

Diet variability in European anchovy: a comparative analysis between larval populations of the inner Bay of Biscay and the NW Mediterranean

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Abstract Feeding is critical for larval survival and it becomes a determining factor in the annual recruitment in species such as European anchovy *Engraulis encrasicolus*. Additionally, since differences in the plankton community may affect the larval feeding patterns, an interregional comparative study may contribute to understand these patterns concerning larval development and environmental features. The diet, feeding pattern and prey selectivity in relation to the ontogeny of the larval anchovy in the Cantabrian Sea (inner Bay of Biscay) and the Catalan Sea (NW Mediterranean) were compared in this study. Larvae

fed preferentially on copepod eggs, nauplii and calanoid postnauplii, selecting them actively. Larval diet was similar before notochord flexion in the two areas. Nonetheless, for larvae of comparable size, prey preferences skewed towards small preys in the Cantabrian Sea, and towards large preys in the Catalan Sea. Differences appeared in the middle-sized larvae (6.5–9 mm) due to prey size and type. Diet differences were attributable (a) to the ability of the Catalan Sea larvae to capture bigger preys at a smaller individual size; and (b) to differences in prey preferences and availability. Therefore, geographic variety in larval populations and food environment features may promote variability in the larval anchovy diet.

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Introduction

European anchovy *Engraulis encrasicolus* L. 1758 is a relevant fishery resource both in the Bay of Biscay (Uriarte et al., 1996; Arregi et al., 2004) and the Western Mediterranean (Pertierra & Leonart, 1996; Palomera et al., 2007). The dynamics of small pelagic fish populations such as anchovy is strongly influenced by environmental variability since changes in habitat conditions affect the survival of the early stages and thus, the recruitment success (Bailey & Houde, 1989;

Cury & Roy, 1989; Cushing, 1990; Palomera et al., 2007). It has also been found that feeding is a key factor affecting larval mortality (May, 1974; Cushing, 1990; Dickmann et al., 2007). Furthermore, the variability in mortality rates of larval populations and the strength of the annual recruitment are linked to larval feeding (Hjort, 1926). It is well known that European anchovy larvae feed on plankton (Tudela & Palomera, 1997; Conway et al., 1998; Tudela et al., 2002; Catalán et al., 2010; Morote et al., 2010), so we can expect that differences in the plankton community may affect their feeding patterns. Although the feeding strategies of fish larvae are complex (Iles & Sinclair, 1982), factors such as their morphological and physiological characteristics play an important role in the feeding behaviour (Sánchez-Velasco, 1998). Therefore, it becomes necessary to know the feeding behaviour of larvae to understand the factors that affect their mortality in the natural environment (Last, 1980).

Provided that almost all marine fish larvae are diurnal plankton visual hunters and that they feed mainly on copepods in different developmental stages (Arthur, 1976; Hunter, 1980), the temporal coupling of zooplankton production and fish larvae peak abundance appears to be a main factor of recruitment variability (Cushing, 1990; Fox et al., 1999; Yasue et al., 2010; Arula et al., 2012). In the case of the European anchovy, feeding ecology of larvae has been studied in depth in the Mediterranean (Bulgakova, 1993; Conway et al., 1998; Tudela et al., 2002; Palomera et al., 2007; Borme et al., 2009; Catalán et al., 2010; Morote et al., 2010; Costalago et al., 2012) and in the North and the Baltic seas (Raab et al., 2011). Even though several studies have been carried out to unravel other aspects of the recruitment of this species in this area, such as those related to the distribution and growth (Irigoiien et al., 2007, 2008; Cotano et al., 2008; Urtizberea et al., 2008; Aldanondo et al., 2010; Urtizberea & Fiksen, 2013), the nutritional condition (Díaz et al., 2007, 2008; Bergeron, 2009), the environmental conditioning (Borja et al., 1996, 2008) or juvenile and adult feeding ecology (Plounevez & Champalbert, 1999, 2000; Bachiller & Irigoien, 2012; Bachiller et al., 2012; Chouvelon et al., 2014), no information on the feeding ecology of anchovy larvae from the Bay of Biscay has been published before.

The comparative method is a very useful tool to identify factors that shape the life history of the species

under study and to investigate these factors quantitatively (Brander, 1994). The interregional comparative study on fishes arises from the interest of providing a framework to systematize the fragmentary information in order to establish generalizations about the impact of various environmental variables (e.g. Costalago et al., 2015). Furthermore, the detection of relationships that might not be as strong as others can gain relevance if they are observed in different environments (Bakun, 1985). This may help us understand the relationship between these populations and the environmental variables which are often difficult to study experimentally (Bakun & Parrish, 1982).

