



Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system

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ABSTRACT

The Peruvian anchovy or anchoveta (*Engraulis ringens*) forages on plankton and is a main prey for marine mammals, seabirds, fish, and fishers, and is therefore a key element of the food web in the Humboldt Current system (HCS). Here, we present results from the analysis of 21,203 anchoveta stomach contents sampled during 23 acoustic surveys over the period 1996–2003. Prey items were identified to the genus level, and the relative dietary importance of different prey was assessed by determination of their carbon content. Variability in stomach fullness was examined relative to the diel cycle, the distance from the coast, sea surface temperature, and latitude, using generalized additive models (GAMs). Whereas phytoplankton largely dominated anchoveta diets in terms of numerical abundance and comprised >99% of ingested prey items, the carbon content of prey items indicated that zooplankton was by far the most important dietary component, with euphausiids contributing 67.5% of dietary carbon followed by copepods (26.3%). Stomach fullness data showed that anchoveta feed mainly during daytime between 07h00 and 18h00, although night-time feeding also made a substantial contribution to total food consumption. Stomach fullness also varied with latitude, distance from the coast, and temperature, but with substantial variability indicating a high degree of plasticity in anchoveta feeding behaviour. The results suggest an ecological role for anchoveta that challenges current understanding of its position in the foodweb, the functioning of the HCS, and trophic models of the HCS.

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1. Introduction

The Peruvian anchovy or anchoveta *Engraulis ringens*, is ecologically and economically the most important pelagic fish species in the Humboldt Current system (HCS). Anchoveta is the major prey of the principal top predators including marine mammals, seabirds, fish and fishers, and more than 250 million tons of anchoveta have been harvested by the purse seine fishery since the 1950s. Anchoveta forage on plankton and is a key element of the marine food web in the HCS and have been the subject of many studies (e.g. the books edited by Pauly and Tsukayama, 1987; Pauly et al., 1989a).

The first trophodynamic studies on anchoveta in Peru concluded that anchoveta subsisted mainly on phytoplankton (Rojas, 1953; Rojas de Mendiola, 1969), and the ability of clupeoids like anchoveta to feed at low trophic levels (directly on primary producers) was suggested as the reason such large populations, biomasses and fisheries could be sustained in upwelling systems (Ryther, 1969). Later studies suggested that in addition to filter-feeding on phytoplankton, anchoveta could also particulate feed

on zooplankton (Rojas de Mendiola, 1989; Alamo, 1989), and zooplankton was sometimes considered equally important as phytoplankton in anchoveta diets (Alamo, 1989; Pauly et al., 1989b; Jahncke et al., 2004). With the exception of Konchina (1991), who suggested that anchoveta preferentially consume zooplankton, all other recent work in the HCS has concluded that anchoveta depends mainly on phytoplankton (Alamo et al., 1996a,b, 1997a,b; Alamo and Espinoza, 1998; Espinoza et al., 1998a,b, 1999, 2000). However, these studies were based on counts of anchoveta prey, a method considered to be inadequate for estimating dietary importance (James, 1987; Konchina and Pavlov, 1995). In contrast, methods based on prey weight (e.g. gravimetric) or on nutritional value (e.g. carbon content, caloric or energetic value) may be more ecologically relevant (Hyslop, 1980; Koslow, 1981; James, 1987; Konchina and Pavlov, 1995; van der Lingen et al. 2006, in press). In other upwelling systems, these latter methods indicate that zooplankton, rather than phytoplankton, support clupeoid populations (e.g. Koslow, 1981; James, 1987; James and Chiappa-Carrara, 1990; Chiappa-Carrara and Gallardo-Cabello, 1993; van der Lingen et al., 2006).

Konchina (1991) results highlighting the significance of zooplankton in the diet of anchoveta were based on gravimetric analysis of prey importance, but his study was based on a very small sample size ($n = 65$ fish). Here we revisit Peruvian anchoveta diet

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and feeding behaviour in Peru using a database which contains information on the stomach contents of 21,203 anchoveta sampled along the Peruvian coast (1996–2003). In particular we assess the relative importance of different prey types to anchoveta using a method which estimates the carbon content of prey items. We also describe variations in anchoveta stomach fullness in relation to the diel cycle, latitude, distance to the coast, and sea surface temperature, using generalized additive models. Our results confirm *Konchima* (1991) finding that Peruvian anchoveta subsist primarily on zooplankton, and suggest an ecological role for anchoveta that challenges current understanding of the functioning of the HCS.

2. Materials and methods

2.1. Sampling

Data were collected during 23 IMARPE (Instituto del Mar del Perú) acoustic surveys between 1996 and 2003 with the aim of estimating pelagic fish abundance in the Peruvian EEZ (Table 1). Fish were collected by pelagic trawling conducted throughout the survey area (Fig. 1), and a sub-sample of 10–50 anchoveta was randomly collected from each trawl. At sea, individual anchoveta were measured (total length) to the nearest 0.5 cm and weighed to the nearest 0.1 g, and the cardiac and pyloric sections of their stomachs were extracted fixed in 5% formalin. In the laboratory, stomach contents were extracted and weighed (wet weight, WW) to the nearest 0.01 g for samples collected between 1996 and the summer of 2001, and to the nearest 0.001 g thereafter. Stomach fullness was calculated by dividing individual stomach content weight by fish wet weight and was expressed as a percentage of fish wet weight (Hureau, 1970). The stomach contents of individual fish were then pooled into 2 cm size classes for each sub-sample, and pooled stomach contents were filtered through a 125 µm mesh. The filtered material was diluted to 100 mL using filtered seawater and a 0.1 mL sub-sample was examined under the compound microscope to identify and count phytoplankton prey. The material that remained on the mesh was diluted to 100 mL using filtered seawater and a 10 mL sub-sample was examined using a stereoscopic microscope to identify (to genus) and count zooplankton prey. All prey counts were then standardized to number per 100 mL, except for anchoveta eggs, for which the whole sample was examined.

2.2. Estimation of prey volume, dry weight and carbon content

Different procedures were followed to estimate the carbon content of phytoplankton and zooplankton and hence determine their relative dietary importance. We did not measure the size of any prey items but instead used information from the literature to estimate prey size; the lack of available references on size and volume for planktonic organisms off Peru led us to use a wide range of references published for other ecosystems. Phytoplankton size was converted to phytoplankton cell volume using references describing the organism's geometric shape and providing equations relating shape to volume, with the coefficients for each equation being obtained from the literature or from estimations made by IMARPE (Table 2). To transform volume into carbon content we used equations given in Menden-Deuer and Lessard (2000) and Verity and Langdon (1984) (Table 4). For zooplankton, prosome or total organism length was estimated from the literature or from some direct measurements made by IMARPE on zooplankton from stomach content samples (Table 3). Zooplankton dry weight and carbon content were calculated using equations given by Alexandrov (2001), Deibel (1986), James (1987), van der Lingen (2002), Parsons et al. (1984) and Sameoto (1971) (Table 4). All prey carbon content values were standardized to µg C, and were expressed as a percentage of all fish examined in each cruise.

2.3. Data analysis

For each survey from which anchoveta were collected for trophodynamic analysis we sought potential relationships between stomach fullness and the diel cycle, latitude, distance to the coast, and sea surface temperature. As the relationships are likely to be nonlinear and multivariate, a generalized additive modelling (GAM) approach was used (Hastie and Tibshirani, 1990) using S-Plus software (Insightful Corporation, Seattle, WA, USA). Cubic spline smoothers were used to estimate these nonparametric functions, and separate GAM models were performed for each survey, and also for all the surveys combined.

3. Results

A total of 21,203 anchoveta (*E. ringens*) ranging from 3 to 18 cm total length were analysed (Table 1). In total, 132 prey taxa were

Table 1
Survey code, start and end date, the number of trawls, and the number, length range (in cm) of anchoveta collected for stomach content analysis during this study.

Survey code	Start date	End date	No. of trawls	No. of stomach	Anchoveta length range (Min–Max)
960204	10 February 1996	01 April 1996	49	633	9–19
960809	11 August 1996	27 September 1996	70	1021	5.5–19.5
961112	16 November 1996	19 December 1996	39	639	9.5–19
970204	13 Feb 1997	23 April 1997	45	739	8–19.5
970910	04 September 1997	05 October 1997	51	1259	6.5–19
980305	27 March 1998	01 May 1998	35	687	9.5–18
980809	23 August 1998	17 September 1998	36	624	4–16
981112	30 November 1998	21 December 1998	36	798	4–16.5
990203	14 February 1999	28 March 1999	75	1266	10–17
990809	28 August 1999	17 September 1999	19	336	10–18
991112	12 November 1999	14 December 1999	70	1412	8–18
000102	20 January 2000	26 February 2000	124	2277	6.5–18.5
000607	10 June 2000	06 July 2000	50	928	7.5–18.5
000809	28 August 2000	23 September 2000	38	574	7–18.5
001011	11 October 2000	13 November 2000	45	846	6.5–18
010204	03 March 2001	10 April 2001	78	1630	8.5–18.5
010708	05 July 2001	06 August 2001	83	1596	6.5–19
020203	21 February 2002	18 March 2002	83	1650	7–18
0208	10 August 2002	31 August 2002	30	281	9.5–17
021011	01 October 2002	13 November 2002	36	416	10–17
030203	26 February 2003	31 March 2003	45	524	6.5–17.5
030809	16 August 2003	15 September 2003	26	243	7.5–17.5
031012	24 October 2003	10 December 2003	36	824	4.5–17.5

