

## Feeding strategy of juvenile (age-0+ year) Argentine hake *Merluccius hubbsi* in the Patagonian nursery ground

B. TEMPERONI\*†‡, M. D. VIÑAS\*† and C. C. BURATTI†

\**Instituto de Investigaciones Marinas y Costeras (IIMyC), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata (UNMdP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Argentina* and †*Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo No. 1, B7602HSA, Mar del Plata, Argentina*

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Age-0+ year juvenile Argentine hake *Merluccius hubbsi* (60–150 mm total length,  $L_T$ ) from San Jorge Gulf, north Patagonian shelf region of the Argentine Sea, had an almost exclusively pelagic diet dominated by the hyperiid amphipod *Themisto gaudichaudii* and the euphausiid *Euphausia lucens*. This suggested that final settlement and permanent demersal habitat utilization might not, as previously reported, occur at earlier sizes (*c.* 20 mm  $L_T$ ). Their feeding strategy involves specialization at a population level towards both the main pelagic prey, indicating a narrow trophic niche. Novel data are provided which contribute to the growing body of information in relation to the age-0+ year transitional stage in demersal fishes and particularly to *M. hubbsi* recruitment in the Argentine Sea.

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Key words: Argentine Sea; diet; feeding behaviour; nursery area; stomach contents.

### INTRODUCTION

Knowledge of the dynamics of mechanisms operating during the early life history of fishes is considered essential to the understanding of interannual recruitment variability (Cushing, 1975; Houde, 1987). Particularly, information regarding the feeding strategy, *i.e.* the complex behaviours of an organism best suited and developed for gathering food in a particular environment, is crucial to understanding species ecology, trophic interrelationships and, ultimately, the flow of energy through ecosystems (Bozzano *et al.*, 1997; Modica *et al.*, 2011). Such information is, however, difficult to obtain from the sea because of limitations in studying this environment (Modica *et al.*, 2011). In spite of this, the analysis of stomach contents in field studies is one of the available means of accessing information on feeding ecology (Amundsen *et al.*, 1996), which can yield species-specific data for potential use in trophic ecosystem modelling (Ainsworth *et al.*, 2010).

Survival of larvae has traditionally been proposed as the primary determinant of recruitment success in fishes (Hjort, 1914; Cushing, 1972; Lasker, 1975; Bailey

‡Author to whom correspondence should be addressed. Tel.: +542234862586 ext. 259; email: btemperoni@inidep.edu.ar

& Houde, 1989), with a major focus on starvation as the main source of mortality (Hunter, 1976). During the last decades, however, overexploitation of the older age classes has led to a reduction in the age of marine fish populations, making recruitment more dependent on the abundance of the youngest age classes (Hidalgo *et al.*, 2009). Therefore, researchers have suggested that the recruitment of some fish stocks may not be exclusively determined during the early larval stages, but that processes occurring during the juvenile stages might also contribute significantly to year-class strength (Sissenwine, 1984; Hüsey *et al.*, 1997). Although predation and adverse oceanographic conditions are considered the two primary agents of juvenile natural mortality (Hüsey *et al.*, 1997), it has been suggested that biological factors such as food limitation cannot be ruled out (Townsend & Cammen, 1988; Koeller *et al.*, 1989), particularly for juveniles of demersal species. Such juveniles, during their first year of life (age-0+ year individuals), undergo a transitional period that involves a shift from a pelagic to a demersal habitat utilization (*i.e.* final settling), with concurrent morphological, physiological, ecological and behavioural changes. Individuals have to face not only major changes in type, size and availability of prey, but also the presence of possible predators in the demersal settlement habitat, thereby establishing this period as potentially critical for survival.

The Argentine hake *Merluccius hubbsi* Marini 1933 is one of the most abundant and economically important fish resources of the Argentine Sea. The species inhabits waters from 34° to 55° S, at depths ranging between 50 and 500 m (Cousseau & Perrota, 1998). Adults of this demersal species make daily vertical migrations to feed in the upper layers of the sea during the night (Angelescu & Prenske, 1987). For assessment purposes, two different stocks were identified: the northern stock (between 34° and 41° S) and the southern one (between 41° and 55° S), also known as the Patagonian stock (Bezzi *et al.*, 1995). The latter is the most abundant, with a spawning biomass of around 200 000 t estimated during 2012 (MAGyP, 2012).

Spawning of the Patagonian stock of *M. hubbsi* takes place during late spring (December) and summer (January to March) in the Isla Escondida sector (43–45° 30' S) (Pájaro *et al.*, 2005) of the north Patagonian region. Individuals undergo a series of pelagic stages from eggs to larvae and juveniles. It has been reported that during late summer and early autumn of their first year of life, at a size of *c.* 20 mm total length ( $L_T$ ), larvae metamorphose to juveniles, settle to the bottom (Bezzi *et al.*, 2004) and begin a diel vertical migratory behaviour similar to that of the adults (occupying pelagic waters during the night and descending close to the bottom during daylight) (Ehrlich, 1998; Buratti & Santos, 2010). These age-0+ year juveniles (*c.* 20–150 mm  $L_T$ ) also undergo an onshore and south-westward drift to reach as far as the inner San Jorge Gulf (SJG; 45–47° S). The settlement ground is then defined as encompassing the spawning ground and extending to the SJG (Fig. 1), which represents their main nursery area (Sabatini, 2004; Álvarez-Colombo *et al.*, 2011). As individuals would be occupying the bottom of the gulf most of the day, an increase in the importance of epibenthic prey in the diet of juveniles could be expected. Preliminary observations in the southern sector of the nursery area (P. Moriondo, pers. comm.) showed, however, that age-0+ year individuals (30–100 mm) prey mainly on pelagic items such as euphausiids. Therefore, further information is needed for a better comprehension of how these juveniles exploit food resources while undergoing the transition from pelagic to demersal habitat utilization in their nursery area. This

