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Diet of sardine (*Sardinops sagax*) in the northern Humboldt Current system and comparison with the diets of clupeoids in this and other eastern boundary upwelling systems

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ABSTRACT

Sardines are one of the main small pelagic fish resources in eastern boundary upwelling systems (EBUS) where they play an important ecological role both as a predator of plankton and as prey of top predators. Sardine trophodynamics have been relatively well studied in three of the EBUS (the Benguela, California and Canary upwelling systems) but not in the Humboldt Current system. In this paper we describe the diet of sardine *Sardinops sagax* in the northern Humboldt Current system (NHCS) off Peru, using an analytical method which assesses relative dietary importance in terms of estimated prey carbon content. We assessed sardine diet by examining a total of 555 stomachs collected during six surveys conducted off Peru during the period 1996–1998, and compare our results with the diet of anchoveta *Engraulis ringens* off Peru and with the diets of sardines from the southern Benguela (also *S. sagax*) and the northern Canary (*Sardina pilchardus*) upwelling systems. The diet of sardine off Peru is based primarily on zooplankton, similar to that observed for anchoveta but with several important differences. Firstly, sardine feed on smaller zooplankton than do anchoveta, with sardine diet consisting of smaller copepods and fewer euphausiids than anchoveta diet. Secondly, whilst phytoplankton represents <2% of sardine dietary carbon, this fraction is dominated by dinoflagellates, whereas diatoms are the dominant phytoplankton consumed by anchoveta. Hence, trophic competition between sardine and anchovy in the northern Humboldt Current system is minimized by their partitioning of the zooplankton food resource based on prey size, as has been reported in other systems. Whereas sardine in the NHCS feed on smaller zooplankton than do anchovy in that system, sardine in the NHCS forage on larger prey and obtain a substantial portion of their dietary carbon from euphausiids compared to sardine from the northern Canary and southern Benguela Current systems.

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1. Introduction

Sardines (the genera *Sardinops* and *Sardina*) and anchovy (the genus *Engraulis*) are the most important commercially-exploited small pelagic fish species worldwide, and are particularly abundant in the eastern boundary current systems (EBUS; including the Benguela, California, Canary and Humboldt Current systems). These fish feed on plankton and are the dominant forage of a variety of fish, marine mammal and seabird predators, and hence are also ecologically important.

A recent synthesis on the trophic dynamics of small pelagic fish from a variety of upwelling and other systems (van der Lingen et al., 2009) has shown that sardine and anchovy derive the bulk of their dietary carbon from zooplankton, a finding that contradicts many previous descriptions of exclusive or near-total phytophagy by these species. For example, Peruvian anchoveta (*Engraulis ringens*) was considered to feed directly on primary producers, which led to the belief that the large populations of anchoveta were supported by an unusually short and efficient food chain (Ryther, 1969; Walsh, 1981). This assumption was recently refuted by Espinoza and Bertrand (2008), who estimated the carbon content of prey items, as opposed to using the numerical method of stomach content analysis which is considered to be subjective (James, 1987), and showed that anchoveta forage mainly on zooplankton. Such findings improve our knowledge of the functioning of the

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northern Humboldt Current system (NHCS) off Peru, and illustrate the need for accurate and appropriate methods. Dietary information derived using carbon content is available for sardine and anchovy from the main EBUS (see van der Lingen et al., 2009) but not for sardine (*Sardinops sagax*) in the Humboldt Current system. To date, sardine in the Humboldt Current system was generally considered as feeding mainly on phytoplankton (Rojas de Mendiola, 1966; Sanchez de Benites et al., 1985; Alamo and Bouchon, 1987). This differs from recent studies on this and similar species' diet in other ecosystems, that demonstrated that sardine derive the majority of their dietary carbon from zooplankton (van der Lingen, 2002; Garrido et al., 2008; van der Lingen et al., 2009). A single study on sardine diet in the NHCS (Konchina, 1991) mentioned that sardine consumed mainly small copepods and tunicates, but this study has seldom been considered.

In this paper we describe the diet of sardine in the NHCS based on a method which assesses relative dietary importance according to estimated prey carbon content (James, 1987; van der Lingen, 2002). We compare our results on sardine diet and prey-size spectrum with those of the anchoveta in the NHCS. We also compare the diet of sardine from the NHCS with data on the diet of sardines in other systems, including *Sardinops sagax* from the southern Benguela (SBCS) off South Africa, *Sardina pilchardus* from the northern Canary system off Portugal (NCCS), and with published work describing clupeid diets in the California Current system (CalCS). We discuss how new insights into the functioning of these systems may be extracted from such a comparative approach. In particular, we re-examine the hypothesis (Ryther, 1969) that upwelling regions are so efficient in terms of fish production because of the direct link between phytoplankton and filter-feeding fishes.

2. Materials and methods

2.1. Sardine diet in the northern Humboldt Current system (NHCS)

Sardines were collected during six acoustic surveys conducted by IMARPE research vessels between 1996 and 1998 with the aim of estimating pelagic fish abundance in the Peruvian EEZ (Table 1). This period encompasses the El Niño of 1997–98, one of the two strongest of the last century (Wolter and Timlin, 1998). Fish were captured using a midwater trawl net ('Engel 124/1800', 12 mm codend mesh) and a sample of 5–20 sardines was randomly collected from each trawl. Individual sardine were measured (total length; cm) and weighed (wet body mass; g) and the cardiac and pyloric sections of their stomachs were extracted onboard and immediately fixed in 5% formalin for later laboratory analysis. In the laboratory stomachs were opened and their contents extracted and weighed (wet weight, WW) to the nearest 0.01 g. The stomach contents of individual fish were then pooled according to fish length (3 cm size-classes) for each sample, and pooled stomach contents were filtered through a 125- μ m 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.