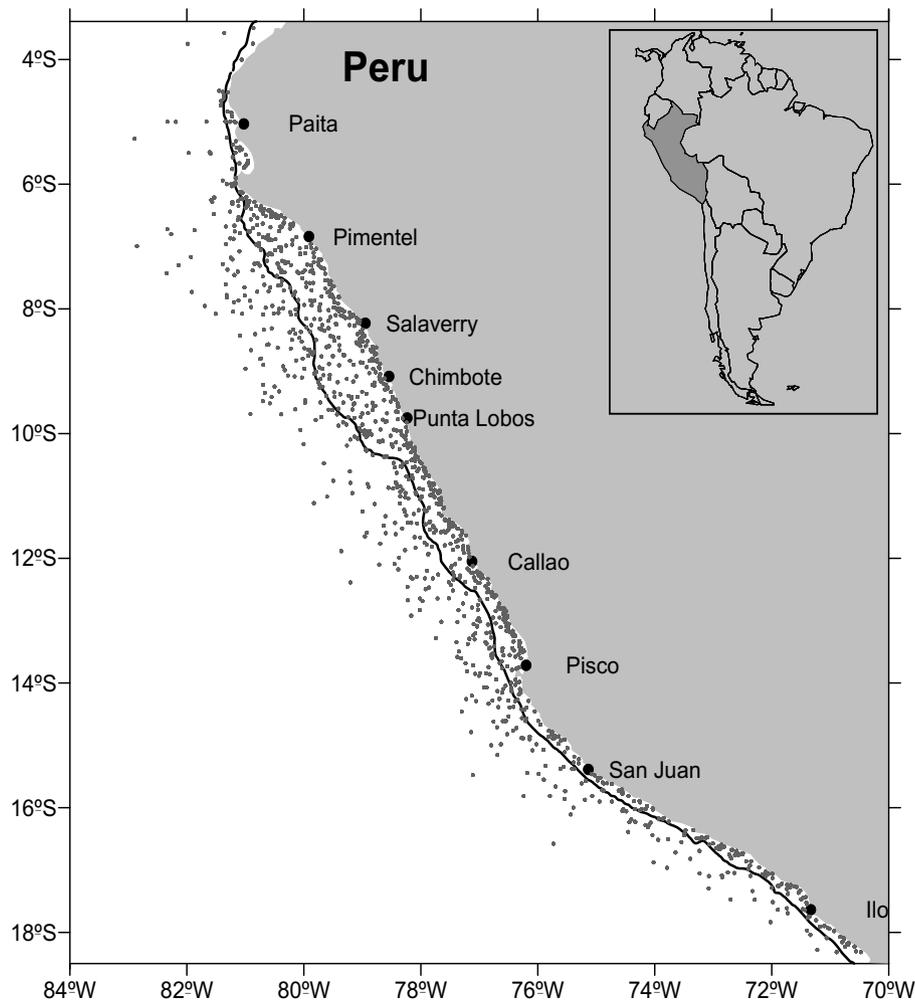


Fig. 1. The locations of trawls (grey dots) from which anchovetas were collected for trophodynamic analysis. The black solid line indicates the 200 m isobaths.

identified: 38 diatoms, 16 dinoflagellates, 2 silicoflagellates, 1 phytoflagellate, 4 microflagellates, 9 tintinnids, 34 copepods, and 28 other items (Tables 2 and 3). Mean stomach fullness was 0.68% of fish WW, and varied between 0.29% WW in February–March 1999 and 1.23% WW in August–September 1998 (Fig. 2).

3.1. Dietary composition

Numerically, phytoplankton dominated anchoveta diet and comprised 99.52% of all ingested prey; copepods represented only 0.07%, euphausiids 0.003%, and other prey items accounted for only 0.40% of the total number of prey (Fig. 2). This view of anchoveta diet changes dramatically when prey carbon content is considered (Fig. 2); zooplankton was by far the most important component and contributed 98.0% of dietary carbon, whilst phytoplankton contributed only 2.0%. Among zooplankters, euphausiids dominated (contributing 67.5% of dietary carbon), followed by copepods (26.3%), and other zooplankton (4.2%). Other groups were much less important in terms of their carbon contribution, including Gastropoda (0.76%), Polychaeta (0.75%), lantern fish (*Vinciguerria luce-tia* and myctophids) (0.45%), anchoveta eggs (0.40%), Amphipoda (0.40%), Bivalvia (0.31%), zoea (0.29%), megalopa (0.29%), and the red shrimp *Pleuroncodes monodon* (0.01%), but their presence illustrates the omnivorous feeding behaviour of anchoveta.

The phytoplankton carbon fraction (2%) was dominated by the diatoms *Coscinodiscus* (54.0%), *Thalassiosira* (14.6%), *Ditylum*

(8.1%), and by the dinoflagellate *Proto-peridinium* (6.7%). The copepod carbon fraction was dominated by the genera *Eucalanus* (69.9%), *Calanus* (12.8%) and *Centropages* (6.6%), whilst *Corycaeus* (1.3%), *Candacia* (1.2%), *Paracalanus* (1.0%) and *Scolecithrix* (1.0%) were of lesser importance.

Our results vary depending on the parameters and relationships used to estimate prey carbon content (Tables 2–4). To test the robustness of our results we re-calculated dietary carbon after increasing twofold the relative volume (and thus carbon content) of phytoplankton items and decreasing the relative size of main zooplankton items by a third. Despite these changes our results were similar to those described above; even in the most ‘extreme’ case where phytoplankton was increased and zooplankton decreased by the maximum amounts the contribution by phytoplankton to anchoveta dietary carbon only reached 6% of the total, which appears to confirm the robustness of our results.

Whereas the relative contribution to anchoveta dietary carbon made by different prey types varied between surveys, no seasonal trend could be identified (Fig. 2). Phytoplankton reached maximum levels (40.7% of total carbon content) in anchoveta diet in August–September 1996, and minimum levels (0.07%) in June–July 2000. The contribution of euphausiids was high ($\geq 80\%$ of total carbon content) during November–December 1996, February–April and September–October 1997, August–September 1999, January–February and August–September 2000, and July–August 2001,

Table 2
Shape, size and volume of phytoplankton cells recorded from anchoveta stomach contents; cell volume was extracted from the literature (see references) or calculated from published geometric shapes and published or estimated cell sizes.

Genus	Geometric shape	Diameter (μm)	Length (μm)	Height (μm)	m^a (μm)	Volume formula ^b	Volume values (μm^3)
Diatoms							
<i>Actinocyclus</i>	Cylinder ^b					$(\pi/4) \cdot d^2 \cdot h$	16,828 ^c
<i>Amphiprora</i>	Elliptic prism ^b	10	35	10		$(\pi/4) \cdot d \cdot l \cdot h$	2749
<i>Amphora</i>	Cymbelloid ^b					$(1/6) \cdot \pi \cdot (2b)^2 \cdot a \cdot (\beta/360)^d$	6187 ^c
<i>Asterionellopsis</i>	Prism on triangle ^b		30	10 ^e	10	$(1/2) \cdot l \cdot m \cdot h$	1500
<i>Asteromphalus</i>	Cylinder ^b	30		5		$(\pi/4) \cdot d^2 \cdot h$	3534
<i>Bacteriatrum</i>	Cylinder ^b	40		80		$(\pi/4) \cdot d^2 \cdot h$	100,531
<i>Cerataulina</i>	Cylinder ^b					$(\pi/4) \cdot d^2 \cdot h$	30,015 ^c
<i>Chaetoceros</i>	Elliptic prism ^b					$(\pi/4) \cdot d \cdot l \cdot h$	3937 ^c
<i>Cocconeis</i>	Elliptic prism ^b					$(\pi/4) \cdot d \cdot l \cdot h$	780 ^c
<i>Corethron</i>	Cylinder + 2 half spheres ^b	20		100		$\pi \cdot r^2 \cdot l + (4/3) \cdot \pi \cdot r^{3f}$	35,605
<i>Coscinodiscus</i>	Cylinder ^b					$(\pi/4) \cdot d^2 \cdot h$	994,625 ^c
<i>Cylindrotheca</i>	Prolate spheroid + 2 cylinders ^b					$(\pi/6) \cdot d^2 \cdot h + 2(\pi/4) \cdot d^2 \cdot h$	158 ^c
<i>Detonula</i>	Cylinder ^b	40		40		$(\pi/4) \cdot d^2 \cdot h$	50,265
<i>Ditylum</i>	Prism on triangle ^b					$(1/2) \cdot l \cdot m \cdot h$	60,495 ^c
<i>Eucampia</i>	Elliptic prism ^b	24	52	30		$(\pi/4) \cdot d \cdot l \cdot h$	9802
<i>Fragilariopsis</i>	Elliptic prism ^b					$(\pi/4) \cdot d \cdot l \cdot h$	190 ^c
<i>Grammatophora</i>	Elliptic prism ^b					$(\pi/4) \cdot d \cdot l \cdot h$	9772 ^c
<i>Guinardia</i>	Cylinder ^b					$(\pi/4) \cdot d^2 \cdot h$	144,013 ^c
<i>Gyrosigma</i>	Prism on parallelogram ^b					$(1/2) \cdot l \cdot b \cdot h^g$	63,513 ^c
<i>Hemiaulus</i>	Elliptic prism ^b	30	90	10		$(\pi/4) \cdot d \cdot l \cdot h$	21,205,75
<i>Lauderia</i>	Cylinder ^b	50		90		$(\pi/4) \cdot d^2 \cdot h$	176,715
<i>Leptocylindrus</i>	Cylinder ^b					$(\pi/4) \cdot d^2 \cdot h$	1608 ^c
<i>Licmophora</i>	Gomphonemoid ^b					^b	11,870 ^c
<i>Lioloma</i>	Box ^b	25	50	25		$l \cdot l' \cdot h^h$	31,250
<i>Lithodesmium</i>	Prism on triangle ^b		34	20 ^e	20	$(1/2) \cdot l \cdot m \cdot h$	6800
<i>Navicula</i>	Elliptic prism ^b					$(\pi/4) \cdot d \cdot l \cdot h$	3013 ^c
<i>Odontella</i>	Elliptic prism ^b					$(\pi/4) \cdot d \cdot l \cdot h$	13,081
<i>Planktoniella</i>	Cylinder ^b	80		15		$(\pi/4) \cdot d^2 \cdot h$	75,398
<i>Pleurosigma</i>	Prism on parallelogram ^b					$(1/2) \cdot l \cdot b \cdot h^g$	36,882
<i>Proboscia</i>	Cylinder ^b					$(\pi/4) \cdot d^2 \cdot h$	13,641
<i>Pseudonitzschia</i>	Prism on parallelogram ^b					$(1/2) \cdot l \cdot b \cdot h^g$	646
<i>Pseudosolenia</i>	Cylinder ^b	50		300		$(\pi/4) \cdot d^2 \cdot h$	589,049
<i>Rhizosolenia</i>	Cylinder ^b					$(\pi/4) \cdot d^2 \cdot h$	108,532
<i>Skeletonema</i>	Cylinder + 2 half spheres ^b					$(\pi) \cdot r^2 \cdot l + (4/3) \cdot \pi \cdot r^{3f}$	459
<i>Stephanopyxis</i>	Cylinder + 2 half spheres ^b	40		60		$(\pi) \cdot r^2 \cdot l + (4/3) \cdot \pi \cdot r^{3f}$	108,909
<i>Thalassionema</i>	Box ^b					$l \cdot l' \cdot h^h$	1252
<i>Thalassiosira</i>	Cylinder ^b					$(\pi/4) \cdot d^2 \cdot h$	14,390
<i>Tropidoneis</i>	Prism on triangle ^b		75	18 ^e	18	$(1/2) \cdot l \cdot m \cdot h$	12,150
Dinoflagellates							
<i>Ceratium</i>	Ellipsoid + 2 cones + cylinder ^b					$(\pi/6) \cdot a \cdot b \cdot l + 2 \cdot (1/3) \cdot \pi \cdot r^2 \cdot z + (\pi/4) \cdot d^2 \cdot h^{jk}$	47,435 ⁱ
<i>Dinophysis</i>	Ellipsoid ^b					$(\pi/6) \cdot a \cdot b \cdot l^i$	50,000 (assumed)
<i>Diplopelta</i>	Ellipsoid ^b					$(\pi/6) \cdot a \cdot b \cdot l^i$	50,000 (assumed)
<i>Diplopsalis</i>	Cone + half sphere ^b					$(1/3) \cdot \pi \cdot r^2 \cdot z + (1/2) \cdot (4/3) \cdot \pi \cdot r^{3fk}$	50,000 (assumed)
<i>Dissodinium</i>							50,000 (assumed)
<i>Goniodoma</i>	Sphere ^b					$(4/3) \cdot \pi \cdot r^{3f}$	50,000 (assumed)
<i>Gonyaulax</i>	2 cones ^b					$2 \cdot (1/3) \cdot \pi \cdot r^2 \cdot z^k$	50,000 (assumed)
<i>Gymnodinium</i>	Ellipsoid ^b					$(\pi/6) \cdot a \cdot b \cdot l^i$	88,099 ^j
<i>Oxophysis</i>	2 cones ^b					$2 \cdot (1/3) \cdot \pi \cdot r^2 \cdot z^j$	50,000 (assumed)
<i>Podolampas</i>	Cone ^b					$(1/3) \cdot \pi \cdot r^2 \cdot z^k$	50,000 (assumed)
<i>Pronoctiluca</i>	Cone + half sphere ^b					$(1/3) \cdot \pi \cdot r^2 \cdot z + (1/2) \cdot (4/3) \cdot \pi \cdot r^{3fk}$	50,000 (assumed)
<i>Proocentrum</i>	Ellipsoid ^b					$(\pi/6) \cdot a \cdot b \cdot l^i$	16,303 ^j
<i>Protoperdinium</i>	2 cones ^b					$2 \cdot (1/3) \cdot \pi \cdot r^2 \cdot z^k$	133,298 ⁱ
<i>Pyrocystis</i>	Ellipsoid ^b					$(\pi/6) \cdot a \cdot b \cdot l^i$	50,000 (assumed)
<i>Pyrophacus</i>	Ellipsoid ^b					$(\pi/6) \cdot a \cdot b \cdot l^i$	50,000 (assumed)
<i>Scrippsiella</i>	Ellipsoid ^b					$(\pi/6) \cdot a \cdot b \cdot l^i$	50,000 (assumed)
Silicoflagellates							
<i>Dictyocha</i>							30,000 (assumed)
<i>Octactis</i>							30,000 (assumed)
Phytoflagellates							
<i>Tetraselmis</i>	Elliptic prism ^b	10	25	5		$(\pi/4) \cdot d \cdot l \cdot h$	1964
Microflagellates							
<i>Olisthodiscus luteus</i>	Prolate spheroid	50	110			$(\pi/6) \cdot d^2 \cdot l$	143,990
Tintinnids							
<i>Amphorellopsis</i>	Cylinder ^l	30		200		$(\pi/4) \cdot d^2 \cdot h$	98,175
<i>Codonella</i>	Cylinder ^l	30		200		$(\pi/4) \cdot d^2 \cdot h$	98,175
<i>Codonellopsis</i>	Cylinder ^l	30		200		$(\pi/4) \cdot d^2 \cdot h$	98,175
<i>Dictyocysta</i>	Cylinder ^l	30		200		$(\pi/4) \cdot d^2 \cdot h$	98,175
<i>Eutintinnus</i>	Cylinder ^l	30		200		$(\pi/4) \cdot d^2 \cdot h$	98,175
<i>Favella</i>	Cylinder ^l	30		200		$(\pi/4) \cdot d^2 \cdot h$	98,175

