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Food and feeding of Argentine hake (*Merluccius hubbsi*) larvae in the Patagonian nursery ground

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ABSTRACT

Feeding success during the early life stages of fish is one of the main factors that determines recruitment and stock fluctuations. In the Argentine Sea, the Patagonian stock of *Merluccius hubbsi* is the most important in biomass, spawning from December to April in the north Patagonian shelf region (43–45°30′). Since previous knowledge about larval feeding of the species in this region is fragmentary, adequate information is required for a complete assessment of its importance in the food web and its effect upon recruitment. Our primary objective was to examine the feeding strategy of *M. hubbsi* larvae in relation with prey availability in the nursery ground. Feeding incidence was 87%; hake larvae consumed mainly calanoid copepodites <2 mm in size, which were preferred prey upon more available items, and that may be nutritionally beneficial for larvae. Hake larvae were specialist at a population level toward such prey, with a narrow trophic niche. There was a clear trophic diel pattern in the number of prey ingested. Results indicate that the nursery area might be favorable for a successful feeding of hake larvae while they grow and develop. Data provided here are relevant not only to determine trophic interactions in the region but also to identify possible causes of recruitment success.

1. Introduction

Interannual fluctuations in the abundance of commercial marine fish stocks have been an important issue in fisheries science since the late nineteenth century (Hjort, 1914). Processes that determine recruitment and stock fluctuations occur during fish larval phase, with predation and starvation as the highest sources of mortality (Bailey and Houde, 1989). Larvae experiencing favorable feeding conditions will grow faster and therefore suffer from lower predation mortality during the larval stage, when vulnerability to numerous predators is most important, thus contributing to recruitment to the population (Cushing, 1975).

Diet information is crucial to our comprehension of species ecology, trophic interrelationships and ultimately, the flow of energy through ecosystems (Brown et al., 2012). The complex of behaviors of a given organism best suited for gathering food in a particular environment, *i.e.* the feeding strategy, is difficult to understand in the sea, because of the limitations in studying this environment (Modica et al., 2011). Thus, in field studies, the analysis of stomach contents is often the only available means of accessing information on feeding ecology (Amundsen et al., 1996), which can yield species-specific data for potential use in trophic ecosystem modeling that provide ecosystem-based fishery management advice (Ainsworth et al., 2010).

In the Argentine Sea, *Merluccius hubbsi* is one of the most abundant fish resources, and it inhabits waters from 34° to 55°S, at depths ranging between 50 and 500 m (Cousseau and Perrota, 1998). For assessment purposes, two different stocks have been identified: the northern stock (between 34° and 41°S) and the southern one, also known as the Patagonian stock (between 41° and 55°S) (Bezzi et al., 1995). The latter is economically the most important, with a spawning biomass of around 200,000 t estimated during 2012 (MAGyP, 2012). Spawning takes place during late spring (December) and summer (January–March) in the north Patagonian shelf, between 43° and 45°30′S (Pájaro et al., 2005), in relation with a highly productive tidal frontal system (Acha et al., 2004). In December, spawning is located in shelf waters of the Isla Escondida area (>50 m in depth), but throughout the summer it extends to the east and south reaching the Bahía Camarones area, where maximum annual densities of eggs and larvae (<20 mm) have been reported (Ehrlich and Ciechomski, 1994).

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Hake larvae are known to prey mainly upon calanoid copepods (Cass-Calay, 2003; Morote et al., 2011; Sumida and Moser, 1980). In the north Patagonian shelf, few studies regarding *M. hubbsi* larval feeding ecology are available (Ciechomski and Weiss, 1974; Viñas and Santos, 2000), but these have neither considered prey selectivity and feeding strategy of the individuals nor have fully covered the nursery ground of the species. Thus, the primary objective of this work is to examine the feeding strategy of *M. hubbsi* larvae in relation with prey availability in the Patagonian nursery ground. Particular objectives include (1) to analyze the diet composition of hake larvae, (2) to evaluate the effect of time of catch and larval size on diet, (3) to describe the larval feeding strategy in terms of degree of generalization/specialization when selecting prey and trophic niche width, (4) to estimate the abundance of hake larvae preferred prey in the field and (5) to assess prey selectivity. Knowledge of the quantitative aspects of hake larval diet will provide further relevant data not only to determine trophic interactions in the region and how hake influences the dynamics of predator–prey interactions within its community but also to identify possible causes of recruitment success.

2. Methods

2.1. Sampling of larvae and zooplankton

M. hubbsi larvae were collected during two research surveys carried out in the north Patagonian shelf by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) during January–February 2010 (EH-01/10) and February 2011 (OB-01/11) (Fig. 1a). Larvae were captured between 46 and 84 m depth, during daylight, by using a Bongo net (300 and 500 μm meshes), an epibenthic sampler (EBS) and a rectangular mid-water trawl sampler (RMT) (Table 1). All of the hake caught were immediately frozen in liquid N_2 at −70 °C to halt the digestion process of the stomach contents. Additionally, to determine the prey availability for hake larvae, oblique mesozooplankton hauls were carried out at the same ichtyoplankton stations (Fig. 1b), with Minibongo (67 and 200 μm mesh) and Bongo (300 and 500 μm mesh) nets. To cover the complete copepod size spectrum, samples obtained with the 67 and 300 μm meshes were analyzed. Filtered water volume was estimated from a Hydrobios flowmeter placed at the mouth of each net. Samples were immediately fixed in a 5% formalin-seawater solution.