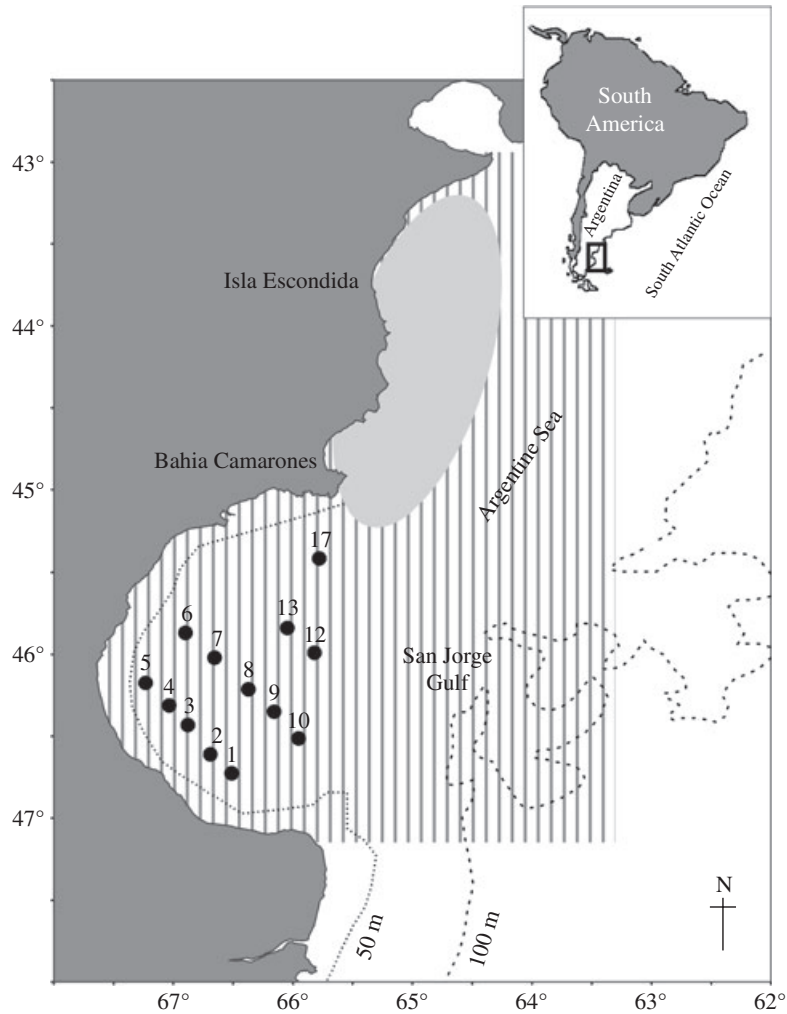


FIG. 1. Location of the *Merluccius hubbsi* survey hauls (●) for age-0+ year juvenile *Merluccius hubbsi* in the San Jorge Gulf. Spawning (■) and nursery (|||||) areas are shown (modified from Sabatini, 2004).

study provides (1) a quantitative taxonomic description of age-0+ year *M. hubbsi* diet within the SJG, (b) an evaluation of the potential effect of  $L_T$ , spatial distribution and time of day on diet composition and (c) an analysis of juvenile *M. hubbsi* feeding strategy in terms of prey incidence, degree of generalization or specialization and trophic niche width. Assessing the feeding habits of these individuals will aid in understanding the dynamics of predator–prey interactions and the key prey selected at this ontogenetic stage. Furthermore, information presented is relevant in the context of recruitment studies as age-0+ year *M. hubbsi* individuals represent a stage prior to the final settling of the juveniles and their further incorporation into the adult population.

TABLE I. Details of the *Merluccius hubbsi* survey hauls and the stomachs sampled per haul in the San Jorge Gulf during January 2010; morning: 0700–1059 hours, afternoon: 1100–1559 hours and sunset: 1600–1900 hours

Haul number	Date	Time of day	Depth (m)	Total stomachs	Full	Empty	Discarded	Mean $\pm$ s.d. $L_T$ (mm)
1	16 January 2010	Afternoon	65	28	27	1	0	134.2 $\pm$ 9.0
2	16 January 2010	Sunset	85	46	38	7	1	124.1 $\pm$ 12.8
3	17 January 2010	Morning	86	33	33	0	0	130.9 $\pm$ 10.3
4	17 January 2010	Morning	84	36	33	3	0	129.3 $\pm$ 13.1
5	17 January 2010	Morning	87	39	35	3	1	124.4 $\pm$ 14.7
6	17 January 2010	Afternoon	88	42	34	7	1	114.0 $\pm$ 13.5
7	17 January 2010	Sunset	94	23	16	6	1	112.6 $\pm$ 17.0
8	18 January 2010	Morning	100	69	54	10	5	107.4 $\pm$ 20.4
9	18 January 2010	Morning	96	62	54	7	1	114.6 $\pm$ 17.8
10	18 January 2010	Morning	87	44	35	6	3	127.1 $\pm$ 13.3
12	18 January 2010	Sunset	97	42	33	9	0	129.7 $\pm$ 12.8
13	18 January 2010	Sunset	98	42	38	3	1	120.8 $\pm$ 16.4
17	20 January 2010	Morning	91	23	22	1	0	128.4 $\pm$ 9.8

$L_T$ , total length.

## MATERIALS AND METHODS

### STUDY AREA AND SAMPLING

The SJG is a half-open basin located between 45° and 47° S and 65° 30' W and the coast, with maximum depths of >110 m in the central region. The gulf is occupied by shelf waters, that are modified by the contribution of low salinity coastal waters (33.0–33.6) flowing from the Magellan Strait. In both extremities of the gulf, which exhibit the lowest depths, the vertical mix affected by winds and tides generates seasonal frontal systems mainly during spring and autumn (Guerrero & Piola, 1997; Fernández *et al.*, 2005). This gulf constitutes an important spawning and fishing area for several species of commercial interest, such as *M. hubbsi* (Bezzi *et al.*, 2004) and shrimp *Pleoticus muelleri* (Fernández *et al.*, 2008).