(continued on next page)

Table 2 (continued)

Genus	Geometric shape	Diameter (μm)	Length (μm)	Height (μm)	m^a (μm)	Volume formula ^b	Volume values (μm ³)
<i>Helicostomella</i>	Cylinder ^d	30		200		$(\pi/4) \cdot d^2 \cdot h$	98,175
<i>Tintinnopsis</i>	Cylinder ^d	30		200		$(\pi/4) \cdot d^2 \cdot h$	98,175
<i>Xystonella</i>	Cylinder ^d	30		200		$(\pi/4) \cdot d^2 \cdot h$	98,175
Foraminiferida	Ellipsoid ^b		200			$(\pi/6) \cdot a \cdot b \cdot \bar{h}$	523,599
Radiolaria	Ellipsoid ^b		110			$(\pi/6) \cdot a \cdot b \cdot \bar{h}$	88,698
<i>Acanthaires</i>	Prolate spheroid ^b	50	75			$(\pi/6) \cdot d^2 \cdot \bar{h}$	98,175

^a m : height of even-sided triangle of the transapical section.

^b Hillebrand et al. (1999).

^c Snoeijs et al. (2002).

^d a : length; b : height.

^e h : base of even-sided triangle of the transapical section.

^f r : radius.

^g b : minor axis; l : major axis, similar to length.

^h l' : minor base of rectangle, similar to diameter (d).

ⁱ Menden-Deuer and Lessard (2000).

^j a : main axis; b : minor axis of cross section (in Foraminiferida: $a = 100$, $b = 50$; Radiolaria: $a = 55$, $b = 28$).

^k z : height of the cone.

^l Chiappa-Carrara and Gallardo-Cabello (1993).

and the lowest value (5.8%) was recorded in November–December 1998. The maximum contribution to dietary carbon (86.7%) from copepods occurred during November–December 1998, at the end of the 1997–1998 El Niño event, and the lowest value (2.0%) was observed during November–December 1996.

3.2. Stomach fullness dynamics

GAM computed on the combined data from all surveys (Fig. 3) show that the main ingestion period for anchoveta occurred during daytime, between 07h00 and 18h00, local time, and this general pattern was observed during most of the surveys, although there were several exceptions (Fig. 3). For instance, during four surveys (990809, 000607, 010204, 0208) the feeding period began earlier at about 02h00 and terminated in the early afternoon, whereas during two other surveys (980305, 030809) feeding occurred mainly at night. In some instances (surveys 961112 and 970910) anchoveta showed a longer (>16 h) feeding period with no clear evacuation period.

In addition to showing a diel pattern, stomach fullness also varied with latitude (Fig. 3), with higher values encountered off both Northern (<6 °S) and Southern (>13 °S) Peru although some surveys presented very different patterns. Indeed the global trend does not seem robust and strong variability in the relationship between stomach fullness and latitude occurred during the time series; for example, high stomach fullness values were observed in the central part of Peru in 960204, 960809, 991112 and 000607 (Fig. 3).

Stomach fullness increased with distance from the coast and reached maximal values at distances >120 km (Fig. 3), but again this general trend obscures strong variability between surveys. When anchoveta were distributed close to the coast, high fullness levels could be observed close to shore, in particular during the 1997–1998 El Niño, but this was also seen in 1999, 2000 or 2001.

Anchoveta stomach fullness was related to temperature, with a minimum observed at 22 °C (Fig. 3). However, the range of temperatures varied strongly depending on the timing of a particular survey, suggesting that this general trend is also not robust. In fact, whereas the general trend was observed for 13 surveys it was not observed in six others (960204, 970910, 990809, 020203, 010204, 010708) during which fullness increased with temperature, in two surveys (980305, 0208) where dome-shaped relationships between SST and stomach fullness were observed, in two

other surveys (960809, 030203) where U-shaped patterns between SST and stomach fullness were observed, nor in one survey (980809) where a bimodal pattern was observed.

4. Discussion

4.1. Dietary composition

Our analysis of the stomach content composition of 21,203 anchoveta illustrates its omnivorous foraging character; this species feeds on both phytoplankton and zooplankton and has a large diversity of prey (132 taxa were identified at the genus level). As shown by Konchina (1991), the size range of anchoveta prey varies by several orders of magnitude, from tens of micrometers (microflagellates) to tens of millimetres (fish, e.g. *V. lucetia*).

When considering only prey numbers, anchoveta diet is dominated by phytoplankton which comprise 99.5% of all prey and the zooplankton fraction appears negligible (Fig. 2). However when the carbon content of prey items is considered, zooplankton becomes by far the most important component and contributes 98.0% of dietary carbon, with a strong dominance of euphausiids (67.5%) followed by copepods (26.3%). These results depend on the parameters and relationships used to estimate prey carbon content (Tables 2–4); the analysis seems robust but the exact proportion of specific taxa should be considered with caution.

The phytoplankton carbon fraction was dominated by the large solitary diatoms *Coscinodiscus* and *Ditylum*, and the chain forming *Thalassiosira*. Similar dominance has been reported for anchovy (*E. encrasicolus*; formerly *E. capensis*) in the Benguela Current system, where the most important phytoplanktonic items were the large solitary diatoms *Rhizosolenia*, *Pleurosigma* and *Coscinodiscus* (James, 1987). Previous studies performed off Peru and based on numerical or frequency of occurrence analysis also highlighted the importance of diatoms in anchoveta diet, in particular nine genera of the Coscinodiscineae: *Coscinodiscus*, *Melosyra*, *Cyclotella*, *Skeletonema*, *Thalassiosira*, *Stephanopyxis*, *Coscinoscira*, *Planktoniella*, and *Asterolampra* (Rojas de Mendiola, 1969, 1971, 1989; Alamo, 1989; Pauly et al., 1989b). Other taxa such as the diatoms *Chaetoceros* and *Asterionellopsis*, and the dinoflagellate *Protoperidinium*, were also considered important to anchoveta diet (Alamo et al., 1996a,b, 1997a,b; Alamo and Espinoza, 1998; Espinoza et al., 1998a,b, 1999, 2000).

Table 3

Type and size of zooplankton recorded from anchoveta stomach contents; length was estimated by IMARPE except where indicated.