2.2. Laboratory analysis

Hake larvae were measured (standard length SL, from the tip of the head to the end of the last vertebrae, excluding the caudal fin, in mm) under a Wild M5 stereoscopic microscope and separated into three length classes: class I (<5 mm, first feeding larvae), class II (5–10 mm, early larvae) and class III (10–30 mm, advanced larvae), slightly modified from the classification proposed for *M. hubbsi* by Ehrlich (1998) based on Hollowed (1992) categories for *M. productus*. Damaged or deformed specimens were discarded. The gut of each individual was removed using fine needles, placed on a glass depression slide and opened to identify prey organisms. A drop of a saturated solution of Toluidine Blue (0.25%) was added to stain crustacean's cuticle, greatly improving the visibility of prey and facilitating their enumeration and measurement. Stomachs damaged during the dissection process were discarded from the analysis.

Adult copepods were identified to species using appropriate taxonomic references. Immature stages were classified as eggs, nauplius or copepodites. Eggs of calanoids were assigned to a single category due to difficulties in identifying species, and the same procedure was applied to nauplius larvae of cyclopoids and calanoids. Although not identified to the species level, copepodites were classified considering four categories of total length, which include mostly members of the more common copepod species in the area (Ramírez, 1970; Viñas et al., 1992) as follows: cyclopoids <1 mm, *Oithona helgolandica*; calanoids <1 mm, early copepodites of Pseudocalanidae (*Drepanopus forcipatus* and *Ctenocalanus vanus*);

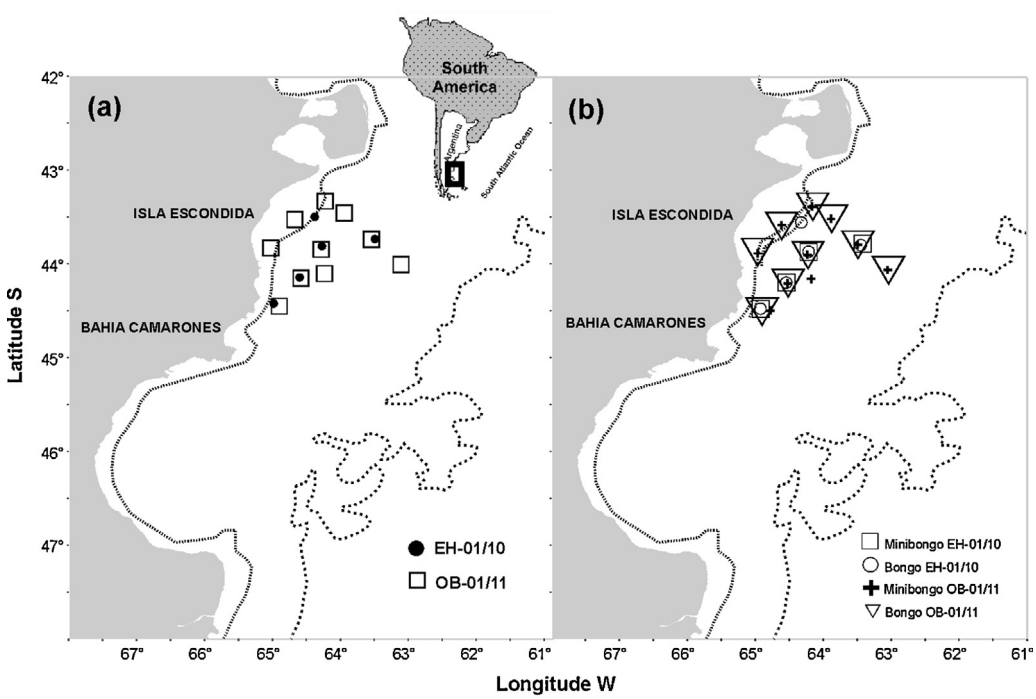

Fig. 1. Location of (a) ichthyoplankton samples to obtain *M. hubbsi* larvae and (b) zooplankton samples with Minibongo and Bongo nets, in the north Patagonian shelf during January–February 2010 and February 2011.

Table 1
Details of the ichthyoplankton samplings to obtain *M. hubbsi* larvae in the north Patagonian shelf during January–February 2010 and February 2011. EBS: epibenthic sampler; RMT: rectangular mid-water trawl sampler; SL: standard length; SD: standard deviation.

	Date	Middle time of catch	Depth (m)	No. of stomachs	Mean SL (±SD, mm)
EH-01/10					
Bongo 18	01.26.10	15:21	76	7	5.04 ± 0.39
Bongo 21	01.27.10	11:03	68	22	5.71 ± 0.54
Bongo 22	01.27.10	14:16	64	21	5.71 ± 0.8
Bongo 24	01.27.10	20:32	53	15	4.38 ± 0.36
EBS 4	02.01.10	18:00	73	13	5.43 ± 0.67
OB-01/11					
Bongo 16	02.02.11	21:40	76	2	14.43 ± 1.87
Bongo 23	02.08.11	06:15	55	1	10.67
Bongo 24	02.08.11	11:20	70	6	4.49 ± 0.45
Bongo 25	02.08.11	16:30	65	15	4.52 ± 0.41
Bongo 26	02.08.11	19:50	45	16	5.61 ± 1.02
Bongo 27	02.09.11	00:45	53	8	5.78 ± 0.91
Bongo 28	02.09.11	02:27	67	25	5.77 ± 1.46
Bongo 29	02.09.11	05:28	69	7	6.76 ± 1
EBS 3	02.10.11	12:18	76	16	7.25 ± 0.46
RMT 2	02.07.11	22:25	15–30	27	13.44 ± 3.06
RMT 3	02.07.11	23:47	25–40	27	10.73 ± 4.49

calanoids 1–2 mm, late copepodites of Pseudocalanidae and early copepodites of *Calanoides carinatus* and calanoids >2 mm, late copepodites of *C. carinatus*.