Samples of *M. hubbsi* juveniles were collected during a research survey carried out by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) in the SJG in January 2010 (Fig. 1). Specimens were captured at depths between 65 and 100 m during daylight, by using a bottom trawl (100 mm mesh at codend with an intranet cover of 20 mm mesh size, headrope of 35.5 m and footrope of 50.0 m; Table I). Speed and time of the survey hauls ( $n = 13$ ) were 4 knots (*c.* 7 km h<sup>-1</sup>) and 30 min. All the *M. hubbsi* caught were immediately frozen at -20° C to ensure that the digestion of the stomach contents was halted.

Once in the laboratory, the specimens were measured ( $L_T$ , mm, and maxilla length  $L_M$ , mm) and weighed (wet mass) to the nearest 0.01 g. Juveniles were placed in three size classes: 60–89, 90–119 and 120–150 mm. The opening of the mouth ( $M_O$ , mm) was calculated according to Shirota (1970), who considered a 90° angle limited by the jaws during the feeding, where  $M_O = 2^{0.5} L_M$ .

### OVERALL DIET COMPOSITION

Stomachs were removed, weighed to the nearest 0.001 g with and without their contents, and the contents were preserved in a 5% formalin solution. Those everted during capture or damaged during dissection were discarded from the analysis. A subjective digestion state, based on appearance and texture, was assigned to each stomach content as follows: 1 = fresh, 2 = partially digested and 3 = totally or almost totally digested.

Prey species were measured and identified to the lowest possible taxon and developmental stage. The eye diameter ( $D_E$ , along the anteroposterior axis, mm), carapace ( $L_C$ , from the tip of the rostrum to the mid-dorsal posterior edge, mm) and sub-total length [ $L_{ST}$ , from the tip of the rostrum to the posterior end of the sixth abdominal somite (Pérez Seijas, 1987), mm] of euphausiids were measured, whereas the eye height ( $H_E$ , mm), eye width ( $W_E$ , mm) and total length [ $L_T$ , from the anterior part of the head, excluding the antennae, to the posterior end of the last pair of uropods (Sheader & Evans, 1975), mm] were measured for amphipods. For copepods, total length ( $L_T$ , from the anterior end of the cephalothorax to the posterior margin of the caudal rami, excluding furcal setae, mm), prosome length ( $L_P$ , mm) and width ( $W_P$ , mm) were measured. Wet or dry mass values for prey items were estimated using length and mass relationships available from the literature (Table II). Biovolumes for copepods were corrected by a 1.025 specific gravity factor to derive wet mass (Chojnacki & Hussein, 1983). For damaged organisms of the hyperiid amphipod *Themisto gaudichaudii* and the euphausiid *Euphausia lucens*, total and sub-total length, respectively, were estimated from their remnants, which resist digestion (eyes and carapace), using the equations proposed by Temperoni *et al.* (2013), as a step prior to calculating their mass.

## DATA ANALYSIS

Feeding incidence ( $I_F$ ) was calculated as the percentage of individuals with at least one prey item in their stomach (Arthur, 1976). A stomach fullness index ( $\%I_{SF}$ ) was calculated following Angelescu (1979) as  $\%I_{SF} = 100 W_c W_f^{-1}$ , where  $W_c$  is the stomach content mass and  $W_f$  is the total mass of the fish. The  $\%I_{SF}$  allowed the establishment of different levels of the fullness scale:  $<5\% = 0-I$  (stomachs with an advanced state of digestion),  $5-10\% = II$  (fullness below 50% of the maximum),  $11-13\% = III$  (fullness above 50% of the maximum) and  $>14\% = IV$  (maximum fullness).

The contribution of each prey category ( $i$ ) to the diet of juvenile *M. hubbsi* was examined through its frequency of occurrence ( $\%O_i$ ), percentage by number ( $\%N_i$ ) and by mass ( $\%W_i$ ). Each of these three measurements provides a different insight into the feeding habits of fishes (Hyslop, 1980). To integrate the three parameters, an index of relative importance ( $I_{RI}$ ) (Pinkas *et al.*, 1971) was calculated as  $I_{RIi} = \%O_i (\%N_i + \%W_i)$ . For each prey item, this index was expressed as  $I_{RI} = 100 I_{RI} \sum I_{RI}^{-1}$  (Cortés, 1997).

Changes in diet composition were assessed by building generalized linear models (GLM) with the R statistical software, version 2.15.1 ([www.r-project.org](http://www.r-project.org)). Fish  $L_T$ , spatial distribution ( $H_{1-13}$ ) (represented by the position of the hauls) and time of day ( $T_{\text{morning}}$ , 0700–1059 hours;  $T_{\text{afternoon}}$ , 1100–1559 hours;  $T_{\text{sunset}}$ , 1600–1900 hours) were used as the explanatory variables and the percentage of stomachs with food and the number of prey for the main consumed items as the response variables. As GLMs assume a linear relationship between the response and the explanatory variables, possible curvilinear relationships were first assessed by fitting generalized additive models (GAM) (Wood, 2006). If GAMs detected a significant non-linear relationship, then appropriate terms were included in the GLMs (*e.g.* quadratic functions) to account for this relationship. Models with the percentage of stomachs with food as the response variable had a binomial error distribution and a link logit, whereas those with count data (number of prey as the response variable), where there are too many zeros and the variance is often much greater than the mean, had a negative binomial error distribution and a log link (Crawley, 2005). The model with the lower value (most plausible model) of the Akaike information criterion (AIC) was selected as the best one and was weighed against the others using Akaike's weight ( $A_w$ ).  $A_w$  values vary between 0 (poor fit) and 1 (good fit) and provide an estimation of the likelihood of the model given the data (Johnson & 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 consumption of a major prey group.