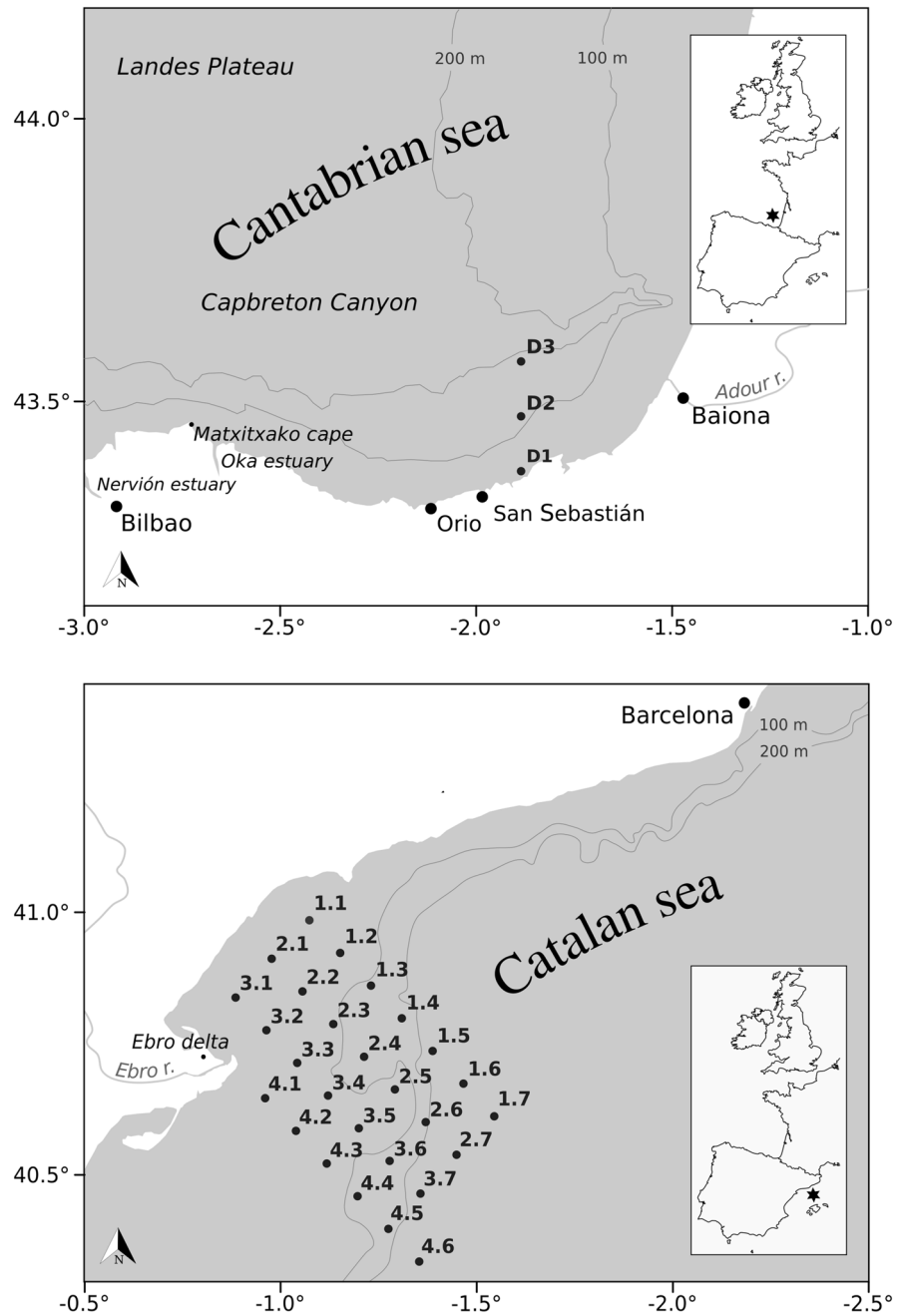
The aim of this study was to give a comparative insight of the trophic dynamics between the larval anchovy populations from the Cantabrian Sea (inner Bay of Biscay) and those from the Catalan Sea (NW Mediterranean) in relation to larval size and developmental stage linked to notochord flexion, so as to contribute to the understanding of the evolution of this species. This was based on the hypothesis that anchovy larvae feeding pattern changes with the ontogeny but presents differences arising from local contrasting environmental conditions. Therefore, comparisons of diet, niche breadth and selectivity patterns in relation to prey availability between the larval populations of the two contrasting areas aim to gather evidence of population distinction that might suggest ecotypical differentiation due to non-homogeneous environmental conditions.

Materials and methods

Study area and sampling

European anchovy larvae and zooplankton samples were collected in the eastern Cantabrian Sea (Inner Bay of Biscay) and in the Catalan Sea (NW Mediterranean Sea). In the Cantabrian Sea, four cruises were conducted in May, June and July of 2000 and June of 2001, coinciding approximately with the spawning peak of the anchovy which occurs between May and June (Motos et al., 1996, 2004). Sampling was carried out at three stations which were 6 nm apart from each other along a single cross-shelf transect (Fig. 1). In the Catalan Sea, three cruises were conducted in June and July of 2003 coinciding with the summer spawning

Fig. 1 Location of the sampling stations for each study area: the Cantabrian Sea (*top*) and the Catalan Sea (*bottom*)



peak in this region (Palomera, 1992; Palomera et al., 2007). Sampling was carried out in a grid of 27 stations, sorted out into 4 cross-shelf transects separated approximately 6 nm from each other (Fig. 1).

Zooplankton was sampled in vertical hauls using a Calvet net with 20 and 200 μm mesh sizes. These hauls were also performed above the thermocline at

depths ranging from 43 to 117 m in the Cantabrian Sea and 42–170 m in the Catalan Sea. The $>20 \mu\text{m}$ sample was filtered through a 200- μm mesh and the $>200 \mu\text{m}$ sample through a 2-mm mesh before preserving them in 5% buffered formalin. Anchovy larvae were sampled in oblique hauls using a 40-cm-diameter Bongo net with a 335- μm mesh size. The volume of

filtered seawater was measured using a flowmeter placed in the mouth of each net. All tows were carried out at a speed of 2 km during daytime and above the thermocline in order to maximize the catch of feeding anchovy larvae (Conway et al., 1998). The thermocline was previously determined at each station by a CTD cast. Sampling depths ranged from 34 to 117 m in the Cantabrian Sea and 42 to 170 m in the Catalan Sea. The whole sample was preserved in 5% buffered formalin for further manipulation in the laboratory.

Laboratory analysis

Microplankton and mesozooplankton were identified and counted from stations where anchovy larvae containing preys were found. The analysis was carried out using a stereoscopic microscope by diluting each sample to 100 ml and by taking aliquots for counting up to 100 individuals of the most abundant taxon and at least 50 individuals of the next one. Identification was made to the lowest possible taxonomic category.

Anchovy larvae were randomly selected from the Bongo samples. Standard length (SL) and jaw width (JW) were measured to the nearest 0.01 mm using an inverted microscope and a micro-ruler. The entire gut was removed and put in a 50%-glycerine-water drop for manipulation. The gut was longitudinally dissected and preys extracted and identified to the lowest possible taxonomic category. The length and maximum width of each prey was also measured to the nearest 0.025 mm by mean of a micro-ruler.

Data analysis

In order to provide a wider view of the available zooplankton, the densities obtained for each group in the two size fractions from a given sampling station were added up and averaged for all the sampling stations in each study area.

The relationship between the number of ingested preys and the larval SL, as well as the prey width and larval SL and JW, was studied using regression analysis.

The trophic niche breadth was calculated following Pearre (1986), and larvae were classified into size classes containing at least 3 prey items. Thus, the standard deviation (SD) of log-transformed prey size in each size class was taken as a measure of the trophic niche breadth.

Diet analysis was performed for three different size classes (larvae < 6.5 mm SL, larvae between 6.5 and 9 mm SL, and larvae > 9 mm SL) and also for two different developmental stages depending on their notochord flexion (preflexion stage and postflexion stage). Since flexion in anchovy larvae from the Catalan Sea has been reported to occur between 6.6 and 8.9 mm (Maynou et al., 2008; Morote et al., 2010), the average flexion length was set at 7.7 mm to differentiate prefixion larvae and postflexion larvae in the larval assemblage of the Catalan Sea. For anchovy larvae from the Southern North Atlantic, flexion has been reported to occur between 9 and 10 mm (Ré, 1986), thus in this case, the average flexion length was set at 9.5 mm to differentiate prefixion larvae and postflexion larvae in the larval assemblage of the Cantabrian Sea.