For adults and copepodites of copepods, total length (TL, from the anterior end of the cephalotorax to the posterior margin of the caudal rami, excluding furcal setae, in mm), prosome length (PL, in mm) and width (PW, in mm) were measured using an ocular micrometer. For nauplius larvae, total length (TL) and width (*W*, mm) were measured whereas for eggs, diameter (*D*, mm) was established.

Zooplankton samples were diluted to a volume of 900 ml and sub-sampled in aliquots. Up to 100 individuals from the most abundant species (adults) or stage were counted, considering the same categories defined for prey identification in the gut content analysis. Eggs and nauplius were only counted in the Minibongo samples (to avoid underestimation of their abundance) while copepodites and adults were counted both on Minibongo and Bongo samples. We compared the abundance assessments of each net and selected, for each category, the mesh that returned the highest estimation. The abundance of each planktonic category, calculated as individuals per cubic meter, was used to estimate a prey selectivity index (Section 2.4).

2.3. Data analysis

Feeding incidence (FI) was calculated as the percentage of the total number of larvae examined having at least one prey item in their gut (Arthur, 1976). The contribution of each prey category (i) to the diet of larvae was examined through frequency of occurrence ($\%O_i$) and by percentage in number ($\%N_i$). Gut content samples of the two studied periods were pooled to increase sample size since no interannual differences were observed among them (Wilcoxon signed-rank test for $\%O_i$: $Z = 0.59$, $p = 0.55$ and for $\%N_i$: $Z = 1.08$, $p = 0.27$; significance level = 0.05). The estimate of the relative importance (RI) of a different prey item in the diet was calculated by multiplying the $\%O_i$ and the $\%N_i$ of such prey in feeding larvae (Laroche, 1982). The diversity of prey items in the diet was calculated using the Shannon index $H' = -\sum_{i=1}^{m}(p_i \times \ln p_i)$ where p_i is the relative abundance of prey item *i* in the diet and m is the number of prey categories (*i.e.* richness).

Dietary shifts were assessed by building GLMs with the R statistical software, version 2.15.1 (R Development Core Team, 2011). Larval standard length (SL) and time of catch ($T_{sunrise}$: 06:00 to 10:59 h, T_{midday}: 11:00 to 14:59 h, $T_{afternoon}$: 15:00 to 19:59 h, T_{sunset}: 20:00 to 23:59 h, T_{night}: 00:00 to 05:59 h) were used as the explanatory variables and the percentage of stomachs with food (PSF) and the number of prey per stomach (NPS) as the response variables. Models with PSF as the response variable have a binomial (contained food or empty) error distribution and a link logit, while those with count data (NPS) have a Poisson error distribution and a link log (Crawley, 2005). The model with the lower value of the Akaike Information Criterion (AIC) (most plausible model) was selected as the best one and was weighed against the others using Akaike's weight (*Aw*). *Aw* values vary between zero (poor fit) and one (good fit) and provide an estimation of the likelihood of the model given the data (Johnson and Omland, 2004). A model without explanatory variables (null model) was also fitted in order to test the hypothesis that none of the variables tested had an effect on the response variable. On the other hand, regression analyses were performed with R to study the relationship between prey number and size (length and width) and larval standard length. Different regression models were tested (linear, exponential, logarithmic, *etc.*) and the best fit was chosen considering the least-squares method, *i.e.* the single regression line best describing predator–prey size relationship that minimizes the sums of squares in prey sizes (*y*) at any predator size (*x*).

2.4. Food niche width and prey selectivity

Food niche width (*B*), which characterizes the food resource spectrum used by a fish species, was calculated with the Levins's standardized index (B; Levins, 1968). B takes values between 0 and 1; values <0.6 represent strongly specialized feeders that prey on few taxa, while values >0.6 indicate generalist feeders with no preference for any taxa (Krebs, 1989).

Feeding selectivity was determined from the relative abundance of the main prey items in hake larvae stomachs and their relative abundance in the zooplankton samples. The alpha index (α_i; Chesson, 1978) was calculated as $\alpha_i = (r_i/p_i)\sum(r_i/p_i)^{-1}$, where r_i and p_i are the percentage abundances of prey item *i* in the larval diet and in the plankton samples, respectively. Only the four most common food categories ingested by the hake larvae were considered for the purpose of focusing on preference for organisms that contributed most to the larval diet, rather than on absolute prey preference (Govoni et al., 1986). The values of α_i range from 0 to 1, with a limit value of $1/n$ (n = number of prey categories), with higher values

