone; and (C) the distance to shelf break (in km, negative inshore and positive offshore). The number of observed stomachs (grey circles) is indicated on the right axis. The estimated index is given for 100 stomachs for years and for 500 stomachs for latitudinal zones and categories of distance to the shelf break.

by El Niño events, in particular when local efficient upwelling occurs as during El Niño 1997–98 (Bertrand et al., 2004b). However additional information is required to disentangle the different mechanisms and understand this paradoxical result.

4.5. When prey diversity decreases with temperature

Although the reasons are still debated (Clarke and Gaston, 2006) temperature and species richness are strongly correlated (e.g. Frank et al., 2007). This pattern leads to a global negative association between taxonomic richness and latitude (e.g. Willig et al., 2003). Interestingly our results challenge such paradigm. Indeed, prey diversity was significantly lower in northern Peru, where the warm tropical and equatorial waters matter (Swartzman et al., 2008), than further south where colder upwelling waters dominate. In addition our findings clearly evidenced such a counterintuitive pattern at a decadal time scale over a large latitudinal range (15°). The system was characterised by warmer conditions between the early 1970s to the mid-1990s than then after. On the basis of the temperature-diversity relationship we would expect more diversity, with an increase of tropical species, before than after the mid-1990 but the opposite was observed with a two-fold increase in diversity during the cooler period. The increase was mainly due to ‘cold species’. Factors other than temperature were thus the dominant drivers of diversity. It is thus important to point out that the period ranging between the early 1970s to the mid 1990s was warmer but also less productive and more oxygenated

compared with the period from the mid 1990s (Chavez et al., 2003; Bertrand et al., 2011; Gutiérrez et al., 2011). In the same sense prey diversity was lower during the ‘warm’ El Niño periods than during neutral or La Niña periods. These spatiotemporal patterns seem to indicate that diversity in the NHCS is probably more driven by productivity than temperature. Interestingly, the latitudinal variability of temperature is peculiar in eastern boundary upwelling systems, since most of it results from combined effects of solar seasonal heating and latitudinal variations in upwelling-favourable wind intensity (Fréon et al., 2009) so to chemical energy. However, oxygen may also play a role. Actually even if some species, such as sardine, are ‘expulsed’ from the system in cold-productive-low oxygen periods (Bertrand et al., 2011), other species associated to cooler conditions, such as the squat lobster, dramatically increase in biomass (Gutiérrez et al., 2008). Furthermore, under conditions of low oxygen and high production (such as in the late 2000s), the epipelagic community is concentrated within a thin surface layer (Bertrand et al., 2011) where ephemeral fine scale oases boost up trophic interactions and thus energetic transfer (Bertrand et al., 2014).

5. Conclusion

In summary, from this long term study of stomach content data, we provided a comprehensive description of the trophic ecology of two important pelagic fish, the jack and chub mackerels according to spatiotemporal patterns. Further, the vast amount of data used

in this study allowed addressing questions beyond classic diet description. Indeed we demonstrated that fish diet composition reveal ecosystem changes but is not always a good indicator of changes in prey biomass since prey accessibility and energy content do matter. In addition we revisited the impact of El Niño events on fish diet and showed that these events have weak but unexpected effects. Finally, our results challenged the paradigm of positive correlation between diversity and temperature in the Humboldt Current system; energy content of forage species and the intensity of the oxygen minimum zone most likely play an important role.

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