## GRAPHICAL ANALYSIS OF FEEDING STRATEGY

The feeding strategy of juvenile *M. hubbsi* was analysed graphically with the method proposed by Amundsen *et al.* (1996), which incorporated the prey-specific abundance (volume, number or mass) into the Costello (1990) analysis. The Amundsen method is

TABLE II. Length and mass relationships applied to estimate the mass of different prey items in stomach contents of age-0+ year *Merluccius hubbsi*

Prey item	Equation	Source	R <sup>2</sup>
<i>Euphausia lucens</i> (♀)	$\ln W_w (g \ 10^{-2}) = -4.6 + 2.07 \times \ln L_{ST} (mm)$	Pérez Seijas (1987)	0.92
<i>Themisto gaudichaudii</i> (♀-♂)	$\ln W_D (mg) = -5.31 + 2.4 \times \ln L_T (mm)$	Álvarez-Colombo & Viñas (1994)	0.92
<i>Munida</i> spp. (♀)	$W_D (g) = 5.66 \times 10^{-4} \times L_C^{3.13} (mm)$	Rodríguez & Bahamonde (1986)	0.94
<i>Munida</i> spp. (♂)	$W_D (g) = 4.16 \times 10^{-4} \times L_C^{3.25} (mm)$		0.96
<i>Peisos petrunkevitchii</i> (♀)	$W_w (mg) = 0.02 \times 10^{-3} \times L_T^{2.75} (mm)$	Mallo & Boschi (1982)	0.91
<i>P. petrunkevitchii</i> (♂)	$W_w (mg) = 0.03 \times 10^{-3} \times L_T^{3.25} (mm)$		0.91
<i>Ctenocalanus vanus</i> (♀-♂)	$\ln_e W_w (mg) = -0.47 + 2.27 \times \ln W_P (mm)$	Mallo & Boschi (1982)	0.83
<i>Drepanopus forcipatus</i> (♀)	$\ln_e W_w (mg) = 0.11 + 2.8 \times \ln W_P (mm)$	Fernández Aráoz (1991)	0.98
<i>D. forcipatus</i> (♀)	$\ln_e W_w (mg) = -2.62 + 3.64 \times \ln W_P (mm)$	Fernández Aráoz (1991)	0.97
<i>D. forcipatus</i> (♂)	$\ln_e W_w (mg) = -2.04 + 2.3 \times \ln L_P (mm)$	Fernández Aráoz (1991)	0.73
<i>Calanus australis</i> (♀)	$\ln_e W_w (mg) = -0.37 + 2.36 \times \ln W_P (mm)$	Fernández Aráoz (1991)	0.91
<i>C. australis</i> (♂)	$\ln_e W_w (mg) = -3.52 + 3.6 \times \ln L_P (mm)$	Fernández Aráoz (1991)	0.91
<i>Calanoides carinatus</i> (♀)	$\ln_e W_w (mg) = 0.24 + 2.04 \times \ln W_P (mm)$	Fernández Aráoz (1991)	0.69
<i>C. carinatus</i> (♂)	$\log V (\mu m^3) = 1.94 + 2.39 \times \log W_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.97
<i>Centropages brachiatus</i> (♀-♂)	$\ln_e W_w (mg) = -0.26 + 2.37 \times \ln_e W_P (mm)$	Fernández Aráoz (1991)	0.94
<i>Acartia tonsa</i> (♀)	$\ln_e W_w (mg) = -0.71 + 1.84 \times \ln_e W_P (mm)$	Fernández Aráoz (1991)	0.78
<i>A. tonsa</i> (♂)	$\ln_e W_w (mg) = -3 + 3.51 \times \ln_e L_P (mm)$	Fernández Aráoz (1991)	0.73
<i>Oithona similis</i>	$W_w (\mu g) = 9.4 \times 10^{-7} \times L_P^{2.16} (\mu m)$	Sabatini & Kiorboe (1994)	0.89
<i>Oithona nana</i> (♀)	$\log V (\mu m^3) = 1.99 + 2.1 \times \log W_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.92
<i>O. nana</i> (♂)	$\log V (\mu m^3) = 3 + 1.65 \times \log W_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.7
<i>Paracalanus parvus</i> (♀)	$\log V (\mu m^3) = 1.9 + 2.24 \times \log W_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.96
<i>P. parvus</i> (♂)	$\log V (\mu m^3) = 0.84 + 2.74 \times \log W_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.98
Calanoid copepodites < 1 mm	$\log V (\mu m^3) = 0.16 + 2.97 \times \log W_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.98
Calanoid copepodites < 1 mm	$\log V (\mu m^3) = -2.31 + 3.43 \times \log L_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.97
Calanoid copepodites 1–2 mm	$\log V (\mu m^3) = 0.16 + 2.97 \times \log W_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.98
Calanoid copepodites 1–2 mm	$\log V (\mu m^3) = -2.31 + 3.43 \times \log L_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.97
Calanoid copepodites > 2 mm	$\log V (\mu m^3) = -0.2 + 3.1 \times \log W_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.99
Cyclopoid copepodites	$\log V (\mu m^3) = 0.57 + 2.71 \times \log W_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.99
Cyclopoid copepodites	$\log V (\mu m^3) = -2.66 + 3.7 \times \log L_P (\mu m)$	Viñas <i>et al.</i> (2010)	0.98

W<sub>w</sub>, wet mass; W<sub>D</sub>, dry mass; L<sub>ST</sub>, sub-total length; L<sub>T</sub>, total length; L<sub>C</sub>, carapace length; L<sub>P</sub>, prosome length; W<sub>P</sub>, prosome width; V, biovolume.

based on a two-dimensional representation where each point relates the % $O_i$  of a prey to its prey-specific number % $N_{pi}$ . In mathematical terms, % $N_{pi} = 100 \sum N_i \sum N_{ti}^{-1}$ , where  $N_i$  is the stomach content (number) comprising prey  $i$  and  $N_{ti}$  is the total stomach content in only those predators with prey  $i$  in their stomach. Then, information about three elements can be extracted, considering the distribution of points along the diagonals and axes of the graph: the prey importance, the feeding strategy in terms of specialization and generalization either at the individual or the population level and the population niche width, which characterizes the food resource spectrum used by individuals and considers both between and within-phenotype variations.