Different procedures were followed to estimate the carbon content of phytoplankton and zooplankton and hence determine their relative dietary importance, and have been described in detail in Espinoza and Bertrand (2008). In summary, we did not measure the size of all prey items but instead estimated prey size using information from the literature and from some direct measurements, taking into account the life cycle stage (e.g. adult *Calanus* were separated from copepodite stages). 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. To transform phytoplankton volume into carbon content we used equations given in Menden-Deuer and Lessard (2000) and Verity and Langdon (1984). For zooplankton, prosome or total length of various zooplankters was taken from the literature or from some direct measurements made by IMARPE on zooplankton from stomach content samples. 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). All prey carbon content values were standardized to μ g C, and the contribution to dietary carbon of a particular prey type was expressed as a percentage of the total estimated carbon content of all fish examined in each cruise. In order to assess temporal (inter-survey) variability of sardine diet off Peru we pooled diet data into seven broad prey categories (dinoflagellates, diatoms, other phytoplankters, copepods, gastropods, euphausiids, and other zooplankters), and present the results for individual surveys and for all surveys pooled. All the equations and conversion factors are available in tables 2–4 of Espinoza and Bertrand (2008).

2.2. Diet comparison

To compare the diet of sardine from the NHCS with that of anchoveta (*Engraulis ringens*) in the same system, and with those of sardines from the southern Benguela (SBCS) and northern Canary (NCCS) systems, we reanalysed data from published work that also examined dietary composition in terms of prey carbon content. For anchoveta we used results reported by Espinoza and Bertrand (2008), which comprised data on anchoveta stomach contents collected during individual surveys and aggregated for all surveys (as has been done for NHCS sardine in this paper). The diet of southern Benguela sardine (*Sardinops sagax*) was described by van der Lingen (2002), using samples collected from midwater trawls deployed during research surveys conducted in 1993 (number of trawls sampled = 10; stomach contents of 10

Table 1
Survey characteristics.

Survey code	Start date	End date	Latitudinal limits	Transect extension (nmi)	No. of trawls	No. of sardine stomachs	Sardine length range (min–max)
1996/11–12	16 November 1996	19 December 1996	5°S–18°S	100	1	16	25–30
1997/02–04	13 February 1997	23 April 1997	5°S–18°S	80–90	5	67	21–30
1997/09–10	04 September 1997	05 October 1997	3°30'S–18°S	80	6	79	10–30
1998/03–05	27 March 1998	01 May 1998	3°30'S–18°S	50	18	287	11–29
1998/05–06	26 May 1998	24 June 1998	4°S–18°S	70	7	59	16–21
1998/08–09	23 August 1998	17 September 1998	5°S–18°S	80	4	47	18–22

sardine per trawl were pooled for analysis) and 1994 (number of trawls sampled = 17; stomach contents of 10 sardine per trawl were pooled for analysis). The average contribution to sardine dietary carbon by prey type (%C_{Type}) and by prey size (%C_{Size}) was calculated for each survey, with the %C_{Type} and %C_{Size} values from each sample receiving equal weighting. For our comparison we calculated average %C_{Type} and %C_{Size} values from all 27 samples, again with equal sample weighting. Garrido et al. (2008) described the diet of 70 sardine (*Sardina pilchardus*) from the northern Canary Current system using samples collected fortnightly from purse-seine catches off the west and south coasts of Portugal, taken during 2002–2004, and those two datasets were also aggregated for our comparison. Further details regarding the sampling and analytical methods used for anchoveta, and sardines from the southern Benguela and northern Canary systems, are provided in Espinoza and Bertrand (2008), van der Lingen (2002), and Garrido et al. (2008), respectively.

In order to facilitate dietary comparisons between species and systems we first grouped diet data into the seven broad prey categories listed above, and present this information in terms of numerical dominance and relative contribution to dietary carbon. To examine the zooplankton component of sardine diet in more detail we then re-grouped the data (in terms of relative contribution to dietary carbon only) from each system/species into the following ten prey categories: (i) diatoms, (ii) dinoflagellates, (iii) other phytoplankters, (iv) calanoid copepods, (v) miscellaneous copepods (mainly cyclopoid, harpacticoid, and poecilostomatoid copepods), (vi) other copepods (including copepod nauplii), (vii) euphausiids, (viii) gastropods, (ix) fish eggs, and (x) other zooplankters (including crustacean eggs). We then compared the prey-size spectra between species and systems by examining the contribution to dietary carbon made by the following six size-classes: $0 < x < 0.5$, $0.5 \leq x < 1.0$, $1.0 \leq x < 2.0$, $2.0 \leq x < 4.0$, $4.0 \leq x < 8.0$, ≥ 8.0 mm. We used the Kruskal–Wallis rank test, a non-parametric alternative to ANOVA (Scherrer, 1984), to assess whether diets between species and systems were significantly different. Because data from the SBCS are only available as percentage contribution to diet by size class and by taxonomic group, standard statistical methods (e.g. chi-square, contingency table, Kruskal–Wallis, and others) could not be used on those data. Consequently, Kruskal–Wallis tests were used to compare the diets of sardine and anchoveta from the NHCS, and of sardine from the NHCS and the NCCS, only.

3. Results

3.1. Sardine diet in the NHCS

A total of 555 sardine from the NHCS ranging from 10 to 30 cm total length were analysed (Table 1). Ninety-one prey taxa were identified, including 24 diatom genera, 10 dinoflagellates, 1 silicoflagellate, 1 phytoflagellate, 4 tintinnids, 1 radiolarian, 32 copepods, and 18 other genera (Table 2).