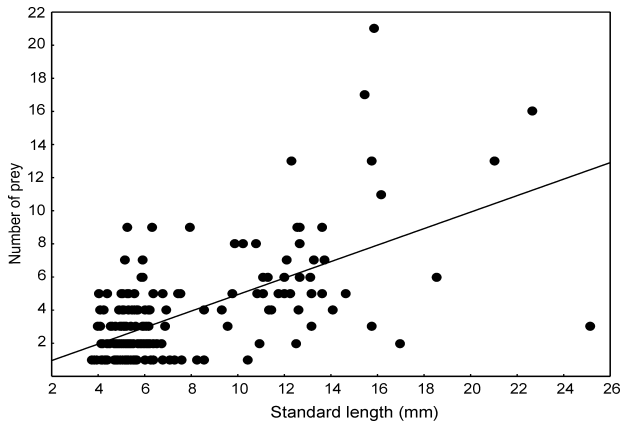

Fig. 2. Relationship between the number of prey consumed and M. hubbsi larval length (SL, mm). Equation of the linear regression is No of prey = −0.042 + 0.5 × SL (R2 = 0.4, $p < 0.001$).

indicating that the larvae ate these prey in greater proportions than they occurred in the environment. Random feeding occurs when $\alpha_i = n^{-1}$; in our study, values of $\alpha_i > 0.25$ or $\alpha_i < 0.25$ were taken to represent selection and avoidance of prey, respectively.

3. Results

A total of 228 intact *M. hubbsi* larvae ($n = 78$ for January–February 2010; $n = 150$ for February 2011) ranging from 3.72 to 25.11 mm SL (mean = 7.22 mm, SD = 3.6) was analyzed. A high number of larvae had identifiable prey in their guts, evidencing a feeding incidence of 87% ($n = 199$), while empty and discarded stomachs represented 9.2% ($n = 21$) and 3.5% ($n = 8$) of the total, respectively. The percentage of stomachs with food did not vary significantly with the time of catch or the standard length of the individuals.

A total of 672 prey items was recorded in all the stomachs. The mean number of prey per stomach (±SD) was 2.95 ± 3.14, with a maximum of 21 items in a 16 mm SL larva. The number of prey per stomach was best described by a model that included standard length and time of catch as the explanatory variables (GLM = 0.55 (0.11) + 0.09 (0.0098) × LS − 0.80 (0.16) × T_{midday}; $\text{AIC}_{\text{model}}$: 953.2; $\text{AIC}_{\text{null model}}$: 1158.8; $Aw = 1$). This indicates that the number of prey consumed increased significantly and positively with larval size (Fig. 2) and was lower during midday (12:00 to 15:59 h). The number of prey per gut increased from a minimum of 1 at midday, to a value of 3 in the afternoon, reaching a maximum of 5 prey per stomach in larvae caught during sunset. Then, values decreased to a value of 2.7 and 2.5 prey per stomach during night and sunrise, respectively.

The four most common components in the diet were calanoid copepodites 1–2 mm and <1 mm in size and adults of *C. carinatus* and *D. forcipatus* (Table 2). There were, however, differences in prey diversity and richness between gut contents of larvae of each size class (class I: $H' = 1.49$, 3 prey categories; class II: $H' = 2.02$, 19 prey categories and class III: $H' = 1.69$, 14 prey categories), with the lowest values in the smallest individuals (<5 mm). Regarding prey size, larvae of the shrimp *Peisos petrunkevitchii* and the euphausiid *Euphausia lucens* were the largest (~5 mm) but rarest items in the guts, found only in larvae from class III. In general, a significant and positive logarithmic relationship was found between mean prosome length (Fig. 3a) and width (Fig. 3b) of copepods and larval standard length. This tendency was also observed when considering different size classes, with individuals of classes I and II consuming, on average, smaller prey than larger individuals from class III (Table 3). However, since hake larvae within the studied size range do not switch to epibenthic or fish prey until much later,