In addition, niche width was estimated quantitatively by means of the Levins's standardized index  $\{B = (n - 1)^{-1} [(\sum_j p_j^2)^{-1} - 1]\}$ , where  $p_j$  = proportion of predator diet that is made up of prey  $j$  and  $n$  = number of prey categories (Levins, 1968).  $B$  takes values between 0 and 1; values <0.6 represent strongly specialized feeders that prey on few taxa, whereas values >0.6 indicate generalist feeders with no preference for any taxa (Krebs, 1989).

## RESULTS

### OVERALL DIET COMPOSITION AND DIETARY SHIFTS

A total of 529 stomachs were examined. Age-0+ year juveniles ranged in size from 68 to 151 mm  $L_T$  (mean  $\pm$  S.D. = 122.4  $\pm$  16.7 mm) (Fig. 2). Feeding incidence was 85% ( $n = 452$ ), while empty stomachs represented 12% ( $n = 63$ ) and discarded (either everted or damaged during dissection) 3% ( $n = 14$ ) of the total. According to % $I_{SF}$  (mean  $\pm$  S.D. = 1.15  $\pm$  1.00%), 98.9% of the stomachs were in state 0–I, *i.e.* stomachs with an advanced state of digestion. Twelve different taxa belonging to eight categories within the crustaceans and the chaetognaths were recorded (Table III). Crustaceans, mainly represented by *T. gaudichaudii* and *E. lucens*, were the principal prey consumed, with frequencies of occurrence of 85 and 61%. Both species accounted for 99% by mass of the total prey items consumed. When considering their relative importance, however, *E. lucens* was the most important prey in the diet of juvenile *M. hubbsi* (% $I_{RI} = 60\%$ ), followed by *T. gaudichaudii* (% $I_{RI} = 40\%$ ).

The percentage of stomachs with food was best explained by a model that included fish  $L_T$  and time of day (afternoon) as explanatory variables ( $AIC_{\text{best model}} = 373.07$ ,  $AIC_{\text{null model}} = 384.17$ ), while it was independent of the spatial distribution. Parameters of the GLM model were (S.E. in parentheses): intercept =  $-1.11$  (0.89),  $L_T = 0.028$  (0.007) and  $T_{\text{afternoon}} = -0.68$  (0.3), which indicate that the percentage of stomachs with food increased with fish  $L_T$ , and was lower during the afternoon. The GLM analyses also showed that the number of the main consumed items (*T. gaudichaudii* and *E. lucens*) increased with fish  $L_T$  (Table IV), even though fish  $L_T$  was not highly correlated with the total number of prey consumed (Spearman rank correlation coefficient  $r = 0.33$ ,  $P < 0.01$ ). In addition, maximum mouth opening of juveniles was significantly and positively correlated with fish  $L_T$  ( $r = 0.89$ ,  $P < 0.01$ ). Most individuals, however, despite their mouth gape and length, ingested prey items within a size range of 5–15 mm (Fig. 3), corresponding to *E. lucens* and *T. gaudichaudii*, and only a few (>110 mm) consumed larger epibenthic prey such as juveniles of *Munida* spp., adults of *Peisos petrunkevitchii* and Stomatopoda larvae.

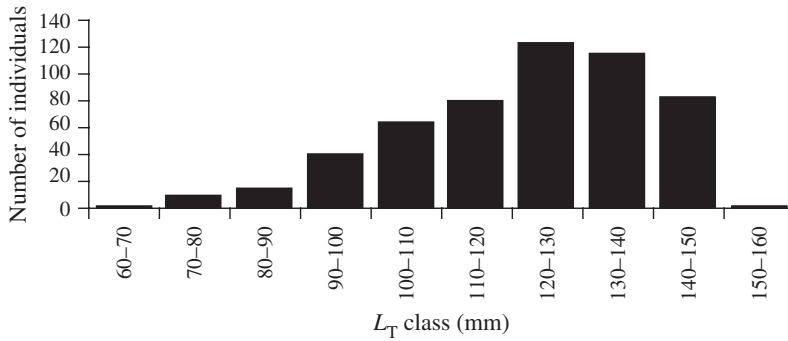


FIG. 2. Total length ( $L_T$ )–frequency distribution of age-0+ year juvenile *Merluccius hubbsi*.

### GRAPHICAL ANALYSIS OF FEEDING STRATEGY

In the Amundsen *et al.* (1996) diagram [Fig. 4(a)], the diagonal from the lower left to the upper right corner provides a measure of prey importance, with dominant prey at the upper, and rare or unimportant prey at the lower end. The present results show that *T. gaudichaudii* and *E. lucens* are the most important prey in the diet of juvenile

TABLE III. Taxonomic list of prey items in age-0+ year *Merluccius hubbsi* diet

Prey item ( <i>i</i> )	% $O_i$	% $N_i$	% $W_i$	$I_{RI}$	% $I_{RI}$	% $N_{Pi}$
Subphylum Crustacea						
Order Amphipoda						
<i>Themisto gaudichaudii</i>	84.65	54.22	6.90	5173.81	39.90	57.77
Gammarids	17.16	4.96	–	–	–	29.23
Order Euphausiacea						
<i>Euphausia lucens</i>	61.40	33.38	92.45	7725.96	59.58	43.75
<i>Nematoscelis megalops</i>	1.58	0.28	–	–	–	5.37
Subclass Copepoda						
Order Cyclopoida	2.93	0.56	<0.01	1.64	0.01	14.05
Order Calanoida	2.48	1.36	0.01	3.40	0.03	13.49
Order Mysida						
<i>Mysidopsis rionegrensis</i>	2.93	2.44	–	–	–	30.00
Order Decapoda						
<i>Peisos petrunkevitchii</i>	2.93	1.16	0.05	3.55	0.03	35.76
Non-identified larvae	0.68	0.09	–	–	–	7.84
<i>Munida</i> spp.	0.45	0.13	0.59	0.32	<0.01	12.77
Order Stomatopoda						
Non-identified larvae	5.64	1.25	–	–	–	12.65
Phylum Chaetognatha						
<i>Sagitta friderici</i>	0.23	0.02	–	–	–	16.67
Other						
Non-identified remains (NI)	0.45	0.15	–	–	–	10.94

% $O_i$ , frequency of occurrence; % $N_i$ , percentage number; % $W_i$ , percentage mass;  $I_{RI}$ , index of relative importance; % $I_{RI}$ , per cent  $I_{RI}$ ; % $N_{Pi}$ , prey-specific number.