Numerical analysis of the diet when data from all the surveys were combined indicated that phytoplankton strongly dominated sardine diet and comprised 99.2% on average of all ingested prey, with copepods representing only 0.7%, euphausiids <0.1%, and other zooplankters <0.1% of the total number of prey (Fig. 1a). However, this view of sardine diet changes when prey carbon content is considered (Fig. 1a); zooplankton was by far the most important component and contributed 98.5% of dietary carbon, whilst phytoplankton contributed the remaining 1.5%. Among zooplankters, copepods dominated and contributed 54.5% of dietary carbon, followed by euphausiids (38.7%) and then other zooplankton (5.3%). The copepod carbon fraction was dominated by *Eucal-*

anus (58.4% of the total copepod contribution to dietary carbon), *Calanus* (21.5%), *Rhincalanus* (5.4%) and *Centropages* (4.5%). The phytoplankton carbon fraction was dominated by the dinoflagellates *Prorocentrum* (31.4% of the total phytoplankton contribution to dietary carbon) and *Ceratium* (16.2%), and the diatom *Coscinodiscus* (27.3%).

When the surveys are considered individually strong variability in dietary composition is seen (Fig. 1a). The maximum contribution to dietary carbon by copepods (90.8%) occurred during November–December 1996, whilst the minimum (33.3%) was observed during February–April 1997. The maximum contribution by euphausiids was observed in February–April 1997 (61.2%) and August–September 1998 (47.5%), whilst the minimum (5.8%) occurred in November–December 1996. The maximum contribution by other zooplankters occurred in March–May 1998 (16.2% of dietary carbon) and June 1998 (26.9%), with gastropods also having their maximum contributions during these surveys. The contribution to dietary carbon made by phytoplankton was very low (<0.3%) during the El Niño 1997–1998, whereas the highest value (4.9%) was observed in February–April 1997 just before the El Niño event.

3.2. Comparative trophic ecology by prey type

In all systems for which data are available the image of sardine diet is dramatically different depending on whether prey items are considered in terms of their numerical contribution or their relative contribution to dietary carbon (Fig. 1b). In terms of numerical dominance the phytoplankton fraction ranged between 47.8% (SBCS) and 99.2% (NHCS), whereas phytoplankton contributed between 1.5% (NHCS) and 17.0% (NCCS) of total dietary carbon. Because the numerical method is not appropriate for adequately characterizing diet, subsequent dietary comparisons will be described in terms of dietary carbon only.

Marked differences are seen between the diet of sardine and anchoveta in the NHCS, and also between sardines from the NHCS, the NCCS, and the SBCS (Fig. 2). Results from the Kruskal–Wallis analysis performed between systems and species (excluding the SBCS sardine) on dietary carbon by prey categories showed highly significant ($p < 0.01$) differences for all prey categories except for “Other zooplankters” ($p > 0.05$). Sardine from the NHCS had only two prey categories that accounted for more than 5% of dietary carbon, namely calanoid copepods (53.0% of dietary carbon) and euphausiids (38.7%). These two categories also dominated anchoveta diet, but in reverse order, with euphausiids (67.5%) being the most important category followed by calanoid copepods (26.3%). Sardine from the NCCS presented a very different prey spectrum and a more even spread of important prey categories, with six categories accounting for more than 8% of dietary carbon: other copepods (26.6%), fish eggs (23.8%), dinoflagellates (13.3%), miscellaneous copepods (12.3%), calanoid copepods (12.2%), and other zooplankters (8.4%). The diet of sardine in the SBCS is intermediate between sardine in the other two systems, with four prey categories accounting for more than 8% of dietary carbon: calanoid copepods (38.2%), miscellaneous copepods (18.2%), other zooplankters (17.5%), and fish eggs (14.6%).

3.3. Comparative trophic ecology by prey-size class

The differences observed in the contribution to dietary carbon by prey category between fish and systems are even more clearly observed when the prey-size spectra are examined (Fig. 3), and results from the Kruskal–Wallis analysis performed between systems and species (excluding the SBCS sardine) on dietary carbon by prey size showed highly significant ($p < 0.01$) differences for all size classes. In the NCCS the sardine prey-size spectrum presents a decreasing trend with smaller prey contributing the majority of

Table 2

Contribution by number (total) and carbon (total and by survey) of the prey in the sardine diet.