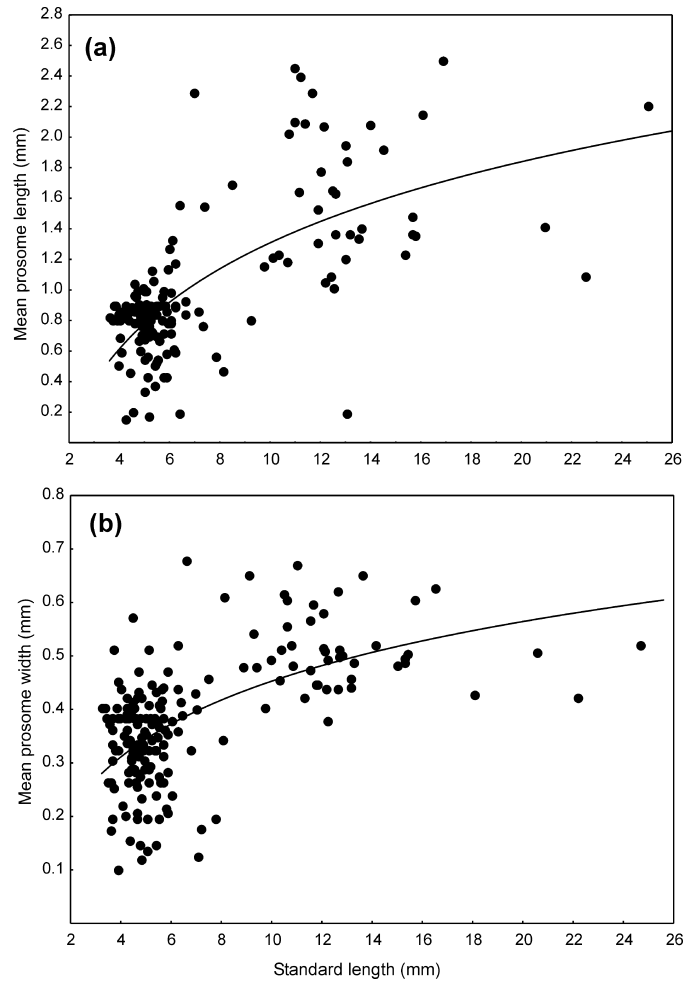

Fig. 3. Relationship between (a) mean prosome length (PL) and (b) mean prosome width (PW) of copepods consumed (mm) and *M. hubbsi* larval length (SL, mm). Equations of the linear regressions are (standard deviation of the coefficients between brackets) (a) PL = −1.3 (0.15) − 0.66 (0.07) × SL ($R^2 = 0.32$, $p < 0.001$) and (b) PW = −1.87 (0.1) + 0.44 (0.05) × SL ($R^2 = 0.27$, $p < 0.001$).

it is likely that copepod size reaches an asymptotic value, as shown in Fig. 3. The analysis of the Levin's index indicated that the diet of hake larvae population was dominated by few prey items, since a value <0.6 ($B = 0.22$) was observed, reflecting a narrow trophic niche with a specialized diet. Although most of the individuals consumed mainly the same prey, small proportions of other items were occasionally consumed by some individuals, particularly at larger sizes. With respect to prey availability, the plankton community was dominated by copepod eggs and nauplii as well as cyclopoid and calanoid copepodites (Table 4). Prey selectivity was different along the three size classes (Fig. 4). While first feeding larvae positively selected adults of *D. forcipatus* and calanoid copepodites 1–2 mm and <1 mm in size, which represented 27% of the community, consuming other more abundant categories (*i.e.* copepod eggs and nauplius, 31% of the community) at a lower proportion than their availability in the field, individuals from classes II and III exclusively selected adults from the species *C. carinatus* and *D. forcipatus*, although both species showed low abundances and only represented <3% of the community.

4. Discussion

Larvae of *M. hubbsi* living in the north Patagonian nursery area exhibited a trophic incidence of 87%, thus reflecting a high feeding

Table 2
Diet composition of *M. hubbsi* larvae. For each prey item: $\%O_i$ = frequency of occurrence; $\%N_i$ = percentage in number; RI: relative importance. Shaded rows indicate the four most common prey items that were included in the selectivity analysis.

Prey item	$\%O_i$	$\%N_i$	RI
Copepods – Developmental stages			
Eggs	4.02	2.83	11.37
Nauplius larvae	3.02	1.04	3.14
Cyclopoid copepodites <1 mm (Ccy)	3.52	1.49	5.23
Calanoid copepodites <1 mm (Cca)	42.71	19.94	851.73
Calanoid copepodites 1–2 mm	60.30	28.72	1731.87
Calanoid copepodites >2 mm	8.04	3.87	31.11
Copepods – Adults			
Family Oithonidae			
Oithona nana (ON)	1.01	0.30	0.30
O. helgolandica (syn. O. similis) (OH)	2.51	1.04	2.62
Family Calanidae			
Calanoides carinatus (CC)	26.63	22.77	606.38
Calanus australis (CA)	4.02	1.49	5.98
Family Pseudocalanidae			
Drepanopus forcipatus (DF)	20.10	8.93	179.47
Ctenocalanus vanus (CV)	10.05	3.27	32.90
Family Centropagidae			
Centropages brachiatus (CBRA)	2.01	0.60	1.20
Family Acartiidae			
Acartia tonsa (AT)	2.01	0.60	1.20
Family Paracalanidae			
Paracalanus parvus (PPa)	3.52	1.19	4.19
Family Ectinosomatidae			
Microsetella norvegica (MN)	0.50	0.30	0.15
Family Euterpinidae			
Euterpina acutifrons (EA)	0.50	0.15	0.07
Other			
Euphausia lucens larvae (EL)	0.50	0.30	0.15
Peisos petrunkevitchii larvae (PPe)	1.51	0.60	0.90
Mysidopsis rionegrensis (MR)	0.50	0.15	0.07
Appendicularians (Append)	2.01	0.45	0.90

success, in agreement with values estimated for other species of the genus (Reiss et al., 2005; Sumida and Moser, 1980; Valenzuela et al., 1995). It has been reported that gadiforms from middle latitudes (30–45°S) often show feeding incidences of about 80% (Llopiz, 2013). One of the factors affecting the feeding incidence may be the larval gut morphology. At a size of approximately 3 mm, gut widening and folding begin (*i.e.* looped gut) in *M. hubbsi* larvae, processes that provide additional space for the accumulation and retention of food items, while preventing their elimination due to external factors such as capture or fixation (Ciechomski and Weiss, 1974).

Table 3
Mean prosome length (PL) and width (PW) in mm of copepod prey in stomach contents of *M. hubbsi* larvae in the three larval length classes (mm). The number of larvae analyzed in each length class is between brackets.