TABLE IV. Best models explaining consumption in numbers of major prey groups in age-0+ year *Merluccius hubbsi*. For each model, parameters, standard errors (in parentheses), Akaike's weights ( $A_w$ ) and Akaike information criterion (AIC) are given

Prey item	Model	AIC	$A_w$
<i>Themisto gaudichaudii</i>	GLM = $-3.73$ (0.6) + $0.026$ (0.003) $L_T$ + $1.8$ (0.36)	2304.1	0.99
	$H_2$ + $3.04$ (0.35) $H_3$ + $2.03$ (0.36) $H_4$ + $2.13$ (0.36)		
	$H_5$ + $2.25$ (0.37) $H_6$ + $1.69$ (0.43) $H_7$ + $2.65$ (0.35)		
	$H_8$ + $1.8$ (0.35) $H_9$ + $1.84$ (0.36) $H_{10}$ + $1.84$ (0.36)		
	$H_{12}$ + $2.38$ (0.36) $H_{13}$ + $2.82$ (0.37) $H_{17}$		
<i>Euphausia lucens</i>	GLM = $-3.66$ (0.78) + $0.03$ (0.005) $L_T$ + $0.99$ (0.4)	1839.1	0.99
	$H_3$ + $1.77$ (0.4) $H_4$ + $1.8$ (0.4) $H_5$ + $1.16$ (0.4)		
	$H_{10}$ + $1.23$ (0.4) $H_{13}$		

$L_T$ , total length;  $H_n$ , survey haul (Table I); GLM, generalized linear model.

*M. hubbsi* [Fig. 4(b)]. The vertical axis represents the feeding strategy in terms of specialization or generalization. The predator has specialized on prey types positioned in the upper part of the graph, whereas prey positioned in the lower part have been eaten less frequently. Juvenile *M. hubbsi* specialized, at a population level, on *T. gaudichaudii* and *E. lucens*, and from a size of *c.* 110 mm ingested epibenthic prey such as gammarids, *P. petrunkevitchii*, *Munida* spp. and *Mysidopsis rionegrensis* [Fig. 4(b)]. There were neither high within nor between-phenotype contributions to the niche width, as no points were located along the diagonal from the upper left to the lower right, which according to Amundsen *et al.* (1996) indicates a narrow niche width for juvenile *M. hubbsi* in the SJG. In agreement, the Levins's index value  $<0.6$  ( $B = 0.12$ ) also suggests that juveniles would be specialized feeders preying on few taxa.

## DISCUSSION

This study constitutes a detailed investigation of the feeding habits of juvenile *M. hubbsi* in the SJG, which constitutes the main nursery ground for the species in the Patagonian region. Even though stomach content studies have the potential disadvantage of either over or underestimating some prey species owing to differential digestion of body structures, these techniques are very useful in species in which direct observation of trophic behaviour in nature is not possible (Ocampo Reinaldo *et al.*, 2011). Such studies are usually associated with difficulties regarding the high incidence of empty stomachs (Ciechomski & Weiss, 1974). Constraints of this kind were not found in this work, however, due to the gut morphology of *M. hubbsi*. At a size of *c.* 3 mm, gut widening takes place and, as development advances, several gut folds appear (Ciechomski & Weiss, 1974), which provide additional space for food accumulation and retention, as reported for Pacific hake *Merluccius productus* (Ayres 1855) (Sumida & Moser, 1980). Thus, a high feeding incidence was observed (85%), suggesting that the resources available in the SJG might be sufficient to sustain the age-0+ year *M. hubbsi* population. High phytoplankton production (Carreto *et al.*, 2007) and elevated abundances of meso and macrozooplankton (Pérez Seijas *et al.*,

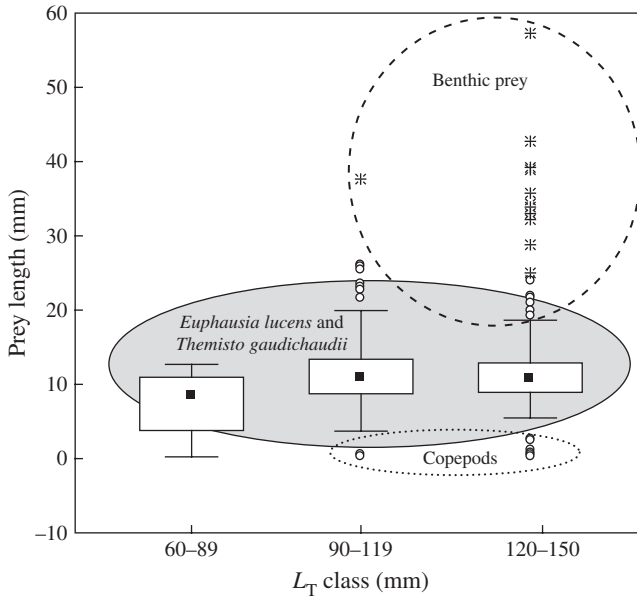


FIG. 3. Box plots of prey length in three different age-0+ year juvenile *Merluccius hubbsi* total length ( $L_T$ ) classes ( $n = 733$ ). The box centre square represents the median of the prey length at each size class, while the box limits are an approximation of the first and third quartiles (Q). The whiskers represent the non-outlier range, *i.e.* the range of values which fall below the upper outlier limit [ $1.5 \times$  (upper value of the box – lower value of the box)] and above the lower outlier limit [ $-1.5 \times$  (upper value of the box – lower value of the box)], with 1.5 corresponding to the outlier coefficient by default. Outliers and extreme values are presented.