Dietary items	Number Total	Carbon content (μg)						
		Total	1996/11–12	1997/02–04	1997/09–10	1998/03–05	1998/05–06	1998/08–09
Diatoms								
<i>Asterionellopsis</i>	43035	4.7	0.0	0.0	0.0	4.4	0.3	0.0
<i>Bacteriastrium</i>	167	3.8	0.0	3.3	0.0	0.1	0.4	0.0
<i>Chaetoceros</i>	47266	91.5	6.6	62.8	10.7	8.5	2.6	0.2
<i>Coscinodiscus</i>	4983	10036.1	610.8	8445.8	631.9	43.7	51.3	252.7
<i>Detonula</i>	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ditylum</i>	126	17.7	0.0	0.0	17.4	0.1	0.2	0.0
<i>Eucampia</i>	92	3.5	3.5	0.0	0.0	0.0	0.0	0.0
<i>Fragilariopsis</i>	43	0.9	0.0	0.9	0.0	0.0	0.0	0.0
<i>Grammatophora</i>	16	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Guinardia</i>	280	1.2	0.0	0.0	0.0	1.2	0.0	0.0
<i>Gyrosigma</i>	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hemiaulus</i>	20	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lauderia</i>	334	1.7	0.0	0.0	0.0	1.7	0.0	0.0
<i>Lithodesmium</i>	277	26.3	0.0	25.9	0.4	0.0	0.1	0.0
<i>Navicula</i>	374	4.5	0.0	3.8	0.6	0.0	0.1	0.0
<i>Planktoniella</i>	42	104.0	36.4	67.6	0.0	0.0	0.0	0.0
<i>Pleurosigma</i>	35	1.5	0.0	1.5	0.0	0.0	0.0	0.0
<i>Pseudo-nitzschia</i>	31014	26.9	0.0	25.2	0.0	1.6	0.1	0.1
<i>Rhizosolenia</i>	905	310.3	97.8	0.0	206.1	0.8	2.1	3.5
<i>Skeletonema</i>	391	5.2	0.0	5.2	0.0	0.0	0.0	0.0
<i>Stephanopyxis</i>	105	28.4	0.0	0.0	28.0	0.3	0.0	0.0
<i>Thalassionema</i>	1924	21.0	0.0	6.6	14.0	0.1	0.0	0.2
<i>Thalassiosira</i>	3798	2374.4	4.7	2362.0	7.5	0.1	0.1	0.0
<i>Lioloma</i>	36	44.5	0.0	44.5	0.0	0.0	0.0	0.0
Dinoflagellates								
<i>Ceratium</i>	1195	5955.9	1747.9	3942.0	239.1	0.3	0.1	26.6
<i>Dinophysis</i>	227	1250.4	39.1	1183.4	27.9	0.0	0.0	0.0
<i>Dissodinium</i>	273	860.3	0.0	809.4	44.7	0.6	0.1	5.6
<i>Gonyaulax</i>	85	474.5	39.1	435.4	0.0	0.0	0.0	0.0
<i>Podolampas</i>	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Proocentrum</i>	119	194.9	0.0	194.9	0.0	0.0	0.0	0.0
<i>Protoperdinium</i>	4023	11553.0	1107.4	9587.8	616.8	43.5	1.4	196.2
<i>Pyrocystis</i>	26	55.9	0.0	0.0	0.0	0.1	0.0	55.8
<i>Scrippsiella</i>	7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Diplopsalis</i>	14	78.1	78.1	0.0	0.0	0.0	0.0	0.0
Silicoflagellates								
<i>Dyctiocha</i>	753	575.6	0.0	566.6	6.9	0.8	1.2	0.0
Phytoflagellates								
<i>Tetraselmis</i>	4175	1.1	0.0	0.0	0.0	0.0	1.1	0.0
Tintinnids								
<i>Eutintinnus</i>	3	23.8	0.0	23.8	0.0	0.0	0.0	0.0
<i>Favella</i>	2	15.9	0.0	7.9	7.9	0.0	0.0	0.0
<i>Helicostomella</i>	48	381.0	222.2	158.7	0.0	0.0	0.0	0.0
<i>Tintinnopsis</i>	212	1682.7	0.0	1682.7	0.0	0.0	0.0	0.0
Radiolaria	115	591.7	0.0	591.7	0.0	0.0	0.0	0.0
Copepoda								
<i>Acartia</i>	139	1959.5	0.0	220.2	528.4	572.5	462.4	176.1
<i>Aetideus</i>	24	3830.8	957.7	0.0	159.6	319.2	0.0	2394.3
<i>Calanus</i>	1099	287891.9	8075.0	27033.8	170979.7	55120.8	10883.7	15798.9
<i>Calocalanus</i>	86	1681.7	0.0	262.8	210.2	630.6	315.3	262.8
<i>Candacia</i>	294	20323.8	1844.0	2806.1	10422.5	4890.5	360.8	0.0
<i>Centropages</i>	441	59617.5	16600.3	10534.8	10694.4	18515.8	1197.1	2075.0
<i>Clausocalanus</i>	466	4689.5	500.4	855.6	1033.1	1372.1	314.8	613.4
<i>Clytemnestra</i>	60	244.6	0.0	125.5	0.0	62.7	56.5	0.0
<i>Copilia</i>	6	509.0	0.0	254.5	0.0	254.5	0.0	0.0
<i>Corycaeus</i>	764	16542.1	708.1	5438.5	5863.4	1784.5	566.5	2181.1
<i>Euaetideus</i>	139	1752.2	0.0	0.0	1338.7	0.0	413.4	0.0
<i>Eucalanus</i>	374	782228.5	75056.4	147767.3	215787.2	199368.6	10554.8	133694.2
<i>Euchaeta</i>	374	18720.6	1946.7	1816.9	6618.7	4672.0	616.5	3049.8
<i>Euchirella</i>	148	17147.3	0.0	0.0	0.0	2588.3	8735.4	5823.6
<i>Euterpina</i>	198	851.8	0.0	138.3	611.6	36.4	65.5	0.0
<i>Lucicutia</i>	22	743.3	514.6	0.0	0.0	171.5	57.2	0.0
<i>Macrosetella</i>	20	28.2	0.0	0.0	0.0	0.0	28.2	0.0
<i>Mecynocera</i>	95	3729.2	0.0	0.0	0.0	3729.2	0.0	0.0
<i>Microsetella</i>	119	788.4	0.0	492.8	0.0	197.1	98.6	0.0
<i>Nonocalanus</i>	10	1596.2	0.0	0.0	1596.2	0.0	0.0	0.0
<i>Oithona</i>	546	2828.5	203.9	458.7	1703.6	247.5	127.4	87.4
<i>Oncaea</i>	1044	10939.7	371.1	3083.6	3928.1	934.0	268.7	2354.3
<i>Paracalanus</i>	552	10863.9	1283.1	1967.5	3763.9	2195.6	541.8	1112.1

(continued on next page)

Table 2 (continued)