Name	Type	Length (mm)
Acartia	Calanoida	0.9375 ^a
Aetideus	Calanoida	1.5
Calanus	Calanoida	2 ^b
Calocalanus	Calanoida	1 ^c
Candacia	Calanoida	1.1666 ^a
Centropages	Calanoida	1.5 ^a
Clausocalanus	Calanoida	0.65 ^b
Clytemnestra	Harpacticoida	0.66 ^b
Copilia	Poecilostomatoida	1.75 ^a
Corycaeus	Cyclopoida	1 ^a
Corycella	Poecilostomatoida	0.65
Euaetideus	Calanoida	0.9 ^b
Eucalanus	Calanoida	4
Euchaeta	Calanoida	1.08 ^b
Euchirella	Calanoida	2.5 ^b
Euterpina	Harpacticoida	0.5 ^c
Haloptilus	Calanoida	1.2 ^a
Lubbockia	Poecilostomatoida	0.8
Lucicutia	Calanoida	1.03 ^a
Macrosetella	Harpacticoida	0.7
Mecynocera	Calanoida	0.899 ^a
Microsetella	Harpacticoida	0.7 ^c
Nonocalanus	Calanoida	1.5
Oithona	Cyclopoida	0.5 ^a
Oncaea	Poecilostomatoida	0.667 ^a
Paracalanus	Calanoida	0.8 ^b
Phaena	Calanoida	0.8
Pleuromamma	Calanoida	1.2 ^b
Pontellina	Calanoida	1.5
Rhincalanus	Calanoida	4
Saphirina	Poecilostomatoida	2.3 ^b
Scolecithrix	Calanoida	1.7 ^b
Scolecithricella	Calanoida	1.8 ^b
Temora	Calanoida	1.2 ^b
Harpacticoida		0.6 ^c
Copepoditos		0.5 ^a
Restos de copépodos		0.25
Euphausiacea		12 ^b
Amphipoda		8 ^b
Ostracoda		0.7
Zoea		2
Megalop		3
Cirriped larvae		0.1
<i>Emerita</i> sp. Larvae		5
Decapod undetermined larvae		5
<i>Pagurus</i> sp.		5
Pleuoncodes monodon		7
Decapoda Reptantia n/i		3
Galatheididae		7
Bivalvia		1.25
Gastropoda		1.25
Anchoveta eggs		vol: 0.27 mm ^{3d}
Apendicularia		10
Echinoderm larvae		1
Chaetognata		8 ^b
Squid remains		10
Polychaeta		10
Anchoa sp. Eggs		vol: 0.27 mm ³
Engraulidae eggs		vol: 0.27 mm ³
Fish eggs		vol: 0.27 mm ³
Fish larvae		15
Fish undetermined		15
Engraulidae		15
Vinciguerria sp.		15
Myctophidae		15

^a <http://earth.leeds.ac.uk/cyclops/data/ncfs-zooplank.xls>.

^b Santander et al. (1981).

^c Tudela and Palomera (1997).

^d Llanos-Rivera and Castro (2004).

Zooplankton dietary carbon was dominated by euphausiids and copepods. The most important copepods were *Eucalanus*, *Calanus* and *Centropages*, in partial agreement with Rojas de Mendiola

(1971, 1989) and Pauly et al. (1989b) who reported that *Calanus*, *Centropages* and *Corycaeus* were frequently-observed in anchoveta stomach contents. During the 1997–1998 El Niño, various studies confirmed the numerical importance of copepods and euphausiids; whereas amphipods, anchoveta eggs, *Vinciguerria* sp., and Myctophidae were of minor importance (Blaskovic' et al., 1999; Espinoza et al., 1998a,b, 1999, 2000).

In spite of the zooplankton dominance in anchoveta diet described above, the contribution made by different prey items varied strongly during the study period (Fig. 2), illustrating the anchoveta's opportunistic feeding ability. For instance, the phytoplankton fraction was high (up to 40% of carbon content) in 1996, but thereafter was never higher than 5%, irrespective of the overall environmental condition (i.e. El Niño 1997–1998 or La Niña 1999). It is difficult to relate these changes in the proportion of dietary phytoplankton to specific conditions. The proportion of anchoveta dietary carbon derived from copepods increased from November–December 1996 (2.0%) to a maximum in November–December 1998 (86.7%) and February–March 1999 (77.1%), after the 1997–1998 El Niño; the copepod fraction also reached high levels (>40%) in June–July 2000, October–November 2000 and August 2002, making the extraction of any seasonal pattern difficult.

4.2. The anchoveta: a predator

Our results demonstrate that anchoveta is a predator foraging at a higher trophic level than has generally been recognised (e.g. by Pauly et al., 1989b; Rojas de Mendiola, 1989), with its main input of carbon coming from zooplankters such as euphausiids and large copepods. Our results differ from the conventional dogma on clupeoid feeding ecology in the HCS, in which diatoms are considered as the major food source. Such feeding low on the food chain has been invoked to explain how such large anchoveta populations can be supported in this system (Rojas de Mendiola 1971). These conclusions now appear incorrect as they are based on counts of very small (phytoplankton) prey who's caloric (carbon) contribution to anchoveta diet is often trivial (Cushing, 1978; Konchina, 1991). James (1987) demonstrated that assessing fish diet from the number of prey items is unsatisfactory due to the preponderance of minute food items and the great difference on size range between phytoplankton and zooplankton (10⁻³ mm for diatoms to 10 mm for zooplankton), which makes the use of carbon or calorie equivalents for assessing the importance of dietary components essential. The determination of prey carbon content helps in determining the true importance of a food type (James, 1988), and this method has been used to highlight the importance of zooplankton over phytoplankton for *E. mordax* off California (Koslow, 1981; Chiappa-Carrara and Gallardo-Cabello, 1993), *E. encrasicolus* and *Sardinops sagax* in the Benguela Current upwelling system (James, 1987; van der Lingen, 2002; van der Lingen et al., 2006), and *Sardina pilchardus* in the north-eastern Atlantic (Garrido et al., 2008); see van der Lingen et al. (2006, in press), for recent reviews of clupeoid trophic ecology. In the Peruvian case, Konchina (1991) was the only scientist to conclude that anchoveta preferentially consumes zooplankton, and that most anchoveta biomass is supported by copepods and euphausiids. Finally, in Central Chile, using isotope analysis, Hückstädt et al. (2007) estimated the trophic level of anchoveta to 3.63, which confirm the dominance of zooplankton in anchoveta diet.

Anchoveta is therefore a 'predator' who select the largest available prey from the phytoplankton and zooplankton communities (Tables 2, 3 and 5). This is shown for zooplankton with the selection of euphausiids and the large copepods *Eucalanus* and *Calanus*, and for phytoplankton with the selection of the large diatom *Coscinodiscus*. Similar selectivity was observed for other anchovy species (e.g. Koslow, 1981; James, 1987; van der Lingen et al., 2006).

Table 4

Relationships employed to calculate dry weight and carbon content of the different categories of phytoplankton and zooplankton. Carbon contents not in μg were transformed in μg for comparison; PL: prosome length (μm); TL: total length (mm); DW: dry weight (μg); WW: wet weight (μg).

Phytoplankton	Volume (μm^3) to Carbon (pg)	
Diatoms	$C = 0.288 \text{ Vol}^{0.811a}$	
Dinoflagellates and other phytop.	$C = 0.760 \text{ Vol}^{0.819a}$	
Tintinnids, Foraminifera, Radiolaria	$C = 445.5 + 0.053 \text{ Vol}^b$	
Zooplankton	Length to dry weight (μg) regression	
Calanoid copepods	$\text{Ln}(\text{DW}) = 2.74\text{Ln}(\text{PL}) - 16.41^c$	dry weight (μg) to carbon (μg)
Cyclopoid copepods	$\text{Ln}(\text{DW}) = 1.96\text{Ln}(\text{PL}) - 11.64^c$	$C = 0.424 \text{ DW}^c$
Harpacticoid copepods	$\text{Ln}(\text{DW}) = 1.96\text{Ln}(\text{PL}) - 11.64^c$	$C = 0.424 \text{ DW}^c$
Poecilostomatoid copepods	$\text{Ln}(\text{DW}) = 1.96\text{Ln}(\text{PL}) - 11.64^c$	$C = 0.424 \text{ DW}^c$
Euphausiacea	$\text{DW} = 0.0012 \text{ TL}^{3.16ci}$	$C = 0.424 \text{ DW}^{cj}$
Amphipoda, Echinoderm larvae	$\text{DW} = 0.005 \text{ TL}^{2.311di}$	$C = 0.370 \text{ DW}^{dj}$
Ostracods, zoea, megalops, crustacea larvae, hermit crab and Galatheidae	$\text{DW} = 3.946 \text{ TL}^{2.436c}$	$C = 0.424 \text{ DW}^c$
Bivalvia, Gasteropod	$\text{DW} = 47.386 \text{ TL}^{3.663d}$	$C = 0.424 \text{ DW}^c$
Fish eggs	$\text{DW} = 0.093 \text{ Vol} + 0.0012^{\text{ck}}$	$C = 0.457 \text{ DW}^c$
Apendicularia	$\text{DW} = 11.3\text{TL}^{1.77e}$	$C = 0.387 \text{ DW}^e$
Chaetognaths	$\text{DW} = 0.00097 \text{ TL}^{2.2365f}$	$C = 0.290 \text{ DW}^f$
Fish, squid and fish larvae	$\text{DW} = 0.0001 \text{ TL}^{3.582di}$	$C = 0.38 \text{ DW}^g$
Polychaeta	$\text{WW} = 0.01 \text{ TL}^{2.136h}$ $\text{DW} = 0.157 \text{ WW}^{hi}$	$C = 0.518 \text{ DW}^{hj}$

^a Menden-Deuer and Lessard (2000).

^b Verity and Langdon (1984).

^c van der Lingen (2002).

^d James (1987).

^e Deibel (1986).

^f Sameoto (1971).

^g Parsons et al. (1984).

^h Alexandrov (2001).

ⁱ DW in mg.

^j C in mg.

^k Volume = 0.27 mm^3 , from Llanos-Rivera and Castro (2004) as anchoveta eggs dominated fish egg fraction.