Diet was described using an index of relative importance (IRI), calculated as the product of the percent frequency of occurrence (%F) of a prey item in the guts of the larvae and the percentage of the total number (%N) of prey items examined (Sassa & Kawaguchi, 2004). Shannon (1948) diversity index (H') was also calculated for ingested preys.

Prey selectivity was quantified using Cheeson's (1978) α index as

$$\alpha_i = (r_i p_i^{-1}) \left(\sum_{j=1}^m r_j p_j^{-1} \right)^{-1}$$

where r_i and p_i are the proportion of an i prey item in the larval diet and the larval habitat, respectively. α values range between 0 and 1 and deviate asymmetrically from the reciprocal of the available (considered) m prey items. Lower values would indicate rejection and higher values would indicate selection. In our study, 10 available prey groups were considered, therefore α 's critical value was set as 1/10.

PCA ordination analyses were performed for IRI values obtained for each prey group in all size classes and flexion stages using CANOCO 4.5.

When necessary, differences between datasets were statistically tested performing t-tests, Mann–Whitney U (M–W U) tests or ANOVAs in SPSS 17 and comparisons between regression lines' intercepts and slopes were tested performing ANCOVA using R software.

Results

Zooplankton availability

The availability of zooplankton groups present in anchovy larvae diet in the Catalan Sea and the Cantabrian Sea is presented in Table 1. The dinoflagellates of the order Peridinales were much more abundant and contributed in a much higher percentage (M–W U , $P < 0.0001$) in the Cantabrian Sea than in the Catalan Sea. In contrast, the cladocerans *Evadne* spp. and *Podon* spp. were the only prey that showed a higher density (M–W U , $P < 0.0047$) and a much higher contribution percentage (M–W U , $P < 0.0001$) in the Catalan Sea than in the Cantabrian Sea. Although the highest density values of the cladocerans *Evadne* spp. and *Podon* spp. were recorded occasionally in this last area, these types of preys were absent in most of the cases in which anchovy larvae with ingested preys were found in the Cantabrian Sea, whereas they were present in most of the cases analysed for the Catalan Sea. Copepod eggs and copepod nauplii showed rather similar densities in both areas but a significantly higher percentage contribution in the Catalan Sea (M–W U , $P < 0.0001$). Similarly, the percentage contributions of harpacticoid postnauplii (M–W U , $P < 0.0001$), calanoid postnauplii (M–W U , $p = 0.0350$) and the cladoceran *Penilia* spp. (M–W U , $P = 0.0047$) were also significantly higher in the Catalan Sea, although density differences were not significant.

Feeding incidence, prey number and size, and niche breadth

Gut content analysis was carried out on 244 larvae from the Cantabrian Sea (larvae containing prey ranging from 3.75 to 16.6 mm) and 318 larvae from the Catalan Sea (larvae containing prey ranging from 2.75 to 16.875 mm). The number of prey in the Cantabrian Sea larvae (average of 1.22 ± 0.599) was significantly lower (t test, $P < 0.01$) than in the Catalan Sea larvae (average of 1.71 ± 1.64), but there was no correlation between increased length of the larvae and prey number in any of the study areas.

The average prey size (measured as maximum width) of Cantabrian Sea larvae ($97.33 \mu\text{m} \pm 53.96$) was significantly (t test, $P < 0.001$) smaller than that of the Catalan Sea larvae ($196.58 \mu\text{m} \pm 96.67$). Prey

size increased significantly with length of larvae (both as SL and JW) in both study areas (Fig. 2a, b) but this trend appeared to be greater in the Catalan Sea larvae, with a significantly higher slope and intercept for SL (ANCOVA, $P < 0.001$) and a significantly higher intercept for JW (ANCOVA, $P < 0.001$). However, larger anchovy larvae also ate small preys. Differences in prey size between larval size classes were significant both in the Cantabrian Sea (ANOVA, $P = 0.002$) and in the Catalan Sea (ANOVA, $P < 0.0001$), while differences in prey size between preflexion and postflexion stages were only significant in the Catalan Sea (ANOVA, $P < 0.0001$) (Fig. 3). Differences between study areas in prey size were only significant for medium size, large size and postflexion larvae (Fig. 3).

Niche breadth analysis was performed with 88 larvae from the Cantabrian Sea and 187 larvae from the Catalan Sea containing preys in their guts. Cantabrian Sea larvae widened significantly their trophic niche breadth as a function of their SL. In contrast, Catalan Sea larvae did not show any significant pattern but a slight trend to narrow their niche breadth with their SL (Fig. 4).

Diet composition and diversity

The number of different prey groups observed in the Catalan Sea larval diet was higher (9) than in the Cantabrian Sea larval diet (7) and the Shannon diversity index was also higher for taxa in the diet of Catalan Sea larvae than in the diet of those from the Cantabrian Sea (Table 2).