Dietary items	Number	Carbon content (μg)						
		Total	1996/11–12	1997/02–04	1997/09–10	1998/03–05	1998/05–06	1998/08–09
<i>Phaena</i>	26	741.4	0.0	57.0	0.0	627.3	0.0	57.0
<i>Pleuromamma</i>	8	692.9	0.0	0.0	0.0	692.9	0.0	0.0
<i>Rhincalanus</i>	31	72710.9	0.0	0.0	68019.9	4691.0	0.0	0.0
<i>Saphirina</i>	5	724.7	0.0	0.0	144.9	579.7	0.0	0.0
<i>Scolecithricella</i>	14	3682.7	0.0	0.0	3682.7	0.0	0.0	0.0
<i>Temora</i>	81	7015.1	0.0	259.8	6062.4	0.0	0.0	692.9
Harpacticoida	177	1092.8	0.0	738.9	0.0	208.2	83.3	62.4
Copepodite	609	2737.5	0.0	715.8	1062.0	306.8	228.1	424.8
Copepods remains	1192	783.6	101.3	143.7	262.6	107.1	68.9	100.1
Other zooplankters								
Euphausiacea	2614	949766.9	6903.4	377145.4	164592.4	239440.1	3270.0	158415.6
Amphipoda	2	4521.1	0.0	0.0	0.0	4521.1	0.0	0.0
Bivalvia	4	1819.9	0.0	0.0	0.0	1819.9	0.0	0.0
Gastropoda	465	105101.6	0.0	1819.9	910.0	88722.1	11829.6	1819.9
Apendicularia	3	1122.9	0.0	0.0	0.0	1122.9	0.0	0.0
Zoea	29	2625.6	0.0	633.8	1358.1	633.8	0.0	0.0
Megalopa	8	1944.8	0.0	0.0	0.0	1944.8	0.0	0.0
Anchovy eggs	60	721.4	0.0	312.6	108.2	276.5	24.0	0.0
White anchovy eggs	16	192.4	0.0	0.0	0.0	192.4	0.0	0.0
Engraulidae eggs	80	961.9	0.0	0.0	0.0	961.9	0.0	0.0
Unidentified fish eggs	326	3919.7	0.0	396.8	709.4	2308.5	408.8	96.2
Cirriped larvae	25	1.0	0.0	0.3	0.6	0.0	0.1	0.0
Unidentified fish larvae	3	836.6	0.0	0.0	836.6	0.0	0.0	0.0
Chaetognata	75	2208.0	0.0	0.0	0.0	0.0	2208.0	0.0
Unidentified fish	1	278.9	0.0	0.0	278.9	0.0	0.0	0.0
Unidentified decapoda	16	3889.6	0.0	0.0	0.0	2431.0	0.0	1458.6
Myctophidae	2	557.8	0.0	557.8	0.0	0.0	0.0	0.0
Polychaeta	2	222.5	0.0	222.5	0.0	0.0	0.0	0.0

total dietary carbon; prey smaller than 0.5 mm contribute 49.7% of dietary carbon and this proportion decreases to zero for prey larger than 4 mm. Sardine in the SBCS also derive the majority (>90% on average) of their dietary carbon from small (<2.0 mm) zooplankton prey, and their prey-size spectra is roughly dome shaped with a mode between 1 and 2 mm. No prey larger than 4 mm were observed in sardine from that system. Finally, the prey-size spectrum of sardine in the NHCS shows an increasing trend, with prey <0.5 mm making a negligible contribution to dietary carbon and prey larger than 8 mm contributing 39.6% of dietary carbon, this size corresponding mainly to euphausiids. A similar, and even more pronounced trend is observed for anchoveta in the NHCS, for which prey larger than 8 mm contribute up to 70.9% of dietary carbon.

4. Discussion

4.1. Sardine diet in the NHCS

Our analysis of the composition of stomach contents of sardine in the NHCS illustrates its capability for foraging on a large variety of prey and over several trophic levels. When considering only prey numbers, sardine diet is dominated by phytoplankton and the zooplankton fraction is negligible (Fig. 1a). However, when the carbon content of prey items is considered, zooplankton becomes by far the most important component of dietary carbon. The zooplankton carbon fraction was dominated by copepods, in particular *Eucalanus* and *Calanus*, followed by euphausiids, and the importance of these taxa was previously recognised by Alamo and Bouchon (1987) and Konchina (1991). The phytoplankton carbon fraction was dominated by large dinoflagellates (mainly *Prorocentrum*, *Ceratium*, and *Coscinodiscus*), as previously observed (Alamo and Bouchon, 1987; Konchina, 1991). This very low proportion of phytoplankton could represent a limitation to sardine growth and development, since phytoplankton has more nitrogen (N) than zooplankton (i.e. the C:N ratio is higher for zooplankton than for phytoplankton). However, sardines (and anchovies) have signifi-

cantly higher N absorption efficiencies from zooplankton than from phytoplankton (van der Lingen, 1998), and that sardine are better able to utilize zooplankton N (and also C and dry mass) than phytoplankton N suggests that this species derives more of its nutritional requirements from zooplankton (van der Lingen, 1998), which is supported by our results.

The contribution made by different prey categories to the diet of sardine in the NHCS strongly varied during the study period (Fig. 1a), illustrating the spatiotemporal opportunistic feeding behaviour of sardine which can forage on a variety of prey according to variations in plankton composition (van der Lingen, 1994; van der Lingen et al., 2006). The relative contribution from phytoplankton was always low but reached a maximum in February–April 1997, prior to the El Niño, and then decreased to very low (<0.5%) levels during the El Niño of 1997–98. The proportion of sardine dietary carbon derived from copepods was highly variable and presented no clear trend (Fig. 1a), being highest in November–December 1996 and lowest a few months later in February–April 1997. Yet, when the contribution to dietary carbon by copepods decreased that from the euphausiids increased, and vice versa. The relative importance of copepods and euphausiids in sardine diet does not match those for anchoveta diet, described by Espinoza and Bertrand (2008) using data collected during the same surveys (Fig. 1a of this paper and Fig. 2 of Espinoza and Bertrand, 2008). For instance, the highest copepod fraction observed in sardine diet in November–December 1996 corresponds to the lowest observed for anchoveta, although the very low number of sardine samples collected during this survey (Table 1) suggests that results should be interpreted with caution. However, this opposite trend was also observed for other surveys (in particular September–October 1997 and March–May 1998) that had a larger sample size. These differences may reflect the fact that these species are ecological neighbours but not ecological analogues (Gutiérrez et al., 2007), and seldom overlap spatially (Bertrand et al., 2004; Gutiérrez et al., 2007; Swartzman et al., 2008).