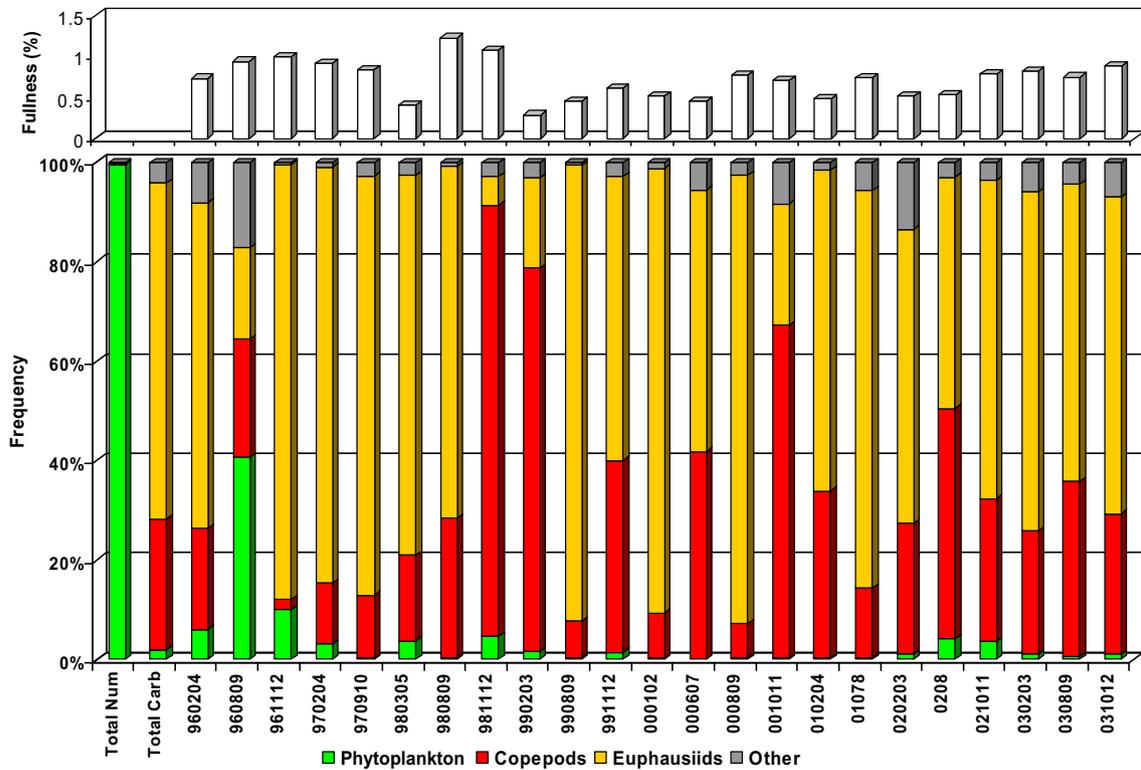


Fig. 2. Percentage contribution of phytoplankton (green), copepods (red), euphausiids (orange) and other zooplankters (grey) by number (total num) and to dietary carbon (total carb) for the total set of 21,203 anchoveta stomach contents. Also shown are the percentage contribution to dietary carbon by prey type for each of the 23 surveys from which anchoveta stomach contents were analyzed; surveys are identified along the x-axis, with the first two numbers corresponding to the year, the following two numbers the start month of the survey, and the last two numbers the end month of the survey.

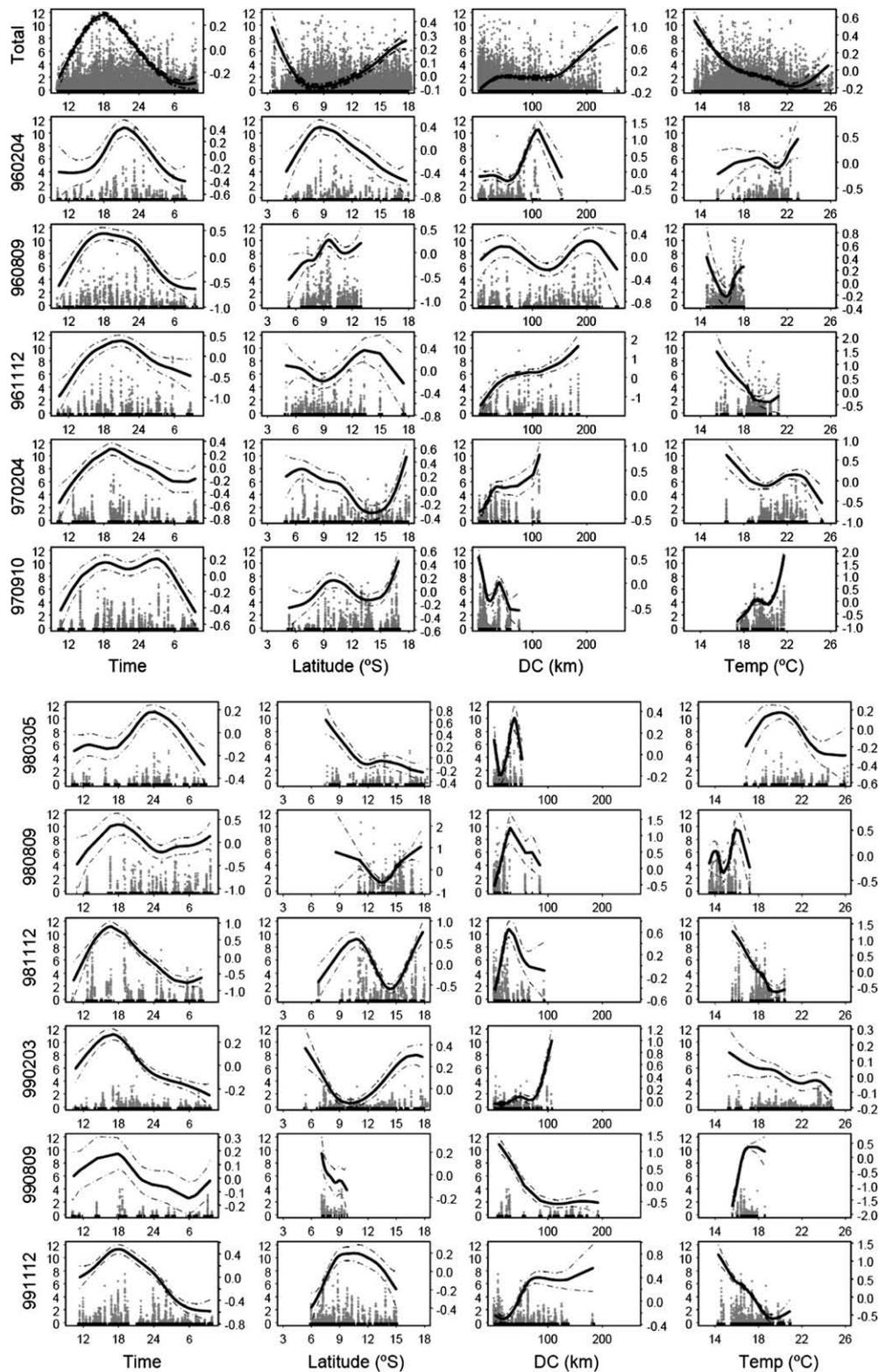


Fig. 3. Scatter plot (grey dots) and cubic spline smoother fits (black solid lines) of GAM models (the black dashed lines show the 95% confidence limits) based on anchoveta stomach fullness according to time of day, latitude, distance from the coast (DC) and sea surface temperature ($^{\circ}\text{C}$) for the complete set of 21,203 stomach contents (top panel) and for each of the 23 surveys from which stomach contents were analyzed (lower panels); surveys are identified along the y-axis, with the first two numbers corresponding to the year, the following two numbers the start month of the survey, and the last two numbers the end month of the survey. The left y-axis shows stomach fullness (% WW) and scaling along the right y-axis is relative and corresponds to the spline smoother that was fitted on the data such that a y-value of zero is the mean effect of the variables on the response.

4.3. Stomach fullness dynamics

As previously observed for *E. encrasicolus* (James, 1987), *E. ringens* displays an extremely high degree of opportunism in fulfilling

its dietary requirements and can shift between prey types according to their availability (Table 2). This flexible feeding behaviour was confirmed by the GAM models (Fig. 3) which illustrated the high variability between surveys when relating stomach fullness

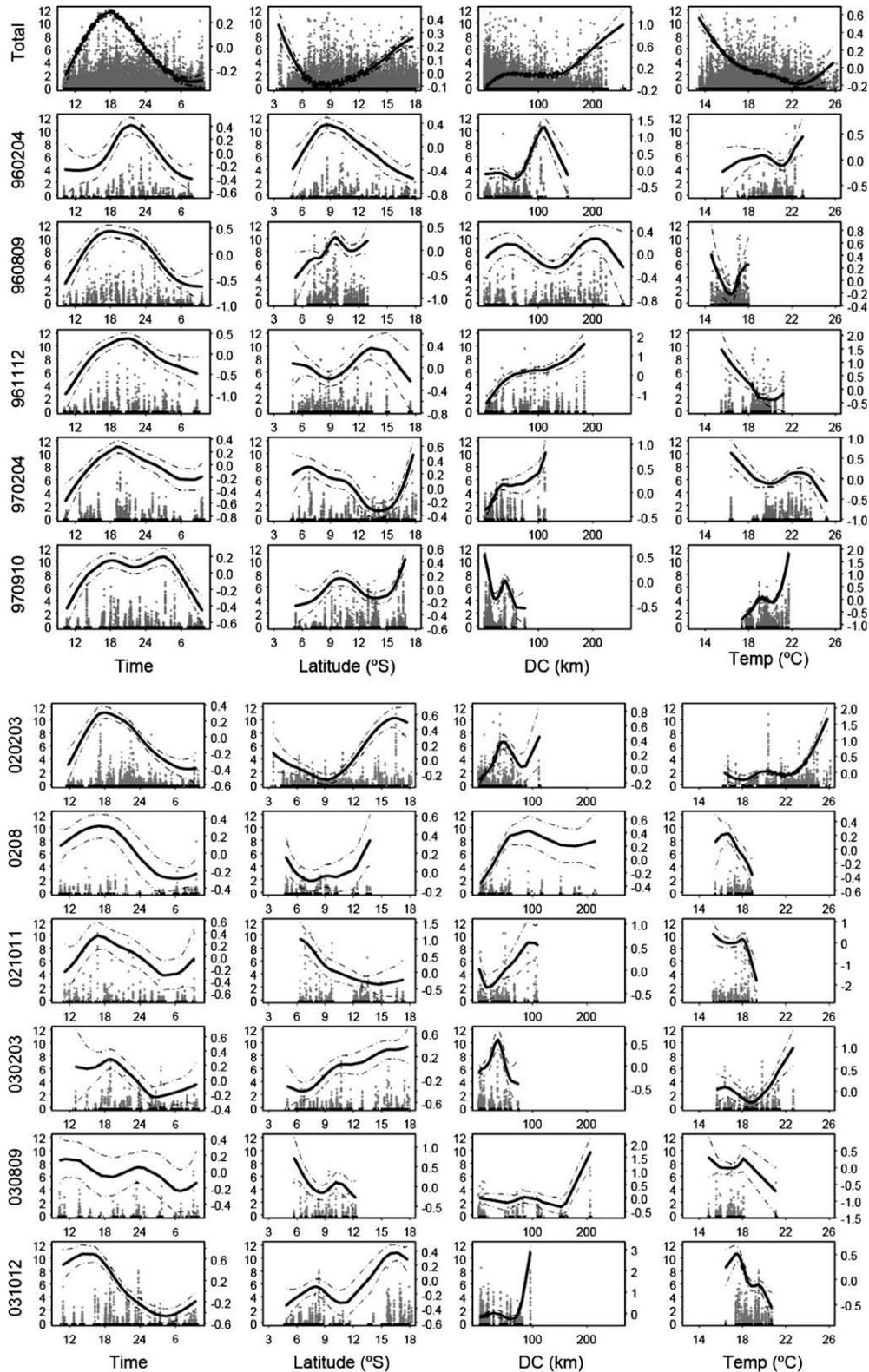


Fig. 3 (continued)

to time, latitude, distance to the coast, or SST. In the highly variable HCS anchoveta have had to evolve adaptive strategies in space and time (Bertrand et al., 2004a), including its spawning behaviour (e.g. Buitrón and Perea, 2000), its mode of spatial distribution (e.g. Bertrand et al., 2004b, 2008; Gutiérrez et al., 2007), or its feeding behaviour as illustrated by this study.