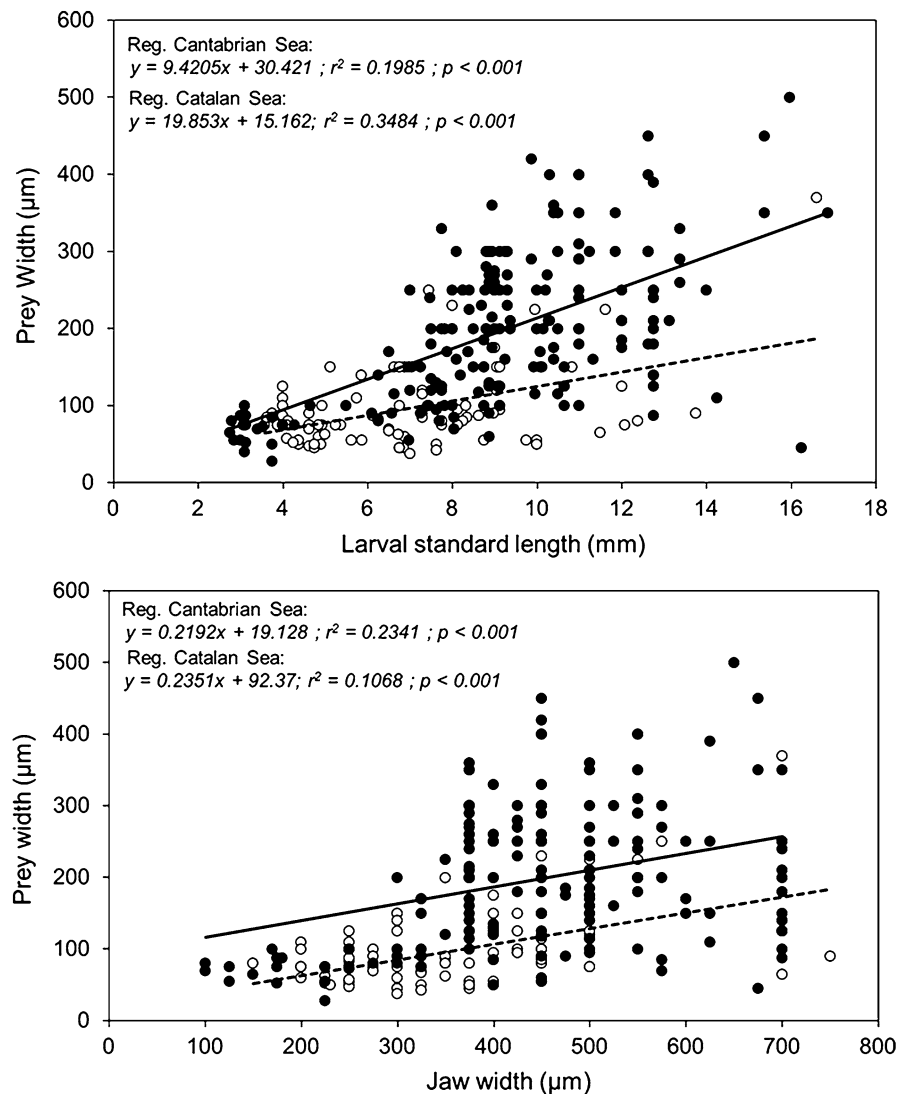
The diet composition showed some differences between sites, larval sizes and flexion stages (Tables 2, 3). The main prey groups for the smallest larvae were the same in the two study areas, i.e. copepod eggs and copepod nauplii. These two groups accounted for >60% of the ingested prey in both areas. However, for the medium-sized larvae, the main groups were copepod nauplii followed by calanoid postnauplii and copepod eggs, and cyclopoid postnauplii in the Cantabrian Sea. In this study area in relation to this larval size, copepod nauplii and postnauplii accounted for ca. 40% and 25% of ingested prey respectively. For the medium-sized larvae from Catalan Sea, however, calanoid postnauplii were the most important prey group followed by copepod nauplii, and the cladocerans *Evadne* spp.

Table 1 Differences between the study areas in density (ind m⁻³) and relative abundance (percentage in the zooplankton assemblage) of the zooplankton groups present in the larval diet

	Peridimiales	Tintinnids	Copepod eggs	Copepod nauplii	Calanoid postnauplii	Cyclopoid postnauplii	Harpacticoid postnauplii	Poecilostomatoid postnauplii	<i>Evadne-Podon</i>	<i>Penilia</i>
Density (ind m⁻³)										
Cantabrian Sea										
Max.	46,593.49	2,385.50	10,773.65	15,759.68	5,898.17	5,511.09	1,465.15	3,565.15	1,169.14	209.54
Min.	1,179.53	0	460.14	1,369.61	61.46	22.90	0	0	0	0
Average	16,703.41	524.85	4,654.18	5,720.79	1,765.96	1,594.17	285.00	805.63	139.73	26.42
SD	16,127.17	830.56	4,129.99	4,647.37	1,920.91	2,121.41	478.33	1,333.41	386.47	69.01
Catalan Sea										
Max.	1,874.20	2,285.71	13,226.38	6,327.99	1,491.71	1,380.83	472.12	338.44	723.36	275.88
Min.	134.45	23.77	912.47	1,153.34	96.47	67.84	44.74	11.98	21.30	0
Average	708.05	263.68	4,923.21	3,105.23	561.58	324.04	211.56	70.37	160.05	54.08
SD	505.18	514.31	3,480.63	1,576.42	374.23	291.96	131.09	72.38	178.45	78.43
M-W U	<0.0001	0.6807	0.5715	0.1358	0.0803	0.3545	0.217	0.217	0.0047	0.0641
<i>P</i>										
Relative importance (%)										
Cantabrian Sea										
Max.	35.23	2.27	8.31	14.55	3.28	3.81	0.66	2.42	0.44	0.20
Min.	4.25	0	1.19	2.55	0.05	0.02	0	0	0	0
Average	15.32	0.40	4.33	7.09	1.99	1.42	0.23	0.66	0.06	0.02
SD	9.56	0.73	2.68	4.43	1.20	1.38	0.24	0.82	0.14	0.07
Catalan Sea										
Max.	8.83	16.57	51.56	40.18	9.11	15.57	2.65	1.80	4.05	2.26
Min	0.97	0.33	13.52	9.52	1.11	0.76	0.32	0.07	0.12	0
Average	4.82	1.82	31.08	21.87	3.95	2.51	1.45	0.53	1.18	0.50
SD	2.34	3.72	11.63	6.75	2.21	3.30	0.63	0.44	1.21	0.74
M-W U	0.0001	0.2698	<0.0001	<0.0001	0.0203	0.3551	<0.0001	0.5894	0.0118	0.0679
<i>P</i>										

Significant ($P < 0.05$) differences have been shown in bold

Fig. 2 Relationship between the larval SL (mm) and the PW (μm) (a) and between the larval JW (μm) and PW (μm) (b) with their corresponding regression lines for the Cantabrian Sea (open circles and dashed lines) and the Catalan Sea (closed circles and continuous line). Regression equations, r^2 values and when significant, P values have also been shown



and *Podon* spp. Different copepod postnauplii accounted for over 45% of the ingested prey and copepod nauplii and total cladocerans each for about 20% in this study area in relation to larval size. For large-sized larvae, copepod eggs were the most important group (45% of the ingested prey) followed by calanoid postnauplii (ca. 32% of ingested prey) and copepod nauplii (ca. 20% of ingested prey) in the Cantabrian Sea, whereas in the Catalan Sea, calanoid postnauplii were the most important prey group (21% of ingested prey) followed by the group of cladocerans *Evadne* spp. and *Podon* spp. (20% of ingested prey), and less importantly by copepod nauplii and the cladoceran *Penilia* spp.