Most of the previous studies on sardine diet in the NHCS were based on qualitative methods (Rojas de Mendiola, 1966; Sanchez

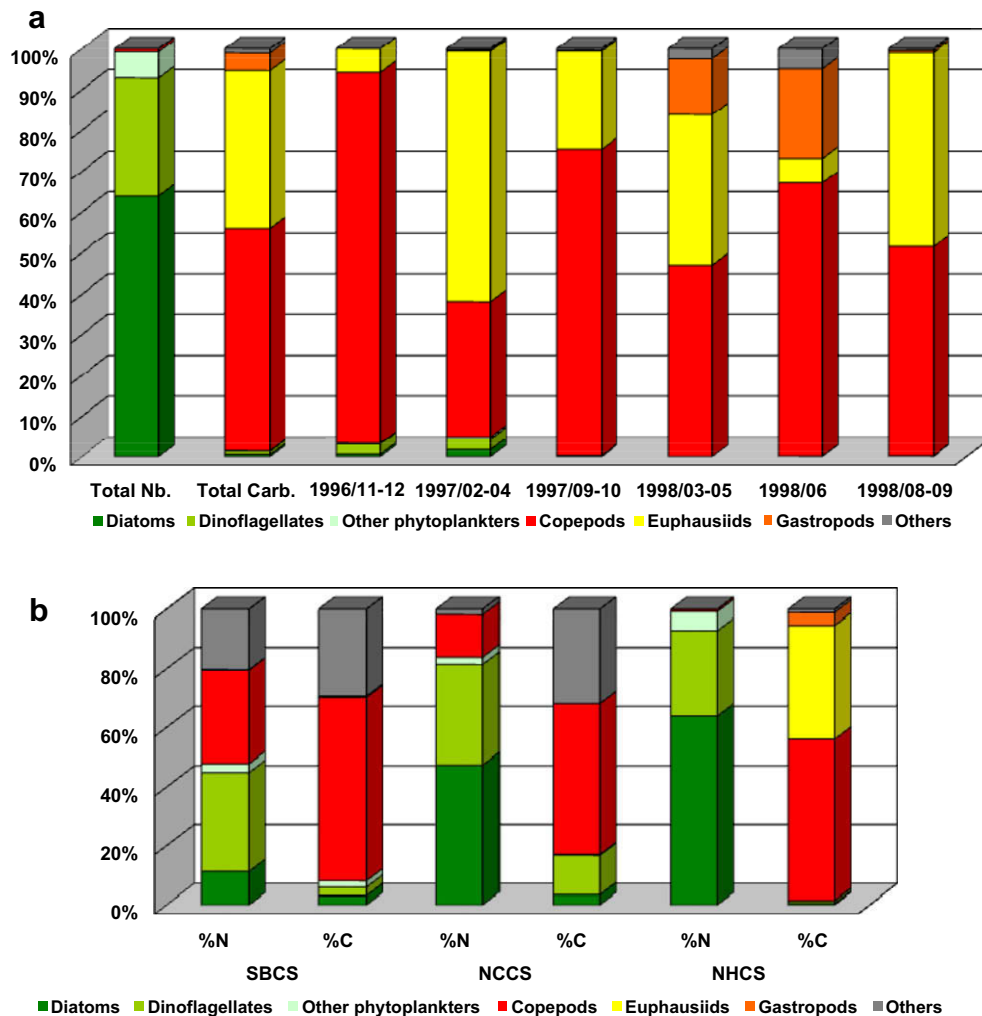


Fig. 1. (a) Percentage contribution of diatoms, dinoflagellates, other phytoplankters, copepods, euphausiids, gastropods and other zooplankters, by number (Total Nb.) and by contribution to dietary carbon (Total Carb.) for (a) the pooled sardine stomach content data (two left histograms), and for each of the 6 surveys from which sardine stomach contents were analyzed off Peru (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), and (b) by number (%N) and by contribution to dietary carbon (%C) for *Sardinops sagax* in the Southern Benguela current system (SBCS), *Sardina pilchardus* in the Northern Canary current system (NCCS), and *S. sagax* in the Northern Humboldt Current system (NHCS).

de Benites et al., 1985; Alamo and Bouchon, 1987), and indicated that sardines depend mainly on phytoplankton with zooplankton only occasionally being important. Konchina's (1991) paper was unique in mentioning that zooplankton was by far the most important dietary component for sardine and anchoveta off Peru. However, his study was based on a relatively small sample size and was not fully recognised in Peru. The present study corroborates Konchina's (1991) results, and clearly shows that in the NHCS sardine derives the bulk of its diet from zooplankton, as is the case for anchoveta (Espinoza and Bertrand, 2008). This result is in agreement with results from other studies (see review by van der Linde et al., 2009) on *S. sagax* diet in the SBCS (van der Linde, 2002) and in the CalCS (Parr, 1930; Emmett et al., 2005; McFarlane et al., 2005), as well as with results for the Iberian sardine *Sardina pilchardus* off Portugal (Garrido et al., 2008). Given that our sampling had limited spatial and temporal coverage, we cannot conclude that this characterization of the diet of sardine off Peru we obtained is perfectly representative of its diet during different periods, e.g. when sardine was more abundant in the system (mid 1970s to the beginning of the 1990s). Additionally, the fact that most of our data were collected during the El Niño of 1997–98 could also impact our dietary characterization, as El Niño events

are known to alter the food web towards a higher dominance of pico- and nanophytoplankton (e.g. Iriarte and González, 2004). The impact of El Niño on the food web and on fish diet has been observed in other cases (e.g., Brodeur and Pearcy, 1992; Arntz and Fahrbach, 1996), although Espinoza and Bertrand (2008) did not observe differences in anchoveta diet during the El Niño of 1997–98 compared to other, non-El Niño periods. This may be due to the fact that during the El Niño of 1997–98 local upwelling cells in the NCCS were strong enough to avoid food limitation for secondary producers (Bertrand et al., 2004). Furthermore, in an analysis of a 35-year time series of zooplankton volume, Ayón et al. (2004) could not relate the variability in zooplankton biomass to El Niño events.