Such variability precludes the determination of robust patterns, and indeed results differ strongly between surveys and therefore from one dataset to another. Our study was based on more than 20,000 stomach content samples collected during an 8 year period which is, to our knowledge, the largest database on anchoveta diet, and the results we obtained from all surveys combined (Fig. 3) can

Table 5

Contribution by number and carbon content of anchoveta dietary items (data from all surveys combined).

Dietary items	Total number	Total carbon (µg)
Diatoms		
<i>Actinoptychus</i>	2,249,000	1733
<i>Amphiprora</i>	107,000	19
<i>Amphora</i>	186,000	64
<i>Asterionellopsis</i>	265,043,000	28,742
<i>Asteromphalus</i>	719,000	156
<i>Bacteriastrium</i>	791,000	2597
<i>Cerataulina</i>	26,000	32
<i>Chaetoceros</i>	206,866,000	49,060
<i>Cocconeis</i>	4000	0.26
<i>Corethron</i>	217,000	307
<i>Coscinodiscus</i>	60,994,000	1,284,639
<i>Cylindrotheca</i>	4000	0.07
<i>Detonula</i>	32,551,000	60,910
<i>Ditylum</i>	89,090,000	193,730
<i>Eucampia</i>	16,313,000	8107
<i>Fragilariopsis</i>	1,487,000	30
<i>Grammatophora</i>	3000	1
<i>Guinardia</i>	1,831,000	8045
<i>Gyrosigma</i>	10,822,000	24,481
<i>Hemiaulus</i>	15,000	14
<i>Lauderia</i>	7000	36
<i>Leptocylindrus</i>	2000	0.23
<i>Licmophora</i>	16,000	9
<i>Lioloma</i>	11,757,000	14,963
<i>Lithodesmium</i>	19,686,000	7273
<i>Navicula</i>	5,025,000	959
<i>Odontella</i>	1,513,000	950
<i>Planktoniella</i>	4,557,000	11,847
<i>Pleurosigma</i>	2,266,000	3299
<i>Proboscia</i>	9000	6
<i>Pseudonitzschia</i>	33,495,000	1834
<i>Pseudosolenia</i>	27,000	372
<i>Rhizosolenia</i>	4,494,000	15,699
<i>Skeletonema</i>	972,395,000	40,361
<i>Stephanopyxis</i>	572,000	2004
<i>Thalassionema</i>	39,032,000	3656
<i>Thalassiosira</i>	513,411,000	348,371
<i>Tropidoneis</i>	2000	1
Dinoflagellates		
<i>Ceratium</i>	8,046,000	42,746
<i>Dinophysis</i>	609,000	3399
<i>Diplopelta</i>	17,000	95
<i>Dipllopsalis</i>	22,000	123
<i>Dissodinium</i>	1,248,000	6966
<i>Goniodoma</i>	1,256,000	7011
<i>Gonyaulax</i>	44,000	246
<i>Gymnodinium</i>	2000	19
<i>Oxophysis</i>	53,000	296
<i>Podolampas</i>	6000	33
<i>Pronoctiluca</i>	1000	6
<i>Prorocentrum</i>	1,340,000	2611
<i>Protoperdinium</i>	11,461,000	160,651
<i>Pyrocystis</i>	704,000	3930
<i>Pyrophacus</i>	16,000	89
<i>Scrippsiella</i>	1,002,000	5593
Silicoflagellates		
<i>Dictyocha</i>	8,469,000	29,262
<i>Octactis</i>	566,000	1956
Phytoflagellates		
<i>Tetraselmis</i>	6000	2
Microflagellates		
<i>Olisthodiscus luteus</i>	1,214,000	9804
Tintinnids		
<i>Amphorellopsis</i>	10,000	79
<i>Codonella</i>	340,000	2699
<i>Codonellopsis</i>	83,000	659
<i>Dictyocysta</i>	337,000	2675
<i>Eutintinnus</i>	216,000	1714
<i>Favella</i>	97,000	770
<i>Helicostomella</i>	3,310,000	26,272
<i>Tintinnopsis</i>	732,000	5810
<i>Xystonella</i>	1,081,000	8580

Table 5 (continued)

Dietary items	Total number	Total carbon (µg)
Foraminiferida	1,040,000	29,323
Radiolaria	1,986,000	10,219
Acanthaires	12,000	68
Zooplankton		
Copepoda		
<i>Acartia</i>	40,020	176,227
<i>Aetideus</i>	16,080	256,667
<i>Calanus</i>	114,300	4,012,932
<i>Calocalanus</i>	2190	11,509
<i>Candacia</i>	47,120	377,775
<i>Centropages</i>	129,440	2,066,103
<i>Clausocalanus</i>	112,340	181,347
<i>Clytemnestra</i>	6810	8543
<i>Copilia</i>	200	1697
<i>Corycaeus</i>	144,420	409,077
<i>Corycella</i>	120	146
<i>Euaetideus</i>	2330	9174
<i>Eucalanus</i>	93,090	21,834,378
<i>Euchaeta</i>	34,450	223,544
<i>Euchirella</i>	280	18,118
<i>Euterpina</i>	19,930	14,510
<i>Haloptilus</i>	10	87
<i>Lubbockia</i>	4910	8981
<i>Lucicutia</i>	18,330	104,803
<i>Macrosetella</i>	10,550	14,853
<i>Mecynocera</i>	3230	12,679
<i>Microsetella</i>	37,960	53,444
<i>Nonocalanus</i>	360	5746
<i>Oithona</i>	126,830	92,338
<i>Oncaea</i>	173,890	222,492
<i>Paracalanus</i>	109,280	311,602
<i>Phaena</i>	8340	23,781
<i>Pleuromamma</i>	400	3464
<i>Pontellina</i>	40	638
<i>Rhincalanus</i>	1070	250,970
<i>Saphirina</i>	570	8261
<i>Scolecithrix</i>	13,390	301,165
<i>Scolecithricella</i>	740	19,466
<i>Temora</i>	3560	30,832
Harpacticoida	52,970	55,130
Copepodites	120,290	94,624
Restos de copépodos	285,570	33,625
Euphausiacea	61,319	80,233,346
Amphipoda	2103	475,392
Ostracoda	150	105
Zoea	38,682	350,220
Megalop	14,205	345,328
Cirriped larvae	7170	44
<i>Emerita</i> sp. Larvae	80	6750
Decapod undetermined larvae	1080	91,125
<i>Pagurus</i> sp.	1	84
<i>Pleuroncodes monodon</i>	48	9192
Decapoda Reptantia n/i	3062	74,438
Galatheididae	1	192
Bivalvia	8090	368,083
Gastropoda	19,910	905,876
Anchoveta eggs	39,611	476,270
Apendicularia	180	14,039
Echinoderm larvae	80	0.17
Chaetognata	2830	83,314
Squid remains	5	873
Polychaeta	7992	888,965
<i>Anchoa</i> sp. Eggs	248	2982
Engraulidae eggs	15	180
Fish eggs	1931	23,218
Fish larvae	361	223,898
Fish undetermined	41	25,429
Engraulidae	2	1240
<i>Vinciguerria</i> sp.	809	501,754
Myctophidae	51	31,631

therefore be considered as representative. However, except in the case of their diel feeding behaviour, we think that the mean signal in anchoveta stomach fullness is not a good representation of the

biological reality at any one moment. Instead, we consider that the most important point arising from our stomach fullness analysis does not reside in the mean patterns but in the variability from one survey to the other (Fig. 3). This variability is another illustration of anchoveta plasticity.

The general trend of diel temporal variation in stomach fullness was the most consistent, and the main feeding period as determined using GAMs ranged between 07h00 and 18h00 (Fig. 3). This general pattern was observed for most surveys, although night-time feeding behaviour made substantial contributions to total ingestion (moon cycle could play a role). Feeding duration also varied from one survey to another, as also shown by Espinoza and Blaskovic' (2000). The primarily diurnal feeding behaviour we observed differs from results of other studies of anchoveta feeding periodicity based on a large database (5245 individuals) from samples collected over the period 1953–1982 (Pauly et al., 1989b; Jarre et al., 1991), which indicated that most feeding occurred between 11h00 and 24h00. This difference cannot be related to the different methods of analysis used i.e., GAM in this study and Sainsbury's method (Sainsbury, 1986) in previous studies, since applying Sainsbury's method to our data does not change the results.

So why did the main feeding period change? At least two hypotheses can be proposed to explain this difference: a shift in the ecosystem, or a problem of data collection. Anchovies in other upwelling systems are considered as daytime (e.g. northern anchovy *E. mordax*; Baxter, 1967; Loukashkin, 1970; Koslow, 1981) or night-time (e.g. Benguela anchovy *E. encrasicolus*; James 1988) foragers. At first sight the main daytime trend we found appears surprising since zooplankton perform diel migrations and a large fraction of zooplankton is generally distributed within or below the oxycline during the day, out of reach of the anchoveta (e.g. Escribano et al., in press; Bertrand et al., 2008). However our results demonstrate that anchoveta can change their feeding period and forage at night if necessary. The HCS experienced 'cold' and 'warm' years during the period (1996–2003) of our study with a dominance of the upwelling-related cold coastal water along the Peruvian coast, except during the 1997–1998 El Niño (Swartzman et al., 2008). That anchoveta fed mainly during the day suggests that, even with the highly stratified conditions typical of enhanced upwelling periods, there were enough prey available during the day to sustain anchoveta. It seems therefore difficult to ascribe the difference between our results and previous studies to changes in climatic conditions. The period 1953–1982 that was previously studied included a wide range of climatic conditions: 'cold' until the beginning of the 1970s, and 'warm' from then until the mid 1980s. Hence we feel that it is more likely that the differences in anchoveta mean feeding periodicity between our and earlier studies was due to potential problems in the data collection (e.g. data sources varied from scientific cruises to fishing boats) for the 1953–1982 series or by the fact that the mean pattern hides important variability from one period to the other. Indeed a refined analysis of the data set used in previous studies revealed a pattern of several feeding periods per day, including some feeding during late night (Jarre-Teichmann, 1992).