Prey item/larval length class	<5 (n = 56)		5–10 (n = 128)		10–30 (n = 44)	
	PL	PW	PL	PW	PL	PW
Nauplius larvae	0.20 ± 0.06	0.08 ± 0.03	0.31 ± 0.23	0.19 ± 0.17	0.36	0.19
Cyclopoid copepodites <1 mm	0.45 ± 0.12	0.18 ± 0.11	0.55 ± 0.20	0.17 ± 0.02	–	–
Calanoid copepodites <1 mm	0.74 ± 0.20	0.25 ± 0.05	0.70 ± 0.15	0.26 ± 0.05	0.72 ± 0.22	0.29 ± 0.03
Calanoid copepodites 1–2 mm	0.90 ± 0.07	0.39 ± 0.05	0.99 ± 0.23	0.40 ± 0.06	1.17 ± 0.34	0.44 ± 0.08
Calanoid copepodites >2 mm	–	–	1.26 ± 0.76	0.64 ± 0.08	1.65 ± 0.18	0.63 ± 0.09
Family Oithonidae						
O. nana	–	–	0.43 ± 0.06	0.19 ± 0	–	–
O. helgolandica	–	–	0.53 ± 0.07	0.16 ± 0.03	–	–
Family Calanidae						
C. carinatus	–	–	2.13 ± 0.33	0.50 ± 0.10	2.01 ± 0.43	0.60 ± 0.08
C. australis	–	–	1.62 ± 0.59	0.52 ± 0.18	2.01 ± 0.4	0.63 ± 0.04
Family Pseudocalanidae						
D. forcipatus	0.94 ± 0.12	0.39 ± 0.04	0.97 ± 0.10	0.39 ± 0.04	0.98 ± 0.09	0.42 ± 0.03
C. vanus	0.93 ± 0.03	0.39 ± 0.04	0.89 ± 0.04	0.36 ± 0.03	0.99 ±± 0.11	0.44 ± 0.08
Family Centropagidae						
C. brachiatus	–	–	–	–	1.05 ± 0.01	0.37 ± 0.03
Family Acartiidae						
A. tonsa	1.04	0.26	1.08	0.32	1.09 ± 0.06	0.39 ± 0.06
Family Paracalanidae						
P. parvus	–	–	0.61 ± 0.05	0.30 ± 0.05	0.88 ± 0.11	0.34 ± 0.08
Family Ectinosomatidae						
M. norvegica	–	–	–	0.12	–	–
Family Euterpinidae						
E. acutifrons	–	–	–	0.17	–	–
Mean	0.80 ± 0.24	0.33 ± 0.10	0.88 ± 0.37	0.35 ± 0.12	1.49 ± 0.61	0.49 ± 0.14

Table 4
Mean abundance (ind m^{-3}) of the zooplanktonic components in January–February 2010 and February 2011.

	Size (mm)	Jan–Feb 2010 (ind m^{-3})	Feb 2011 (ind m^{-3})	Mean (ind m^{-3})	% in the community
Copepods – Developmental stages					
Eggs	<1	1036.95	1442.91	1239.93	13.63
Nauplius larvae	<1	377.76	2834.66	1606.21	17.66
Cyclopoid copepodites <1 mm	<1	585.11	2320.55	1452.83	15.97
Calanoid copepodites <1 mm	<1	378.33	2196.90	1287.61	14.16
Calanoid copepodites 1–2 mm	1–2	518.87	1741.92	1130.39	12.43
Calanoid copepodites >2 mm	>2	209.89	314.02	261.95	2.88
Copepods – Adults					
Family Oithonidae					
O. nana	<1	14.98	88.55	51.77	0.57
O. helgolandica	<1	69.39	1359.96	714.68	7.86
O. atlantica	<1	4.08	0.58	2.33	0.03
Family Calanidae					
C. carinatus	>2	176.39	140.81	158.60	1.74
C. australis	>2	1.54	0.22	0.88	0.01
Family Pseudocalanidae					
D. forcipatus	1–2	244.23	243.57	243.90	2.68
C. vanus	1–2	211.50	726.10	468.80	5.15
Family Paracalanidae					
P. parvus	<1	1.23	1.23	1.23	0.01
Family Centropagidae					
C. brachiatus	1–2	36.77	81.88	59.32	0.65
Family Ectinosomatidae					
M. norvegica	<1	11.85	519.30	265.57	2.92
Family Euterpinidae					
E. acutifrons	<1	11.46	76.11	43.79	0.48
Family Acartiidae					
A. tonsa	1–2	152.33	60.41	106.37	1.17
Appendicularians		80.19	763.81	422	4.43
Euphausiids					
E. lucens larvae		1.75	15.72	8.74	0.09

Similar results were reported for larvae of merluccid (Sumida and Moser, 1980) and non-merluccid gadoids such as *Gadus morhua* (Voss et al., 2003). Furthermore, an early development of the structures associated with feeding, such as the caudal peduncle, the head and the gut, may favor the pursuing and handling of prey items (Palomera et al., 2005). Also, the mechanic support provided by a full development of the fins (Ciechomski and Weiss, 1974) is a decisive factor in the trophic ecology of the larvae, since it improves not only the frequency of encounter but also the effectivity of capture of the prey.