4.2. Diet comparison

The diets of sardine and anchoveta in the NHCS are broadly similar and in both species are dominated by copepods and euphausiids, although in different proportions (Fig. 2). A second difference is related to dinoflagellates, that are consumed noticeably only by sardine. The apparent similarity in the diet of sardine and anchoveta is puzzling, since these species have very different feeding

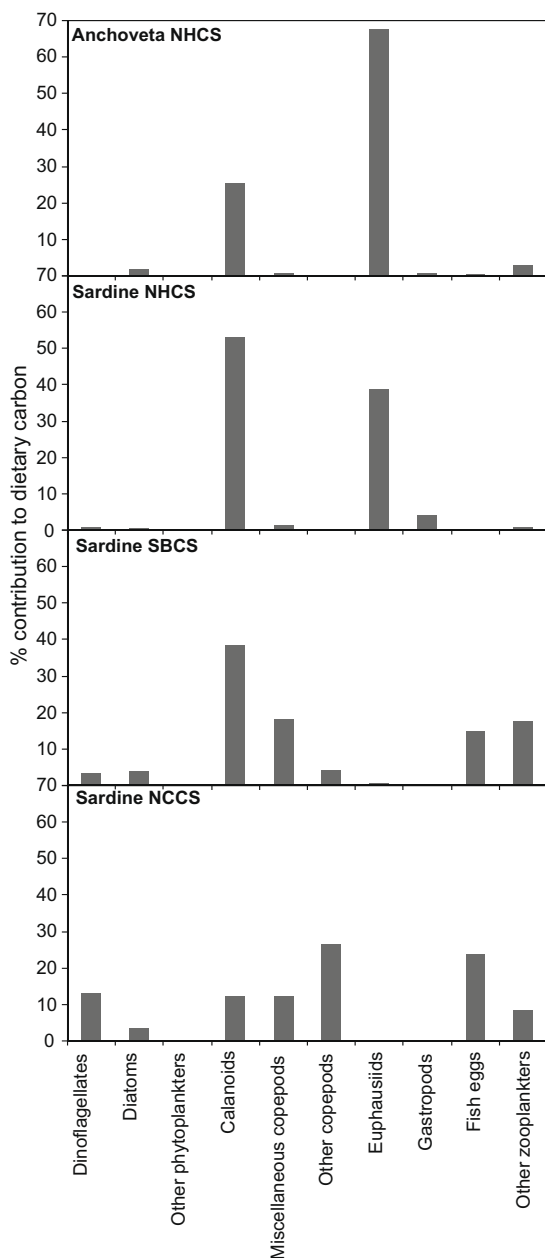


Fig. 2. Average percentage contribution to dietary carbon (%) by prey category for *Engraulis ringens* and *Sardinops sagax* in the Northern Humboldt Current system, *S. sagax* in the Southern Benguela system, and *Sardina pilchardus* in the Northern Canary Current system.

capabilities and foraging behaviours, at least in the SBCS (van der Lingen et al., 2006). However, when sardine diet is compared between systems, important differences appear, even if zooplankton is always by far the most important dietary component (Figs. 1 and 2). Copepods are always the dominant prey item, but whereas calanoids are by far the most important copepod in the diet of sardine in the NHCS, they represent less than 40% in sardine from the SBCS and only 12.2% in those from the NCCS (Fig. 2). The contribution to sardine dietary carbon made by phytoplankton appears to be negligible (<2%) in the NHCS, and ranges between 7% and 17% in the other systems. Most of the samples from the NHCS were collected during the El Niño of 1997–98, which could have biased our results toward an underestimation of the phytoplankton fraction (note that the number of samples is also rather low in the case of the other systems), although even before El Niño the phytoplankton

fraction accounted for less than 5% of sardine diet (i.e. less than in other systems). Finally, fish eggs are important prey items of sardine in the NCCS and SBCS, but apparently not in the NHCS. However, sardine in the NHCS have been observed to forage on fish eggs, with Santander et al. (1983) reporting an average of 16 anchoveta eggs in each sardine stomach for fish collected during August–September 1981, and the differences between that and our study likely reflect sampling limitations.

The differences in prey composition observed between sardine and anchovy and also between sardine from the three systems are related to marked differences in the modal sizes of ingested prey (Fig. 3). Within the NHCS, sardine and anchoveta forage principally on large items. This is particularly true for anchoveta, for which prey larger or equal to 8 mm contribute 70.9% of dietary carbon. Sardine in the NHCS derive the majority of their dietary carbon from items larger than 4 mm, and it is interesting to note that euphausiids observed in sardine stomachs were smaller (~8 mm) than those typically seen in anchoveta stomach contents (~12 mm). Also interesting is the difference in modal prey size of sardine diet between systems. If we take into account our results (Fig. 3) and published studies from the CalCS (e.g. Emmett et al., 2005; McFarlane et al., 2005; Miller and Brodeur, 2007; van der Lingen et al., 2009), we can rank the size of sardine prey between systems in the following order: Canary < Benguela < California and Humboldt.

In the NCCS most of the sardine dietary carbon comes from small copepods, fish eggs and phytoplankton that are <2 mm and have a mode of <0.5 mm. The main prey of sardine in the SBCS (calanoid and cyclopoid copepods and fish eggs) are also <2 mm and have a mode between 1 and 2 mm. Finally it is only in the Humboldt and California systems that large prey, in particular euphausiids, are important in sardine diet. Therefore, it seems that in the NHCS sardine are possibly not primarily non-selective filter-feeders as in the SBCS (see van der Lingen, 2002; van der Lingen et al., 2006) and probably in the NCCS (Garrido et al., 2007), possibly due to local adaptations to different environments. More detailed research on sardine and anchoveta feeding behaviour should be performed in the future.