If data are analysed by flexion stages (Table 3), we can see that copepod nauplii were the main prey group for preflexion larvae in both study areas, followed by either copepod eggs or calanoid postnauplii. Copepod eggs and nauplii constituted more than 50% of the ingested prey of preflexion larvae in both areas. For the postflexion larvae, however, larger differences were identified between sites. In the Cantabrian Sea, copepod eggs were found to be the most important group and formed the majority followed by copepod nauplii and copepod postnauplii, with copepod eggs together with copepod nauplii constituting >75% of ingested prey. In the Catalan Sea, calanoid postnauplii were the most important prey group followed by the

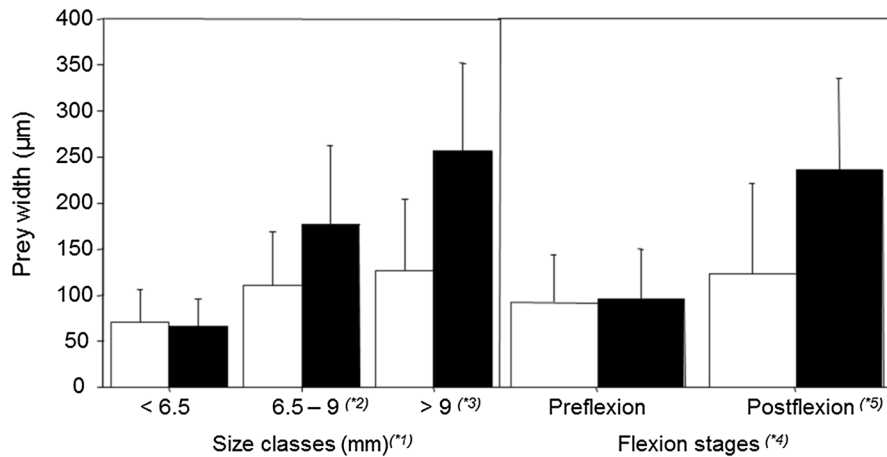
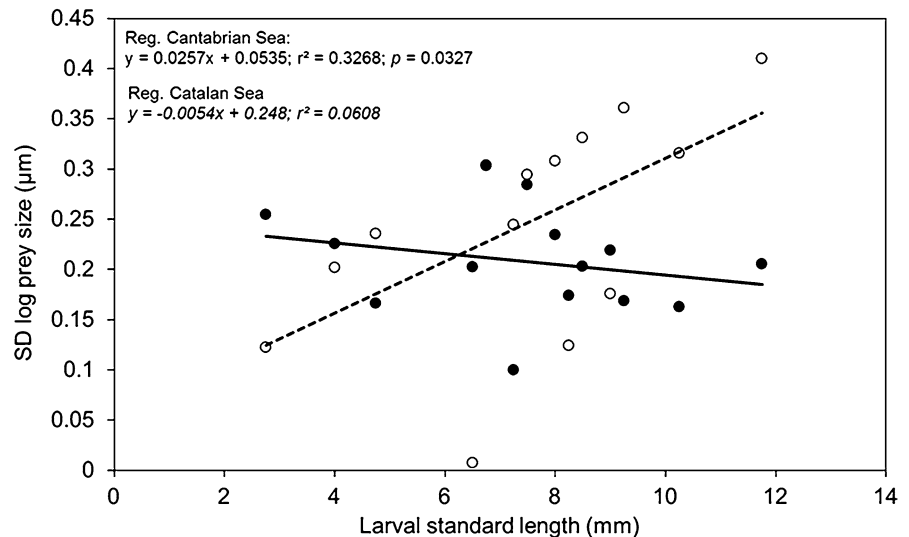


Fig. 3 Average and standard deviations of PW (µm) in each size class and flexion stage for the Cantabrian Sea (white bars) and the Catalan Sea (black bars) larvae. Significant differences were found between size classes in both study areas (*1), and

between the study areas in the medium-sized (*2) and large-sized larvae (*3). Significant differences were also found between flexion stages in the Catalan Sea (*4) and between study areas in the postflexion stage (*5)

Fig. 4 Relationship between anchovy larvae SL and trophic niche breadth in the Cantabrian Sea and the Catalan Sea. Symbols and lines are as in Fig. 2



cladocerans *Evadne* spp. and *Podon* spp. and copepod nauplii—the sum of the first two groups accounting for >50% of ingested prey with copepod eggs reaching <20%.

Accordingly, PCA performed with the IRI values showed the first axis separating postflexion stage larvae, larvae ≥ 9 mm of the Cantabrian Sea and copepod eggs, from the other larvae and prey groups (Fig. 5). The second axis mainly separated the smallest size class of the Catalan Sea, associated to copepod nauplii, from the other two size classes and the postflexion stage from the same area, these being

associated to calanoid and harpacticoid postnauplii and cladocerans. The preflexion stages of both the Cantabrian Sea and the Catalan Sea, and the smallest and the medium size classes of the Cantabrian Sea appeared nearby in the space (Fig. 5).

Prey selectivity

Prey selectivity patterns were detected both for the different larval size classes (Table 4) as well as for the different flexion stages (Table 5) in the two study areas. In the Cantabrian Sea, the strongest preferences

Table 2 Larval diet composition of different size classes in the Cantabrian Sea and the Catalan Sea

Size class	<6.5 mm			6.5–9 mm			≥9 mm		
No. of larvae (total: 83)	34			16			33		
H' (total: 1.66)	1.28			1.83			1.17		
Taxa	%N	%F	%IRI	%N	%F	%IRI	%N	%F	%IRI
Cantabrian Sea									
Peridiniales				2.44	3.03	0.30			
Tintinnids				2.44	3.03	0.30			
Copepod eggs	32.69	47.06	44.08	12.20	15.15	7.46	45.45	56.25	66.67
Copepod nauplii	30.77	41.18	36.30	39.02	45.45	71.64	18.18	25.00	11.85
Calanoid postnauplii	7.69	11.76	2.59	12.20	15.15	7.46	31.82	25.00	20.74
Cyclopoid postnauplii				9.76	12.12	4.78			
Harpacticoid postnauplii				2.44	3.03	0.30			
Poecilostomatoid postnauplii									
<i>Evadne–Podon</i>									
<i>Penilia</i> sp.									
Crustacean parts				12.20	12.12	5.97			
Unidentified	28.85	20.59	17.02	7.32	6.06	1.79	4.55	6.25	0.74
Catalan Sea									
Peridiniales	5.56	8.70	1.52	1.37	2.08	0.12			
Tintinnids									
Copepod eggs	19.44	21.74	13.26	1.37	2.08	0.12	2.34	6.25	0.63
Copepod nauplii	41.67	56.52	73.86	21.92	33.33	29.84	14.06	25.00	15.22
Calanoid postnauplii	2.78	4.35	0.38	32.88	39.58	53.15	21.09	35.42	32.35
Cyclopoid postnauplii	2.78	4.35	0.38	6.85	6.25	1.75	3.91	10.42	1.76
Harpacticoid postnauplii				4.11	4.17	0.70	4.69	6.25	1.27
Poecilostomatoid postnauplii				2.74	4.17	0.47	3.13	8.33	1.13
<i>Evadne -Podon</i>				16.44	14.58	9.79	20.31	29.17	25.65
<i>Penilia</i> sp.				4.11	6.25	1.05	7.03	12.50	3.81
Crustacean parts	2.78	4.35	0.38	6.85	10.42	2.91	10.94	14.58	6.91
Unidentified	25.00	13.04	10.23	1.37	2.08	0.12	12.50	20.83	11.28