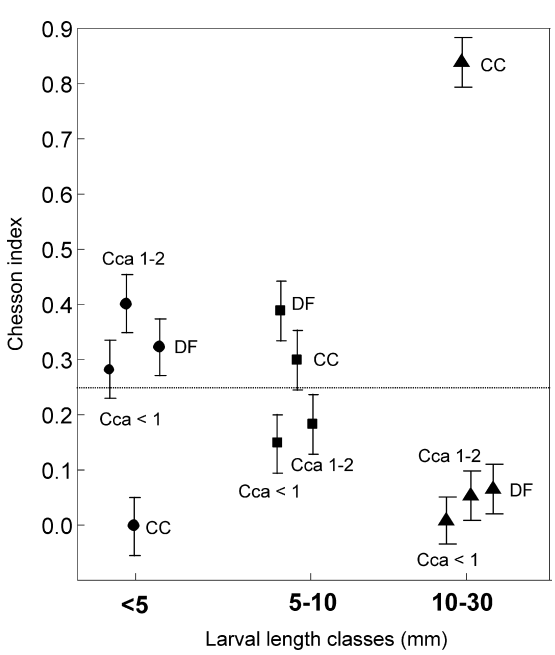

Fig. 4. Mean Chesson's index values (± standard deviation) for the four most common prey items of *M. hubbsi* larvae in three length classes (mm). The dotted line indicates minimum threshold values (1/*n*) for random selection. See references in Table 2.

Trophic incidence was not related to the time of catch, as previously demonstrated for mackerel larvae (Robert et al., 2009). On the contrary, the number of prey per stomach evidenced a marked diel cycle, with a minimum at midday, a gradual increase during the afternoon, a maximum at sunset and a decrease during night and sunrise hours, when digestion and evacuation of the gut might occur. This is the first report of a trophic diel pattern in the number of ingested prey for *M. hubbsi* larvae. Considering that most fish larvae are primarily visual predators (Hunter, 1980), the feeding peak should have been expected during daylight hours. However, it has been shown that the larval visual system of gadids such as *M. merluccius* (Morote et al., 2011) and *G. morhua* (Huse, 1994) is able to cope with a wide range of photic conditions, hence allowing the individuals to forage even at low light intensity. It is also probably the case of *M. hubbsi* larvae. Additionally, the general metabolic activity of hake larvae is known to decline at sunset (Sumida and Moser, 1980), thus diminishing the gut evacuation rate and consequently producing a post-sunset feeding peak.

Hake larvae diet in the spawning area focused on calanoid copepodites and adults, mainly corresponding to the Pseudocalanidae (*D. forcipatus*) and Calanidae (*C. carinatus*) families. Copepodites of medium and large-size calanoid species are the preferred prey in the larval stages of numerous species (Robert et al., 2008 and references therein), with those families mentioned as the main items in *M. hubbsi* (Ciechomski and Weiss, 1974) and *G. morhua* (reviewed by Heath and Lough, 2007) diet. Copepodites predominance might be explained considering the preferendum in prey size, which reflects the optimum of the ratio between energy gain and energy spent for the capture of prey. Below the preferred size interval, prey are not as valuable in terms of energy balance due to an insufficient gain relative to the basic foraging energy demand

(*i.e.* small prey), while over the interval there is an excessive average attack cost compared with the potential energy benefits (*i.e.* large prey). Furthermore, individuals foraging optimally can adjust their food preferences to take into account prey quality (*i.e.* energy density) rather than prey abundance (Anthony et al., 2000). Since energy density of lipid is about twice that of protein and carbohydrate (Schmidt-Nielsen, 1997), a lipid-rich diet provides enough metabolic energy for maintenance, so dietary protein can be allocated to tissue synthesis and growth (Pinnegar et al., 2003). It has been demonstrated that accumulation of fatty acids can be a key factor in larvae survival and subsequent recruitment (Sargent et al., 1999). Thus, the high incidence of calanoids in the diet may be related to their potential nutritional benefit due to high levels of highly unsaturated fatty acids in the form of phospholipids (Moreno et al., 1979; Vogedes et al., 2010). The positive selection observed for copepodites and adults of *C. carinatus* and *D. forcipatus*, which are highly lipid-rich species (Cripps and Atkinson, 2000; Verheye et al., 2005; Vogedes et al., 2010), supports this hypothesis.

Our results indicate that larvae would feed on small prey at the onset of feeding and replace them with larger prey as they grow. In fact, the presence of *E. lucens* and *P. petrunkevitchii* larvae in the diet was observed in individuals >18 mm. Surprisingly, first-feeding larvae (<5 mm) did not include copepod nauplii and/or eggs as main prey, as previously observed for *Merluccius* (Cass-Calay, 2003; Viñas and Santos, 2000) and other gadids (Robert et al., 2008). Viñas and Santos (2000) suggested that, within the north Patagonian shelf, larval ability of taking advantage of small-scale patches of nauplii in the water column may account for their high dominance in the diet. In fact, their reported nauplii abundances (mean = 4609 ind m^{-3}, SD = 3281) were markedly higher than our values, and the same was observed for eggs abundance (mean = 6323 ind m^{-3}, SD = 260), which may be explained considering the high dynamism of the tidal frontal system that characterizes the spawning ground, and that may determine the year-to-year distribution patterns of zooplankton (Sabatini and Martos, 2002). However, since individuals do not depend exclusively on such dense patches due to a large mouth (even at small sizes) they can also feed upon larger prey (*i.e.* copepodites), thus having a wider choice of prey and an energetic advantage. Moreover, this fact would reduce the competition for resources with anchovy (*Engraulis anchoita*) first-feeding larvae that also nurse in the area and prey exclusively on copepod eggs and nauplii due to a mouth gape limitation (Viñas and Ramírez, 1996). Besides copepod eggs and nauplii, there is growing evidence that soft organisms such as heterotrophic protists, which are undetectable with standard larval gut content studies, can play an important role in larval nutrition, either through consumption or indirectly due to their presence (de Figueiredo et al., 2007; Fukami et al., 1999; Overton et al., 2010). Thus, further studies considering alternative techniques, such as the fatty-acid trophic markers or stable isotopes approaches, should be carried out to establish the importance of these prey items in hake larvae diet, as has been previously done for different species (Pepin and Dower, 2007; Rossi et al., 2006).