The main difference in sardine prey composition between systems is related to the euphausiids, that are absent from sardine stomach contents in the eastern Atlantic (NCCS and SBCS) but are important in the eastern Pacific (NHCS, this study; and CalCS, Emmett et al., 2005; McFarlane et al., 2005; Miller and Brodeur, 2007). This is a crucial finding because large prey such as euphausiids have a very high energy content per individual, which may favour or accelerate pelagic fish growth. In the Atlantic, euphausiids are less available to sardines, and fish eggs may supplant euphausiids in sardine diet, at least to a degree. We assume that the importance of euphausiids for sardine diet in the eastern Pacific is due to a higher availability of these organisms, attributable to a narrower shelf compared with Canary and Benguela systems. In the NHCS for instance, the rich, cold coastal waters can extend far away from the shelf when the upwelling is strong. This allows the coastal community, including small pelagic fish, to extend their range of distribution far away from the shelf (Swartzman et al., 2008) and hence have access to the offshore vertically migrating communities, in particular the euphausiids. As stated by Espinoza and Bertrand (2008), a strong connection between the coastal and the offshore pelagic ecosystems may allow sardine and anchoveta to gain access to high energy prey such as euphausiids, which is likely one of the reasons for the high fish productivity of the NHCS (see Espinoza and Bertrand, 2008) compared to other systems (see Hutchings, 1992; Chavez et al., 2008).

Local and seasonal changes in food composition are high in all systems, reflecting the impact of environmental dynamics on the specific composition of prey patches (Konchina, 1991). Gregarious

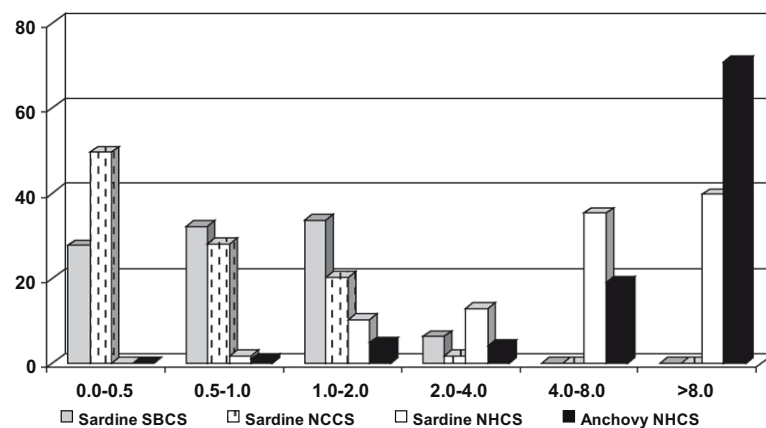


Fig. 3. Average percentage contribution to dietary carbon (%C) by prey size class (mm) for *Sardinops sagax* in the Southern Benguela system, *Sardina pilchardus* in the Northern Canary system (Iberian coast), and *S. sagax* (sard) and *Engraulis ringens* (anch) in the Northern Humboldt system.

fish such as sardine and anchovy are sensitive to processes (in particular patchiness) occurring at a continuum of spatial scales from the individual (dm) to populations (100s km) (Fréon et al., 2005; Bertrand et al., 2008). They exhibit a highly flexible feeding behaviour and can shift between filter or particulate feeding according to the available prey (van der Lingen, 2002; Garrido et al., 2007), and this opportunistic foraging behaviour allows them to cope with variability in the conditions they meet.

4.3. Summary

Our characterization of the diet of sardine in the NHCS based on prey carbon contents has shown that the diet of sardine off Peru is based primarily on zooplankton, similar to that observed for anchoveta *Engraulis ringens* (Espinoza and Bertrand, 2008), but with several important differences. Firstly, sardine feed on smaller zooplankton (smaller copepods and fewer euphausiids) than does anchoveta. Secondly, whilst phytoplankton represents <2% of sardine dietary carbon, this fraction is dominated by dinoflagellates, whereas diatoms are the dominant phytoplankton consumed by anchoveta. Hence, trophic competition between sardine and anchovy in the NHCS is minimized by their partitioning of the zooplankton food resource based on prey size, as has been reported in other systems (van der Lingen et al., 2009). Sardine in the NHCS (this study) and in the CalCS (Emmett et al., 2005; McFarlane et al., 2005; Miller and Brodeur, 2007) forage on larger prey and obtain a substantial portion of their dietary carbon from euphausiids, compared to those from the NCCS and SBCS. We relate this difference to the narrower shelf in the eastern Pacific compared with the eastern Atlantic that allows clupeids to distribute over the shelf break and in offshore areas where euphausiids are abundant. Euphausiids have a high energetic content, which may favour fish growth relative to when feeding on other prey types. Additionally, the high availability of euphausiids in the eastern Pacific may limit sardine predation on fish eggs, which is very high in the NCCS and the SBCS compared with the NHCS. These last two points are probably key factors explaining the secret of the fish productivity in the NHCS. Finally our results provide an opportunity to re-examine the hypothesis of Ryther (1969) who attributed the high abundance of small pelagic fish in upwelling systems to their ability to feed directly on phytoplankton and hence benefit from a very short and efficient food chain. This theory based on phytophagy was questioned decades ago in other systems (Cushing, 1978; James, 1987) but was still considered to be the case off Peru. The 'Peruvian short food chain' hypothesis has now been discredited (this study; Konchina, 1991; Espinoza and Bertrand, 2008; van der Lingen et al.,

2009). Off Peru, anchoveta and sardine not only forage mainly on zooplankton but select large, energetically-rich zooplankters. This indicates that the energy transfer from primary production to fish through zooplankton is particularly efficient, and that the zooplankton biomass is higher than supposed. Recent estimates of zooplankton biomass, based on acoustic methods, seem to confirm the presence of high biomass of macro-zooplankton off Peru (M. Ballón, IMARPE unpublished data), but more research in this field is crucial.

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