The index of relative importance (IRI) was calculated as the product of the percent of total prey number (%N) and the percent frequency of occurrence (%F) and presented as %IRI for a given prey group in each size class. Shannon–Weaver diversity index (H') of the diet has also been indicated

were for both copepod eggs and copepod nauplii in small-sized larvae, whereas the medium-sized larvae showed a preferential selection for copepod nauplii and a lower one for copepod eggs. However, the

highest selection was for copepod eggs in large-sized larvae. Analysis based on flexion stages showed that preflexion and postflexion larvae selected the same prey groups (i.e. copepod eggs, copepod nauplii and

Table 3 Larval diet composition of different flexion stages for the two study areas

Study area	Cantabrian Sea						Catalan Sea					
	Preflexion			Postflexion			Preflexion			Postflexion		
No. of larvae	71			12			41			78		
H'	1.70			1.12			1.85			2.05		
Taxa	%N	%F	%IRI	%N	%F	%IRI	%N	%F	%IRI	%N	%F	%IRI
<i>Peridinales</i>	0.99	1.41	0.05				5.26	7.32	1.55			
Tintinnids	0.99	1.41	0.05									
Copepod eggs	23.76	32.39	29.10	57.14	58.33	80.00	12.28	12.20	6.02	2.22	5.13	0.49
Copepod nauplii	32.67	42.25	52.19	21.43	25.00	12.86	38.60	48.78	75.73	15.00	26.92	17.52
Calanoid postnauplii	13.86	15.49	8.12	14.29	16.67	5.71	12.28	17.07	8.43	25.00	38.46	41.72
Cyclopoid postnauplii	3.96	5.63	0.84				5.26	7.32	1.55	4.44	7.69	1.48
Harpacticoid postnauplii	0.99	1.41	0.05							5.00	6.41	1.39
Poecilostomatoid postnauplii							1.75	2.44	0.17	2.78	6.41	0.77
<i>Evadne–Podon</i>							1.75	2.44	0.17	20.56	25.64	22.87
<i>Penilia</i> sp.							1.75	2.44	0.17	6.11	10.26	2.72
Crustacean parts	4.95	5.63	1.05				5.26	7.32	1.55	9.44	12.82	5.25
Unidentified	17.82	12.68	8.54	7.14	8.33	1.43	15.79	7.32	4.65	9.44	14.10	5.78

The Shannon–Weaver diversity index (H') of the diet has also been indicated. Encoding information as in Table 2

calanoid postnauplii). However, copepod nauplii were the most strongly selected group in the preflexion stage, copepod eggs were preferentially selected in the postflexion stage. In the Catalan Sea, however, medium- and large-sized larvae actively ingested larger prey with a stronger selectivity than small-sized larvae did. The same pattern was evident when data were analysed by larval flexion stages. Thus, larvae in preflexion stage actively selected copepod eggs, copepod nauplii and calanoid postnauplii, with the strongest selection for copepod nauplii, whereas larvae in postflexion stage did not actively select copepod eggs, instead they selected copepod nauplii, calanoid postnauplii and the cladocerans *Evadne* spp. and *Podon* spp., with the highest preference for calanoid postnauplii.

Discussion

This study is relevant for two reasons: it is the first time that a description of the diet of larval anchovy in the Cantabrian Sea is published; in addition to this, it is the first time the diet of larval anchovy is compared for populations in the Cantabrian Sea and in the Catalan

Sea. The low number of larvae containing prey suggests a low feeding incidence for the two areas, in line with values reported in the literature for clupeiforms (Arthur, 1976; Munuera & Gonzalez-Quiros, 2007) and specifically for European anchovy larvae (Conway et al., 1998; Tudela et al., 2002; Morote et al., 2010). These recurrent low numbers of larvae containing preys have been related to capturing procedures: it could be that nets capture the weakest or malnourished larvae, or that due to their straight stomach, stress of capture and handling leads to a greater tendency to regurgitation (Arthur, 1976; Conway et al., 1998) but other factors such as the preys that are not accounted for in the gut content analysis because they cannot be identified with regular analytical methods or because they are very easily digested, may bias our perception of the feeding incidence as well.

The average prey number per gut was similar to that reported for European anchovy larvae of similar size ranges by Morote et al. (2010), and Catalán et al. (2010) (1.7) or Tudela et al. (2002) (1.66), but higher values were also reported by Conway et al. (1998) (1.96–2.53). The low prey number per gut may be explained by an intermediate stage of gut

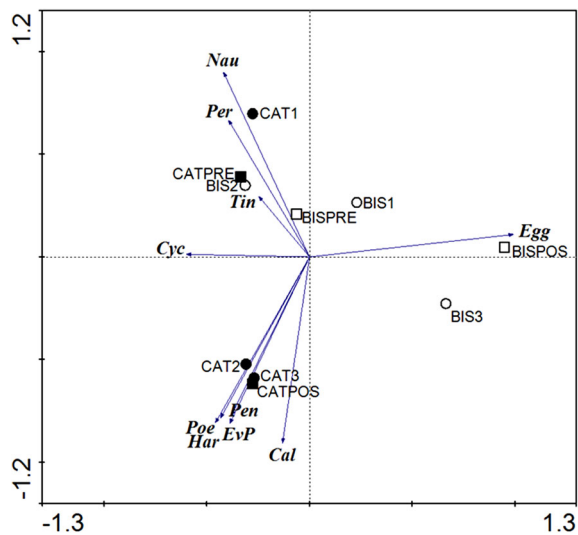


Fig. 5 PCA for the IRI values of the zooplankton groups present in the diet of all the larval size classes and flexion stages in each study area. The encoding is as follows: Zooplankton groups in italics: *Per* Peridinales, *Tin* tintinnids, *Egg* copepod eggs, *Nau* copepod nauplii, *Cal* calanoid postnauplii, *Cyc* cyclopoid postnauplii, *Har* harpacticoid postnauplii; *Poe* Poecilostomatoid postnauplii; *EvP* *Evadne* spp. and *Podon* spp., *Pen* *Penilia* spp. Larval size classes have been noted with circles and flexion stages with squares (open for Cantabrian Sea larvae and closed for Catalan Sea larvae). Labels for each data point are shown as follows: BIS1: larvae < 6.5 mm, BIS2: larvae between 6.5 and 9 mm, BIS3: larvae > 9 mm, BISPRE: preflexion larvae, BISPOS: postflexion larvae. Larval groups in the Catalan sea: CAT1: larvae < 6.5 mm, CAT2: larvae between 6.5 and 9 mm, CAT3: larvae > 9 mm, CATPRE: preflexion larvae, CATPOS: postflexion larvae