The plasticity in anchoveta foraging periodicity was even more obvious when considering the distance to the coast, latitude or SST, where mean patterns were not representative of the observations from a single survey. Inside its range of overall viable conditions anchoveta is therefore able to forage efficiently at any time, any place, or any temperature. In other words, inside its cold coastal water-related habitat (see Bertrand et al., 2004a; Gutiérrez et al., 2007; Bertrand et al., 2008; Swartzman et al., 2008), anchoveta were probably distributed where prey were abundant and available, rather independently of other parameters (Bertrand et al., 2008).

4.4. A new vision of HCS functioning

If anchoveta is a predator that uses large zooplankters as the main source of dietary carbon, then our vision of HCS functioning must change. The HCS is by far the most productive eastern boundary current system in the world in terms of fish catches, but these high catches do not appear to be supported by exceptionally rates of primary production far higher than those observed in the other eastern boundary current systems (Carr, 2002; Carr and Kearns, 2003). The high fish production in the HCS could be related to a more efficient use of primary production due to, for example, a short trophic chain, and this assumption has been prevalent in the last few decades since anchoveta was considered to feed directly on primary producers and hence rely on a complete very short and efficient food chain (Ryther, 1969; Walsh, 1981). But if this is not the case, and anchoveta do not, in fact, benefit from a 2-step food chain, then the explanation for the high fish productivity in the HCS must be found elsewhere. Konchina (1991) stated that the ability of anchoveta to utilize food from several trophic levels and to choose energetically advantageous food enables it to achieve enormous biomass in a relatively short time. Yet all trophic models of the HCS developed to date, even recently, still consider that the anchoveta consumes at least as much carbon from phytoplankton as from zooplankton (e.g. Jahncke et al., 2004; Neira et al., 2004). Our results indicate that carbon flows in trophic models of the HCS must be re-evaluated, since the tremendous importance of anchoveta in the coastal pelagic ecosystem means that a major change in its diet should affect all the other components of that system. In particular, the fact that anchoveta forages at a higher trophic level than previously been considered implies that the primary and secondary production of the HCS may be higher than supposed (for primary production see Echevin et al., 2008). No absolute estimation of zooplankton production is available (see Ayón et al., 2004, 2008 for trends in zooplankton biovolume) but we hypothesize that zooplankton production could be higher in the HCS than in other upwelling systems, and this higher secondary production could be related to a more efficient use of primary production by zooplankton and/or a strong connection between the coastal and the offshore pelagic ecosystems. This last argument may particularly apply to the euphausiids, which were the main source of dietary carbon for anchoveta and which inhabit both near- and offshore ecosystems.

The hypothesis of higher zooplankton biomass in the HCS compared to other systems highlights the urgent need for more studies on zooplankton diversity, abundance and dynamics in the HCS, particularly for large zooplankters like euphausiids (Antezana, 2002). Studying these organisms is difficult, however, as they avoid standard samplers such as bongo nets, but new, multi-frequency acoustic measurements permit estimation of the biomass of the main zooplankton groups and facilitate the study of their distribution patterns in 2-D and 3-D (e.g. Lebourges-Dhaussy et al., 2004).

Our results also bring into question current thinking on anchoveta distribution. Because of the westward drift of water masses in the HCS there is usually a spatial separation between areas of peak phytoplankton abundance and areas of peak zooplankton abundance. Hence the relationship between anchoveta distribution and chlorophyll concentration, as observed from satellite, is not necessarily direct, and it is therefore important to take into account the characteristics of the available habitat, including zooplankton abundance, to understand anchoveta distribution patterns and also changes in abundance (cf. the habitat-based hypothesis in Bertrand et al., 2004a). It is not sufficient to use temperature or chlorophyll concentration as indicators of anchoveta distribution, since the plasticity of the genus *Engraulis* in general (Bakun, 1996) and *E. ringens* in particular allows it to feed successfully and distribute across a broad range of environmental variability. The dependence

of anchoveta on zooplankton has previously been illustrated by Alheit and Ñiquen (2004) and Ayón et al. (2008), who showed bottom-up control of anchoveta where its abundance in the HCS was linked to overall zooplankton abundance. At a smaller scale, Ayón et al. (2008) also showed that this apparent bottom-up control was accompanied by a local depletion effect, as zooplankton biomass was lower in places where anchoveta was abundant.

4.5. Synthesis: plastic is fantastic!

Our results have demonstrated that the diet of anchoveta in Peru is based primarily on large zooplankters, but also that this species shows tremendous plasticity in its diet and feeding behaviour; anchoveta utilize food from several trophic levels, can choose energetically advantageous food types, and can fit its foraging period and duration to prey. Trophic plasticity is apparently an evolved adaptive strategy; other strategies include the ability to track and concentrate in refuge areas when conditions are adverse (Bertrand et al., 2004a), change its reproductive behaviour (Buitrón and Perea, 2000), and distribute its population over a rather large temperature range (Bertrand et al., 2004a; Gutiérrez et al., 2008). In combination these characteristics may explain the 'anchoveta paradox': how a fish which (i) performs very small migrations and cannot escape adverse conditions, (ii) is mainly distributed in dense surface aggregations and is thus highly accessible to predators (fish, cephalopods, birds, mammals and fishers), and (iii) is very slow in its avoidance reactions to predators (Gerlotto et al., 2006), can achieve such enormous biomass in a relatively short time.

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References

- Alamo, A., 1989. Stomach contents of anchoveta (*Engraulis ringens*), 1974–1982. In: Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.), The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings, vol. 18, pp. 105–108.
- Alamo, A., Navarro, I., Espinoza, P., Zubiato, P., 1996a. Espectro alimentario y ración de alimentación de *Engraulis ringens* y de *Sardinops sagax* sagax, y mortalidad de huevos de la anchoveta peruana por predación. Informe Instituto del Mar del Perú 119, 34–42 (in Spanish, with abstract in English).
- Alamo, A., Navarro, I., Espinoza, P., Zubiato, P., 1996b. Relaciones tróficas, espectro alimentario y ración de alimentación de las principales especies pelágicas en el verano 1996. Informe Instituto del Mar del Perú 122, 36–46 (in Spanish, with abstract in English).
- Alamo, A., Espinoza, P., Zubiato, P., Navarro, I., 1997a. Comportamiento alimentario de la anchoveta peruana *Engraulis ringens*, durante el invierno de 1996. Crucero BIC Humboldt 9608-09. Informe Instituto del Mar del Perú 123, 38–46 (in Spanish, with abstract in English).
- Alamo, A., Espinoza, P., Zubiato, P., Navarro, I., 1997b. Comportamiento alimentario de los principales recursos pelágicos peruanos en verano y comienzos de otoño 1997. Informe Instituto del Mar del Perú 127, 82–89 (in Spanish, with abstract in English).
- Alamo, A., Espinoza, P., 1998. Variaciones alimentarias en *Engraulis ringens* y otros recursos pelágicos durante invierno-primavera de 1997. Informe Instituto del Mar del Perú 130, 45–52 (in Spanish, with abstract in English).
- Alexandrov, B.G., 2001. Caloric content of the Black Sea invertebrates: 1 Zooplankton and meiobenthos. In: *Ecologiya Morya (Ecology of the Sea)*, ISSN:1726-6777, pp. 5–10 (in Russian).
- Alheit, J., Ñiquen, M., 2004. Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography* 60, 201–222.
- Antezana, T., 2002. Adaptive behavior of *Euphausia mucronata* in relation to the oxygen minimum layer of the Humboldt Current. In: Färber Lorda, J. (Ed.), *Oceanography of the Eastern Pacific*. Editorial CICESE, vol. II, pp. 29–40.
- Ayón, P., Purca, S., Guevara-Carrasco, R., 2004. Zooplankton volume trends off Peru between 1964 and 2001. *ICES Journal of Marine Science* 61, 478–484.
- Ayón, P., Swartzman, G., Bertrand, A., Gutiérrez, M., Bertrand, S., 2008. Zooplankton and forage fish species off Peru: Large-scale bottom-up forcing and local-scale depletion. *Progress in Oceanography* 79, 208–214.
- Bakun, A., 1996. Patterns in the ocean: ocean process and marine population dynamics. Centro de Investigaciones biológicas del Nordeste. La Paz, Mexico and University of California Sea Grant, San Diego, USA.
- Baxter, J.L., 1967. Summary of biological information on the northern anchovy *Engraulis mordax* Girard. California Cooperative Fisheries Investigation Reports 11, pp. 110–116.
- Bertrand, A., Segura, M., Gutiérrez, M., Vásquez, L., 2004a. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. *Fish and Fisheries* 5, 296–316.
- Bertrand, S., Díaz, E., Ñiquen, M., 2004b. Interactions between fish and fisher's spatial distribution and behaviour: the anchovy (*Engraulis ringens*) fishery off Peru. *ICES Journal of Marine Science* 61, 1127–1136.
- Bertrand, A., Gerlotto, F., Bertrand, S., Gutiérrez, M., Alza, L., Chipollini, A., Diaz, E., Espinoza, P., Ledesma, L., Quesquén, R., Peraltilla, S., Chavez, 2008. Schooling behaviour and environmental forcing in relation to anchoveta distribution: an analysis across multiple spatial scales. *Progress in Oceanography* 79, 264–277.
- Blaskovic, V., Espinoza, P., Torriani, F., Navarro, I., 1999. Hábitos alimentarios de la anchoveta frente al litoral peruano durante la primavera 1998. Crucero BIC José Olaya Balandra 9811-12. Informe Instituto del Mar del Perú 146, 77–84 (in Spanish, with abstract in English).
- Buitrón, B., Perea, A., 2000. Aspectos reproductivos de la anchoveta peruana durante el período 1992–2000. *Boletín del Instituto del Mar del Perú* 19, 45–54 (in Spanish, with English abstract).
- Carr, M.-E., 2002. Estimation of potential productivity in Eastern Boundary Currents using remote sensing. *Deep Sea Research II* 49, 59–80.
- Carr, M.-E., Kearns, E.J., 2003. Production regimes in four Eastern Boundary Current systems. *Deep Sea Research II* 50, 3199–3221.
- Chiappa-Carrara, X., Gallardo-Cabello, M., 1993. Estudio del régimen y hábitos alimentarios de la anchoveta *Engraulis mordax* Girard (Pisces: Engraulidae), en Baja California, Mexico. *Ciencias Marinas* 19, pp. 285–305.
- Cushing, D.H., 1978. Upper trophic levels in upwelling areas. In: Boje, R., Tomczak, N. (Eds.), *Upwelling Ecosystems*. Springer-Verlag, Heidelberg, Berlin, pp. 101–110.
- Deibel, D., 1986. Feeding mechanism and house of the appendicularian *Oikopleura vanhoeffeni*. *Marine Biology* 93, 429–436.
- Echevin, V., Aumont, O., Ledesma, J., Flores, G., 2008. The seasonal cycle of surface chlorophyll in the Peru upwelling system: a modelling study. *Progress in Oceanography* 79, 167–176.
- Escribano, R., Hidalgo, P., Krautz, C., in press. Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000. *Deep Sea Research II*.
- Espinoza, P., Navarro, I., Torriani, F., 1998a. Variaciones en el espectro alimentario de los principales recursos pelágicos durante otoño 1998. Crucero BIC Humboldt 9803-05 de Tumbes a Tacna. Informe Instituto del Mar del Perú 135, pp. 134–142 (in Spanish, with abstract in English).
- Espinoza, P., Blaskovic, V., Navarro, I., 1998b. Comportamiento alimentario de *Engraulis ringens*, a finales del invierno 1998. Crucero de evaluación hidroacústica de recursos pelágicos 9808-09. Informe Instituto del Mar del Perú 141, pp. 67–71 (in Spanish, with abstract in English).
- Espinoza, P., Blaskovic, V., Torriani, F., Navarro, I., 1999. Dieta de la anchoveta *Engraulis ringens* según intervalos de talla. Crucero BIC José Olaya Balandra y BIC Humboldt 9906. Informe Instituto del Mar del Perú 149, pp. 41–48 (in Spanish, with abstract in English).
- Espinoza, P., Navarro, I., Torriani, F., 2000. Variaciones espaciales en la dieta de la anchoveta a finales de la primavera 1999. Crucero BIC José Olaya Balandra y SNP-2 9911-12. Informe Instituto del Mar del Perú 157, pp. 72–76 (in Spanish, with abstract in English).
- Espinoza, P., Blaskovic, V., 2000. Cambios en la dieta de la anchoveta *Engraulis ringens* y su influencia en la dinámica de alimentación. *Boletín Instituto del Mar del Perú* 19, 21–27 (in Spanish, with abstract in English).
- Garrido, S., Ben-Hamadou, R., Oliveira, P.B., Cunha, M.E., Chicharo, M.A., van der Lingen, C.D., 2008. Diet and feeding intensity of sardine *Sardina pilchardus*: correlation with satellite-derived chlorophyll data. *Marine Ecology Progress Series* 354, 245–256.
- Gerlotto, F., Bertrand, S., Bez, N., Gutiérrez, M., 2006. Waves of agitation inside anchovy schools observed with multibeam sonar: a way to transmit information in response to predation. *ICES Journal of Marine Science* 63, 1405–1417.
- Gutiérrez, M., Swartzman, G., Bertrand, A., Bertrand, S., 2007. Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983–2003. *Fisheries Oceanography* 16, 155–168.