A central aspect of niche theory and feeding strategies is the generalist–specialist dichotomy (Pianka, 1988). A generalist predator has a broad dietary niche, whereas the food niche of a specialist is narrow. Results suggest that, in the nursery area, hake larvae are specialist predators in calanoid copepods <2 mm in size. Most larvae were feeding on this particular prey taxon, thus exhibiting a narrow trophic niche, but small proportions of other prey types were included occasionally in the diet of some individuals. The foraging environment of a species must be taken into account when analyzing trophic ecology (Morote et al., 2011). In the present study, high abundances of eggs, nauplii and copepodites of cyclopoids and calanoids were found in the nursery area of the species, which *a priori* indicate a suitable prey field. However, and despite the fact that nauplii and cyclopoid copepodites dominated the copepod community during the study period, they were not positively selected by hake larvae, while calanoid copepodites <2 mm, that showed lower abundances, were clearly the preferred prey. Some factors, such as color or behavior may affect the prey–predator encounter rate. Calanoid copepodites have a well-developed lipid sac that usually occupy a large part of the body cavity (Vogedes et al., 2010) and is pale yellow to bright orange in color (Ceballos et al., 2006), which could increase their visibility when larvae forage during daylight hours. Also, Pseudocalanidae species are known to be more vulnerable to predation because of their poor escape response (McLaren and Avendaño, 1995; Petrik et al., 2009; Viitasalo et al., 2002).

Not only the high trophic incidence value reported here but also the preference for calanoid copepodites would indicate that the north Patagonian shelf region might be favorable and appropriate for a successful feeding of hake larvae while they grow and develop. One of the most outstanding features of this region is the presence of a major and highly productive frontal system located from near Península Valdés and extending southwards along the Patagonian coast up to 45°S (Carreto et al., 2007; Sabatini and Martos, 2002). The distinct physical environments characterizing the northern and southern boundaries of the tidal front, mainly due to differential wind/tidal relative forcing, led to the occurrence of different plankton assemblages (Sabatini and Martos, 2002). While cyclopoids, cladocerans and appendicularians are conspicuous toward north (Península Valdés), suggesting that matter and energy transfer may be channeled through a microbial food web, further south (Isla Escondida), where the intensive spawn and nursery of *M. hubbsi* Patagonian stock occurs, calanoid copepods are dominant, evidencing a classic food web mainly herbivorous. These authors estimated an abundance of 4000 ind m^{-3} for calanoids in December, while maximum values estimated for the following months (January and February–March) would be over 6000 ind m^{-3} (Temperoni et al., unpublished data). Thus, availability of *M. hubbsi* larvae preferred prey would be higher in the Isla Escondida sector along the spawning season.

Encounter in the water column between hake larvae and their prey might be favored by several factors. Firstly, larvae would be retained in this highly dynamic system due to a coupling between circulation and behavioral patterns (Álvarez-Colombo et al., 2011). According to these authors, circulation in the region involves a two-layered flow with a surface layer moving offshore and a bottom layer directed onshore. Thus, the smaller larvae (<5 mm) would be scarce or absent in the surface layer due to the strong currents that would advecte them offshore, but would be highly concentrated in the bottom one, where a low motion level develops. This spatial location of the bulk of first feeding larvae might explain their low number in our samplings, even though a higher number was expected since the reproductive peak occurs in January (Pájaro et al., 2005). Such position in the water column probably left them out of the nets range. Once they grow, a functional swimming bladder would allow the larger individuals (>5 mm) to perform daily vertical migrations from near the bottom to the level immediately below the thermocline at night. On the other hand, the high chlorophyll *a* values registered at the thermocline level (Viñas and Ramírez, 1996) probably favor the occurrence of high densities of herbivorous calanoid copepods (Derisio, 2012), the preferred prey for larvae. Particularly for *C. carinatus* and *D. forcipatus*, a diel vertical migratory behavior has been demonstrated, which allows these species to ascend at night to the chlorophyll-rich upper layer of the water column, and descend to the bottom during daylight hours, when predation risk due to increased visibility is higher (Guglielmo et al., 2011; Verheye and Field, 1992). Hence, migratory behavior allows the larvae not only to follow the movement of their main prey, thus ensuring a successful foraging throughout the day (probably favored by a highly adapted visual system, as mentioned

before), but also counteract the advective forces of the system by moving toward the bottom layer during the day.

Since variability in feeding success might have a significant effect on post-larval mortality (Sissenwine, 1984), the information provided here could be useful in the context of predicting the future pre-recruits number which will incorporate to the adult fraction of the *M. hubbsi* population in the Argentine Sea. In addition, these new insights on trophic ecology of *M. hubbsi* larvae provide a better understanding of their ecological role and food web interactions within the north Patagonian shelf ecosystem. As concluding remarks of this article we highlight that hake larvae in the north Patagonian shelf were specialist at a population level toward calanoid copepodites and adults from the Pseudocalanidae and Calanidae families, and positively selected prey which were not the most available in the field, mainly characterized by high lipid content and, consequently, nutritional benefit. For the first time, a daily feeding rhythm is reported for *M. hubbsi* in the north Patagonian shelf.

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