development, where a completely straight disposal makes smaller larvae very likely to expel their gut contents as a result of sampling trauma (Conway et al., 1998). The increase in the feeding incidence with anchovy larvae size reported in some other works (Islam & Tanaka, 2009; Catalán et al., 2010) may be due to the fact that larger larvae with further development of the digestive tract have a greater ability to retain the preys. Furthermore, the reduction of prey number with larval size has been related to the lack of suitable food when the larvae begin a more selective type of feeding (Ciechowski, 1967; Conway et al., 1998). However, the abundance of suitable preys found in the Cantabrian Sea and the Catalan Sea does not support the idea of prey scarcity for the Cantabrian Sea larvae, even more if we take into account that suitable prey abundances were lower in the Catalan Sea and no decrease in the number of preys with larvae

size was observed. Therefore, low prey number seems more likely to be related to the low number of larvae containing preys.

The increase in the size of the ingested prey with larvae length was found to be significantly higher in the Catalan Sea than in the Cantabrian Sea, both in terms of pattern (slope) and magnitude (intercept) for the SL. Taking into account (a) that notochord flexion is a key milestone in the ontogenetic process for anchovy larvae (Somarakis & Nikolioudakis, 2007, 2010) because the caudal fin and the subsequent structures develop to confer higher individual mobility; (b) that flexion occurs at smaller lengths in larval anchovies from the Catalan Sea than in those from the Cantabrian Sea (Maynou et al., 2008; Ré, 1986); and (c) that anchovy larvae are more robust after the flexion event (Bergeron, 2009), we could expect larvae of the Catalan Sea to capture larger or more motile preys than those of the Cantabrian Sea of similar size. However, even though the size of the largest prey in the diet increased significantly with larval size, large larvae continued eating also small prey items, in agreement with observations by Conway et al. (1998) for the Adriatic Sea, probably because these are easier to capture. Although it has commonly been reported that niche breadth does not change during larval development (Pearre, 1986; Sabatés & Saiz, 2000; Voss et al., 2003; Sassa & Kawaguchi, 2004), both increases (Pepin & Penney, 1997; Sassa, 2009) and decreases (Llopiz & Cowen, 2009) have been reported for some species and specifically for European anchovy larvae (Catalán et al., 2010). Our results showed some divergence, as niche breadth widened significantly in the Cantabrian Sea larvae but not in the Catalan Sea larvae, which reinforces the idea that niche breadth does not really change during the development of anchovy larvae. In addition, despite the significant increase in the amplitude of the trophic niche regarding larval size, prey diversity decreased. This apparent contradiction can be explained due to the low number of larvae for this size class in this region and also as a result of few prey groups with very different sizes.

European anchovy larval diet has been described for several regions, such as the Adriatic Sea (Conway et al., 1998; Borme et al., 2009; Catalán et al., 2010), the Black Sea (Pavlovskaja, 1961; Bulgakova, 1993), the NW Mediterranean (Tudela et al., 2002; Morote et al., 2010; Costalago et al., 2012) or the Portuguese

Table 4 Cheeson's α index for the three different size classes in each study area

Area	Cantabrian Sea				Catalan Sea				
	<6.5	6.5–9	≥ 9		<6.5	6.5–9	≥ 9		
Size class (mm)									
<i>N</i> larvae	30	28	16		21	38	32		
Taxa	<i>N</i> prey	α	SD	<i>N</i> prey	α	SD	<i>N</i> prey	α	SD
Peridinales	1	0.036	0.189	2	0.088	0.279	1	0.026	0.162
Tintinnids	1	0.023	0.121						
Copepod eggs	17	0.444	0.475	5	0.147	0.355	10	0.527	0.500
Copepod nauplii	16	0.423	0.472	16	0.468	0.504	4	0.223	0.411
Calanoid postnauplii	4	0.133	0.346	5	0.148	0.355	7	0.250	0.447
Cyclopoid postnauplii	4	0.143	0.356	1	0.048	0.218	5	0.077	0.268
Harpacticoid postnauplii	1	0.035	0.184	1	0.026	0.162	3	0.013	0.074
Poecilostomatoid postnauplii				1	0.026	0.162	3	0.040	0.181
<i>Evadne-Podon</i>				7	0.122	0.323	18	0.195	0.372
<i>Penilia</i> sp.				3	0.076	0.265	8	0.092	0.262

Positive selection over the critical value of 0.1 has been noted in bold

Table 5 Cheeson's α index for the different flexion stages in each study area

Area	Cantabrian Sea						Catalan Sea					
	Preflexion			Postflexion			Preflexion			Postflexion		
	SL < 9.5			SL \geq 9.5			SL < 7.7			SL \geq 7.7		
Larvae number	62			12			37			54		
Taxa	<i>N</i> prey	α	SD	<i>N</i> prey	α	SD	<i>N</i> prey	α	SD	<i>N</i> prey	α	SD
Peridiniales	1	0.016	0.127				3	0.077	0.263			
Tintinnids	1	0.010	0.081									
Copepod eggs	24	0.304	0.442	8	0.583	0.515	7	0.135	0.347	2	0.019	0.136
Copepod nauplii	33	0.425	0.478	3	0.250	0.452	21	0.465	0.501	20	0.194	0.389
Calanoid postnauplii	14	0.164	0.370	2	0.167	0.389	7	0.189	0.397	34	0.368	0.466
Cyclopoid postnauplii	4	0.065	0.248				3	0.080	0.271	8	0.078	0.257
Harpacticoid postnauplii	1	0.016	0.124							4	0.026	0.146
Poecilostomatoid postnauplii										4	0.042	0.193
<i>Evadne</i> – <i>Podon</i>							1	0.027	0.164	24	0.183	0.366
<i>Penilia</i> sp.							1	0.027	0.164	10	0.090	0.267

Positive selection over the critical value of 0.1 has been noted in bold

coast (Ferreira & Ré, 1993). In general, anchovy larvae feed mainly on crustaceans and according to our data, the most important groups in the two study areas and for the various size classes were different developmental stages of copepods. This is consistent with results from other studies for engraulid and other clupeiform species (Ciechomski, 1967; Tudela et al., 2002; Sampey et al., 2007; Morote et al., 2008, 2010; Catalán et al., 2010; Yasue et al., 2010). However, our data revealed that anchovy larvae do not have a homogeneous diet, because they showed differences between study areas, larval sizes and developmental stages.