- Gutiérrez, M., Bertrand, S., Ramirez, A., Morón, O., Bertrand, A., 2008. Ecological niches and areas of overlap of the squat lobster 'munida' (*Pleuroncodes monodon*) and anchoveta (*Engraulis ringens*) off Peru. *Progress in Oceanography* 79, 256–263.
- Hastie, T., Tibshirani, R., 1990. *Generalized Additive Models*. Chapman and Hall, London.
- Hillebrand, H., Dürselen, C.-D., Kirschtel, D., Pollinger, U., Zohary, T., 1999. Biovolume calculations for pelagic and benthic microalgae. *Journal of Phycology* 35, 403–424.
- Hückstädt, L.A., Rojas, C.P., Antezana, T., 2007. Stable isotope analysis reveals pelagic foraging by the Southern sea lion in central Chile. *Journal of Experimental Marine Biology and Ecology* 347, 123–133.
- Hureau, J.-C., 1970. Biologie compare de quelques poissons antarctiques (Nototheniidae). *Bulletin de l'Institut Oceanographique Monaco* 68, 244.
- Hyslop, E.J., 1980. Stomach contents analysis – a review of methods and their application. *Journal of Fish Biology* 17, 411–429.
- Jahncke, J., Checkley, D.M. Jr., Hunt Jr., G.L., 2004. Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. *Fisheries Oceanography* 13, 208–223.
- James, A.G., 1987. Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. In: Payne, A.I.L., Gulland, J.A., Brink K.H. (Eds.), *The Benguela and Comparable Ecosystems South African Journal of Marine Science* 5, 673–692.
- James, A.G., 1988. Are clupeid microphagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *South African Journal of Marine Science* 7, 161–177.
- James, A.G., Chiappa-Carrara, X., 1990. A comparison of field based studies on the trophic ecology of *Engraulis capensis* and *E. mordax*. In: Barnes, M., Gibson, R.N. (Eds.), *Trophic relationships in the marine environment*. Aberdeen University Press, pp. 208–221.
- Jarre, A., Muck, P., Pauly, D., 1991. Two approaches for modelling fish stock interactions in the Peruvian upwelling ecosystem. *ICES Marine Science Symposia* 193, 171–184.
- Jarre-[Teichmann], A., 1992. Steady-state modelling of the Peruvian upwelling ecosystem. Doctoral dissertation, University of Bremen, Germany, 153.
- Konchina, Y.V., 1991. Trophic status of the Peruvian anchovy and sardine. *Journal of Ichthyology* 31, 59–72.
- Konchina, Y.V., Pavlov, Y.P., 1995. On methods of determining the trophic status of species in ichthyocenoses. *Journal of Ichthyology* 35, 150–166.
- Koslow, J.A., 1981. Feeding selectivity of schools of northern anchovy, *Engraulis mordax*, in the southern California. *Fishery Bulletin* 79, 131–142.
- Lebourges-Dhaussy, A., Knutsen, T., Korneliussen, R.J., 2004. Acoustic backscatter from zooplankton and fish explored through an optimised model framework. *ICES, CM 2004/R:39*.
- Llanos-Rivera, A., Castro, L.R., 2004. Latitudinal and seasonal egg-size variation of the anchoveta (*Engraulis ringens*) off the Chilean coast. *Fishery Bulletin* 102, 207–212.
- Loukashkin, A.S., 1970. On the diet and feeding behaviour of the northern anchovy, *Engraulis mordax* (Girard). In: *Proceedings of the California Academy of Sciences (Series 4)* 37, 419–458.
- Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology and Oceanography* 45, 569–579.
- Neira, S., Arancibia, H., Cubillos, L., 2004. Comparative analysis of trophic structure of commercial fishery species off Central Chile in 1992 and 1998. *Ecological Modelling* 172, 233–248.
- Parsons, T.R., Takahashi, M., Hargraves, B., 1984. *Biological Oceanographic Processes*. Pergamon, Oxford.
- Pauly, D., Tsukayama, I., 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. *ICLARM Studies and Reviews*, 15.
- Pauly, D., Muck, P., Mendo, J., Tsukayama, I., 1989a. The Peruvian upwelling ecosystem: dynamics and interactions. In: *ICLARM Conference Proceedings*, vol. 18.
- Pauly, D., Jarre, A., Luna, S., Sambilay Jr., V., Rojas de Mendiola, B., Alamo, A., 1989b. On the quantity and types of food ingested by Peruvian anchoveta, 1953–1982. In: Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.), *The Peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conference Proceedings, vol. 18, pp. 109–124.
- Rojas, B., 1953. Estudios preliminares del contenido estomacal de las anchovetas. *Bol. Cient. Cía. Adm. Guano* 1, 33–42.
- Rojas de Mendiola, B., 1969. The food of the Peruvian anchovy. *Journal du Conseil International pour l'Exploration de la Mer* 32, 433–434.
- Rojas de Mendiola, B., 1971. Some observations on the feeding of the Peruvian anchoveta *Engraulis ringens* J. in two regions of the Peruvian coast. In: Costlow, J.D. (Ed.), *Fertility of the Sea*. Gordon and Breach Science Publisher, New York, pp. 17–440.
- Rojas de Mendiola, B., 1989. Stomach contents of anchoveta (*Engraulis ringens*), 1953–1974. In: Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.) *The Peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conference Proceedings, vol. 18, pp. 97–104.
- Ryther, J.H., 1969. Photosynthesis and fish production in the sea. *Science* 166, 72–76.
- Sainsbury, K.J., 1986. Estimation of food consumption from field observation of fish feeding cycles. *Journal of Fish Biology* 29, 23–36.
- Sameoto, D., 1971. Life history ecological production and empirical mathematical model of the population of *Sagitta elegans* in St. Margaret's Bay Nova Scotia. *Journal of Fisheries Research Board of Canada* 28, 971–985.
- Santander, H., Luyo, G., Carrasco, S., Veliz, M., Sandoval de Castillo, O., 1981. Catalogo de zooplankton en el mar peruano. *Boletín Intituto del Mar del Perú* 6, 1–75 (in Spanish).
- Snoeijs, P., Busse, S., Potapova, M., 2002. The importance of diatom cell size in community analysis. *Journal of Phycology* 38, 265–272.
- Swartzman, G., Bertrand, A., Gutiérrez, M., Bertrand, S., Vasquez, L., 2008. The relationship of anchovy and sardine to water masses in the Peruvian Humboldt Current System from 1983–2005. *Progress in Oceanography* 79, 228–237.
- Tudela, S., Palomera, I., 1997. Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea. *Marine Ecology Progress Series* 160, 121–134.
- van der Lingen, C.D., 2002. Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *South African Journal of Marine Science* 24, 301–316.
- van der Lingen, C.D., Hutchings, L., Field, J.G., 2006. Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? *African Journal of Marine Science* 28, 465–477.
- van der Lingen, C.D., Bertrand, A., Bode, A., Brodeur, R., Cubillos, L., Espinoza, P., Friedland, K., Garrido, S., Irigoien, X., Möllman, C., Rodriguez-Sanchez, R., Tanaka, H., Temming, A., in press. Trophic dynamics of small pelagic fish. In: Checkley, D.M., Jr., Roy, C., Alheit, J. (Eds.), *Climate Change and Small Pelagic Fish (Chapter 8)*.
- Verity, P.G., Langdon, C., 1984. Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *Journal of Plankton Research* 6, 859–868.
- Walsh, J.J., 1981. A carbon budget for overfishing off Peru. *Nature* 290, 300–304.