1987; Viñas *et al.*, 1992; Santos, 1994), shrimps (Bezzi *et al.*, 2004) and decapods (Vinuesa & Varisco, 2007) have been reported in this gulf.

The diet of juvenile *M. hubbsi* in the SJG was almost exclusively pelagic, represented mainly by the hyperiid amphipod *T. gaudichaudii* and the euphausiid *E. lucens*. Pelagic feeding occurs at night, as a high proportion (almost 99%) of stomachs in the lowest state of satiation was observed during daylight, as previously described by Angelescu & Prenski (1987). The low incidence of epibenthic prey found only in larger individuals ( $>110$  mm  $L_T$ ) suggests a gradual transition to fully developed demersal habitat utilization, as reported for other gadids (Bowman, 1981). In agreement, the incorporation of higher proportions of epibenthic and fish prey was observed in the diet of age-1+ and age-2+ year juveniles ( $>150$  mm  $L_T$ ) within the gulf in summer, indicating a reduction in the amplitude of vertical migrations by larger individuals that remain close to the bottom for longer periods. Pelagic crustaceans, however, such as *E. lucens* and *T. gaudichaudii*, were among the main food items (Sánchez & García de la Rosa, 1999; Sánchez, 2009).

The importance of amphipods and euphausiids in the diet of age-0+ year juveniles has previously been pointed out for European hake *Merluccius merluccius* (L. 1758) (Mahe *et al.*, 2007), cape hake *Merluccius capensis* Castelnau 1861 (Pillar & Barange, 1993) and silver hake *Merluccius bilinearis* (Mitchill 1814) (Koeller *et al.*, 1989). The energetic gain from feeding on lower trophic levels as a result of reduced

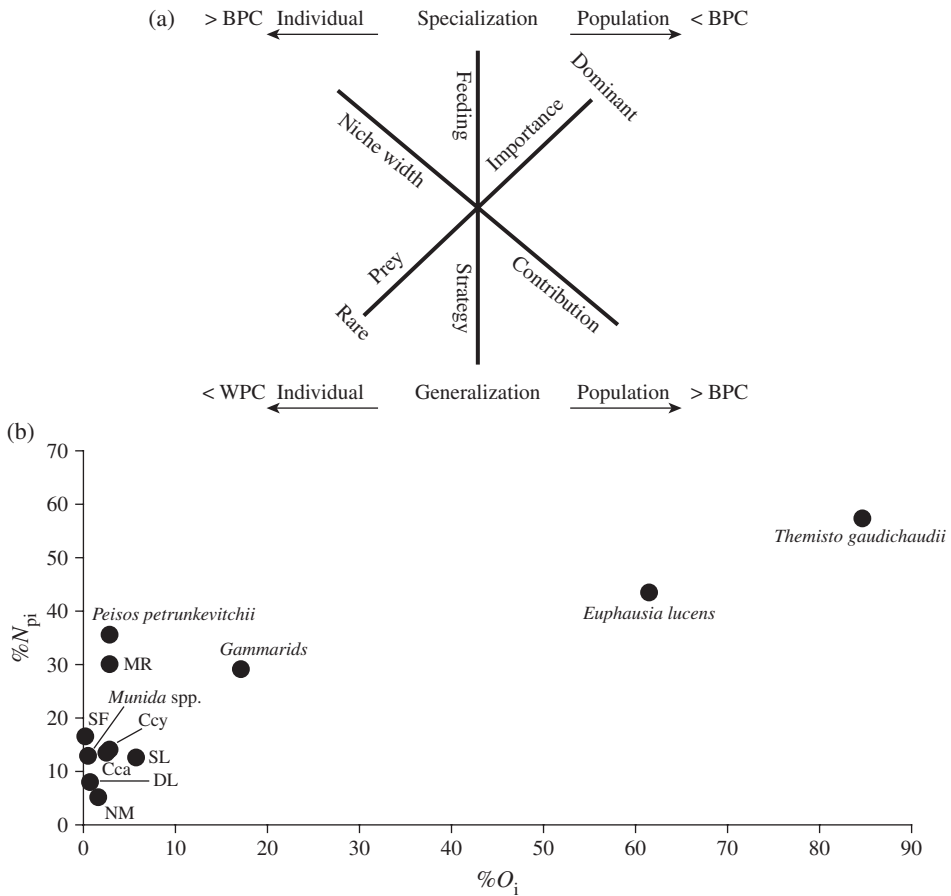


FIG. 4. (a) Amundsen *et al.* (1996) diagram relating frequency of occurrence ( $%O_i$ ) of a prey to its specific number ( $%N_{pi}$ ) to interpret prey importance, feeding strategy and trophic niche width of a predator and (b) schematic representation of age 0+ year juvenile *Merluccius hubbsi* feeding strategy according to the Amundsen *et al.* (1996) method. BPC, between-phenotype component; WPC, within-phenotype component; MR, *Mysidopsis rionegrensis*; NM, *Nematoscelis megalops*; SF, *Sagitta friderici*; DL, Decapoda larvae; SL, Stomatopoda larvae; Cca, calanoid copepods; Ccy, cylopoid copepods.

cost of capture due to lack of pursuit and lesser handling time justifies the high incidence of zooplankton over fish prey in the diet during the entire life cycle of the species (Sánchez & García de la Rosa, 1999). Also, a swarming behaviour has been reported for *T. gaudichaudii* and *E. lucens* (Gray & McHardy, 1967; Nicol *et al.*, 1987), allowing the juveniles to feed without investing much energy. Furthermore, both a rapid adaptation to self-propulsion and the mechanical support due to the complete development of the fins (Ciechomski & Weiss, 1974; Palomera *et al.*, 2005; Betti *et al.*, 2009) might be decisive factors in juvenile trophic ecology, affecting not only the frequency of encounter with prey but also the capture efficiency.