In larvae of the Catalan Sea, there was a clear diet shift from small- to medium-sized larvae, characterized by a widening of the prey range and an increase in prey size. Thus, in medium-sized larvae, calanoid postnauplii became the most important and predominantly selected group, and the cladocerans *Evadne* spp. and *Podon* spp. appeared and were selected in the diet. The inclusion in the diet and the positive selection of these by anchovy larvae and by other larvae of clupeiforms such as *Sardinella aurita* Valenciennes 1847 has been reported as a feature of the diet evolution of these larvae when they exceed 6–6.5 mm in length (Morote et al., 2008). Nonetheless, the

absence of this prey group in the diet of anchovy larvae from the Cantabrian Sea could be attributed to prey availability since both the density and the percentage contribution to total zooplankton of cladocerans (*Podon* spp. and *Evadne* spp. together) were higher in the Catalan Sea than in the Cantabrian Sea. Moreover, cladocerans are highly seasonal and in the NW Mediterranean, they are mainly found during the summer months (Calbet et al., 2001) when one of the highest abundances of anchovy larvae occur (Palomera, 1992; Palomera et al., 2007).

Cyclopoid postnauplii, harpacticoid postnauplii and poecilostomatoid postnauplii were the other prey groups present in the diet of the medium-sized larvae of the Catalan Sea, although much less abundantly and only cyclopoid postnauplii were actively selected. Cyclopoid postnauplii have also been reported to be part of the diet of the Japanese anchovy *Engraulis japonicus* Temminck & Schlegel 1846 (Yasue et al., 2010) and the occurrence of harpacticoid postnauplii and poecilostomatoid postnauplii has previously been reported in the diet of anchovy larvae as they grow (Catalán et al., 2010). In large larvae of the Catalan Sea, the diet remained complex.

This pattern was not so clear in Cantabrian Sea larvae, since the diet of large larvae was found to be

less diverse than the diet of larvae of smaller size: it was predominantly composed by eggs and copepod nauplii. Given that an increase in the contribution of copepod postnauplii, and a decrease in the contribution of copepod eggs to the larvae diet was observed from the small-sized larvae to the medium-sized larvae, the break in the diet pattern shown by the large-sized larvae from the Cantabrian Sea can only be interpreted as a spurious result due to the low number of larvae analysed in the large size class.

Moreover, our data suggest that changes in the diet composition and selectivity of prey with larval development were associated to the notochord flexion rather than to larval size itself. In the Catalan Sea, a clear shift was observed in larval diet between preflexion and postflexion stages in agreement with studies that claim that copepod postnauplii gradually gain importance with anchovy developmental stage (Conway et al., 1998; Morote et al., 2010). It is also consistent with data described for European pilchard *Sardina pilchardus* (Walbaum, 1792) in the Cantabrian Sea (Munuera & Gonzalez-Quiros, 2007) or for round sardinella in the Catalan Sea (Morote et al., 2008). This shift in prey size from flexion to postflexion stages was not observed, however, for the larval population of the Cantabrian Sea, but this is likely due to the fact that flexion phenomena occurred at a larger size of individuals in the Cantabrian Sea, and that, as mentioned above, data for large larvae, which were in postflexion stage, were really scarce for this area. Results evidenced that an initial similar diet can be set in the two study areas, but as flexion occurs, a differentiation happens from the previous stage but in a different way for each study area.

Even if prey width is the main selection factor for fish larvae, as it is also claimed by other works (e.g. Detwyler & Houde, 1970; Checkley, 1982; Dabrowski, 1984), our data suggest that there are additional factors influencing this selection since medium- and large-sized larvae from the Catalan Sea select large preys such as calanoid postnauplii and the cladocerans *Evadne* spp. and *Podon* spp. However, the largest larvae still select small prey groups such as copepod nauplii with similar selection strength as other larger prey such as cladocerans *Evadne* spp. and *Podon* spp. In addition, a clear discrimination pattern in copepod nauplii capture, even at the species level has been reported in the literature (Hillgruber et al., 1995). This leads us to support the idea that prey

selection by larval fishes is also based on the type of prey, as suggested by Checkley (1982), Govoni et al. (1986) and Morote et al. (2010) among others.

Other differences between sites cannot be attributed to site-specific differences in prey availability. For example, copepod eggs had a higher contribution to the diet of the Cantabrian Sea larval population than to the diet of the Catalan Sea larval population, but copepod egg density did not differ between the studied areas, and the percent contribution of copepod eggs to the total available zooplankton was significantly higher in the Catalan Sea. In comparative larval diet analysis of different species in the Pacific, copepod eggs were found to be the primary diet of herring *Clupea harengus* L. 1758 larvae, whilst copepod nauplii and postnauplii were the primary diet of Pacific hake *Merluccius productus* (Ayres, 1855) and Alaska pollock *Theragra chalcogramma* (Pallas 1814) larvae (Neville & Beamish, 2007). In our case, however, this discrimination among the different developmental stages of copepod preys was observed for larval populations of the same species but from different geographic areas. The skewed diet and preference towards copepod nauplii and postnauplii in the Catalan Sea larvae might be related to the higher swimming capability as may be inferred from the morphometric differences observed between the larvae of these two areas for the entire larval size range analysed in this study (Intxausti, 2016). Strydom et al. (2014) suggest that some fish larvae can capture the sac of eggs when this is still attached to the adult copepod and just swallow the eggs, rejecting the adult. However, considering the fact that free copepod eggs are non-motile preys, it seems reasonable to consider that the increased presence of eggs in the diet of the larvae of Cantabrian Sea may be related to limitations on the swimming ability in comparison to the Catalan Sea larvae.

In conclusion, diet and prey selection clearly appeared to be linked not only to prey size but also to other larval and prey features. Although, in general, the larval populations that we studied keep similar feeding patterns as those described in the literature, our results revealed that there is a clear diet shift due to the flexion event which makes larvae change both diet and selection pattern at a different size in each area. In addition, differences in the motility of larvae in relation to the motility of preys (i.e. copepod eggs vs. nauplii and postnauplii), and differences in the

feeding scenarios (i.e. cladocerans availability) are found to contribute to the diet variability of larval populations of the same species from different areas.

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