The present results following Amundsen's criterion and the Levins's index show that, within their nursery ground, all individuals in the age-0+ year juvenile population are specialist predators with a narrow trophic niche of two dominant prey

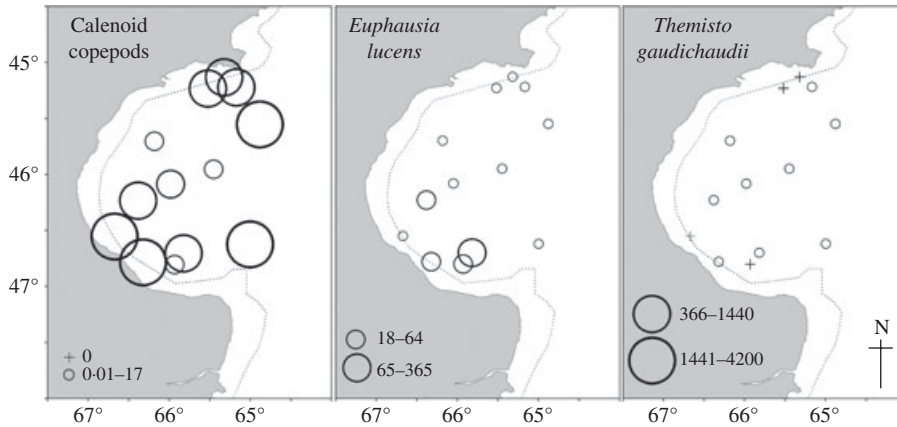


FIG. 5. Abundance (individuals  $m^{-3}$ ) of the zooplankton components within the San Jorge Gulf in January 1985. Modified from Pérez Seijas *et al.* (1987).

(*T. gaudichaudii* and *E. lucens*), although they include small proportions of other items in the diet. Similar results were reported for age-0+ year *M. hubbsi* in the San Matías Gulf (Ocampo Reinaldo *et al.*, 2011). When considering prey choice, age-0+ year *M. hubbsi* juveniles may not be simple opportunistic feeders, adapting to the available zooplankton prey, as found in other species of the genus (Koeller *et al.*, 1989). For instance, *T. gaudichaudii* and *E. lucens* were preferred to others, even though previous data showed that their abundances are low in the area in January, while copepods represent a more available prey [Pérez Seijas *et al.* (1987); Fig. 5]. Moreover, *Munida* spp. was not selected as a main prey, although it is highly abundant in the SJG (Vinuesa & Varisco, 2007). A similar behaviour was found for *M. capensis* (Pillar & Barange, 1993) and *M. merluccius* (Bozzano *et al.*, 1997; Mahe *et al.*, 2007). While balancing the cost and the benefits, predators foraging optimally can adjust their preferences to take into account prey quality rather than prey abundance (Anthony *et al.*, 2000). Interestingly, *T. gaudichaudii* and *E. lucens* tend to be more lipid-rich than other available prey in the environment (Nelson *et al.*, 2001; Gigliotti *et al.*, 2010). A diet high in lipids provides sufficient metabolic energy for maintenance, so dietary protein can be allocated to tissue synthesis and growth (Pinnegar *et al.*, 2003). Thus, these crustaceans may constitute the nutritionally beneficial items to sustain age-0+ year juveniles while growing in their nursery area, before they recruit to the pre-adult and adult fractions of the population in shelf waters (Macchi *et al.*, 2007).

The almost exclusively pelagic prey found in age-0+ year juveniles (60–150 mm  $L_T$ ) suggest that final settling and permanent demersal habitat utilization might not occur at the early size of 20 mm, as previously reported, but would be at larger sizes. In this sense, recent observations within the SJG based on acoustic surveys and confirmed by pelagic trawls showed that age-0+ year juveniles school during daylight in a thick layer (*c.* 10–12 m in height) as far as *c.* 10–15 m from the bottom, but are dispersed in the water column at night (G. Álvarez Colombo, pers. comm.), probably following the migration pattern of their main prey (Williams & Robins, 1981; Gibbons *et al.*, 1991). Analogous findings have been reported for other

gadoids worldwide (Olsen & Soldal, 1989; Grant & Brown, 1998). The distribution of juveniles *c.* 10–15 m from the bottom during daylight could be an avoidance strategy against intercohort cannibalism, mainly by age-1+ and age-2+ year conspecifics already settled at the bottom and able to migrate only a few metres from it (Sánchez & García de la Rosa, 1999). A similar behaviour was described for *M. capensis* (Huse *et al.*, 1998). Moreover, SJG seabed is characterized by the presence of the stomatopod *Pterygosquilla armata*, *Munida gregaria*, and the bivalves *Corbula patagonica* and *Nucula* sp. (Bremec *et al.*, 2012) and lack the physical structure that could provide shelter for age-0+ year individuals, as found in other gadids (Gotceitas & Brown, 1993; Lindholm *et al.*, 1999). Hence, the age-0+ year *M. hubbsi*'s pelagic behaviour pattern may successfully maintain an adequate food intake while reducing predation risk.

Age-0+ year *M. hubbsi* feeding behaviour highlights the importance of this stage as a major intermediate in the energy flow between shallower (pelagic) and deeper (epibenthic) water communities, as has been stated for *M. merluccius* (Modica *et al.*, 2011). Although further studies are needed to clearly comprehend the events taking place during such an important phase, novel data presented here contribute to the knowledge of the biology and ecology of the age-0+ year stage in demersal fishes. Furthermore, this information could be useful in approaching the complex problem of determining the main factors controlling year-class strength of *M. hubbsi* in the Argentine Sea.

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