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Feeding strategy and cannibalism of the Argentine hake *Merluccius hubbsi*

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The diet composition and feeding strategy of the Argentine hake *Merluccius hubbsi* in the San Matías Gulf were analysed in order to use this information for the sustainable management of the fishery. *Merluccius hubbsi* behaved as an opportunistic predator. Small *M. hubbsi* consumed planktonic crustaceans, whereas medium and large fish ate numerous prey taxa with low frequency of occurrence and variable specific abundance. Intra- and intercohort cannibalism were detected in all size groups and were particularly significant in large *M. hubbsi*. Medium-sized *M. hubbsi* consumed small conspecifics and large-sized *M. hubbsi* consumed both small and medium *M. hubbsi*. These results indicate that the removal of large *M. hubbsi* by fishing may increase the risk of overfishing by two combined effects: a direct effect of recruitment-overfishing and an indirect effect of growth-overfishing through an enhanced cannibalism of medium *M. hubbsi* on small *M. hubbsi*. Intra- and intercohort cannibalism and other trophic relationships in the *M. hubbsi* should therefore be considered explicitly in stock assessment models.

Key words: bottom trawl fishery; diet; longline fishery; predation; San Matías Gulf, Patagonia; stomach contents.

INTRODUCTION

Most intermediate predatory fishes are generalist feeders that switch to invertebrate prey or cannibalism and eat many species of fishes at different stages in their life history (Kaiser & Jennings, 2002). Fishes can act as predators and prey and are capable of switching their diet and feeding behaviour in response to prey availability (Mittelbach, 2002). In various marine ecosystems, humans act as predators by fishing, causing a direct impact on the abundance of target species, and size-selective fishing results in a general decrease in the proportion of large individuals within populations (Pauly *et al.*, 2002; Hidalgo *et al.*, 2009). In temperate systems, the strongest evidence for the predator-based control of prey species comes from the impact of

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humans on their target species. The strength of this relationship is likely to result from the conservative fishing strategies used by humans (Kaiser & Jennings, 2002).

The Argentine hake *Merluccius hubbsi* Marini 1933 (Teleostei: Merlucciidae) is a target of the commercial trawl fishery in Argentina, Uruguay and Brazil. *Merluccius hubbsi* is a pelagic and demersal species that makes daily vertical migrations to feed in the upper layers of the sea during the night (Angelescu & Prenski, 1987). Previous studies have shown that *M. hubbsi* is an active and opportunistic predator that changes its diet during its lifetime (Angelescu & Prenski, 1987; Cousseau & Perrotta, 2004). Other variations in the diet of this species are determined by the seasonal occurrence of different prey, inter- and intracohort cannibalism and different feeding habits between sexes at maturity (Sánchez & García de la Rosa, 1999).

Two main stocks of *M. hubbsi* have been identified in the Argentine continental shelf (ACS) ('Northern stock' and 'Patagonian stock'; Fig. 1). These stocks are considered overexploited (Aubone *et al.,* 2004; Vaz-dos-Santos & Rossi-Wongtschowski, 2005; Vaz-dos-Santos *et al*., 2010). A third stock located within the San Matías Gulf (SMG; Fig. 1) is fished by both industrial bottom trawl and artisanal semi-pelagic near-bottom longline fleets, and several studies have shown that this stock completes its life cycle within SMG, constituting an independent demographic unit with its own spawning season in October to November (Di Giácomo *et al.,* 1993; Sardella & Timi, 2004; González *et al*., 2007; Ocampo Reinaldo, 2010; Machado Schiaffino *et al.,* 2011). The population structure of the stock of SMG seems to be well preserved since the beginning of the trawl fishery in 1971 (Ocampo Reinaldo, 2010; Romero *et al.,* 2010). Historically, *M. hubbsi* has constituted on average up to 80% of the annual landings in this fishery, being the most important species in economic terms (Fishery Statistics of Rio Negro Province, 2009; Romero *et al*., 2010).

Angelescu *et al*. (1958) postulated that the trophic relationships of the marine community of the north and centre of the marine Patagonian shelf are structured around the triad formed by *M. hubbsi*, the anchovy *Engraulis anchoita* Hubbs & Marini 1935 and squid (mainly the short-finned squid *Illex argentinus*). The most relevant trophic-fishing relationships that include *M. hubbsi* are: *M. hubbsi* and *E. anchoita*, *M. hubbsi* and squid and *M. hubbsi* and *M. hubbsi*. The first one includes *E. anchoita*, which is the most frequent species in food webs in the ACS, while the last one refers to cannibalism. *Merluccius hubbsi*, squid and *E. anchoita* are also prey of numerous top predators like marine mammals, sharks and rays (Angelescu & Prenski, 1987; Koen Alonso *et al.,* 1998, 2000, 2001; Dans *et al.,* 2003; Koen Alonso & Yodzis, 2005; Romero *et al*., in press).

Studies on the structure of marine communities and their trophic relationships in SMG started only very recently (Ocampo Reinaldo, 2010). In this ecosystem, some fishery species that play an important role in food webs show dramatic interannual abundance variations for unclear reasons (*e.g. I. argentinus*), while other species show seasonal variations apparently related to cyclical oceanographic processes, *e.g.* silver warehou *Seriolella porosa* Guichenot 1848 and Patagonian hoki *Macruronus magellanicus* Lönnberg 1907 (Romero *et al.,* 2007; Williams *et al.,* 2010).

Considering that *M. hubbsi* in SMG is the most important species in landings, biomass removal by fishing could be causing different effects over several components of the food web that are either directly or indirectly related to *M. hubbsi*. From a narrow perspective, fishing may also be affecting the demographic structure of the *M. hubbsi* stock and consequently cannibalistic pressure. The main objective of the

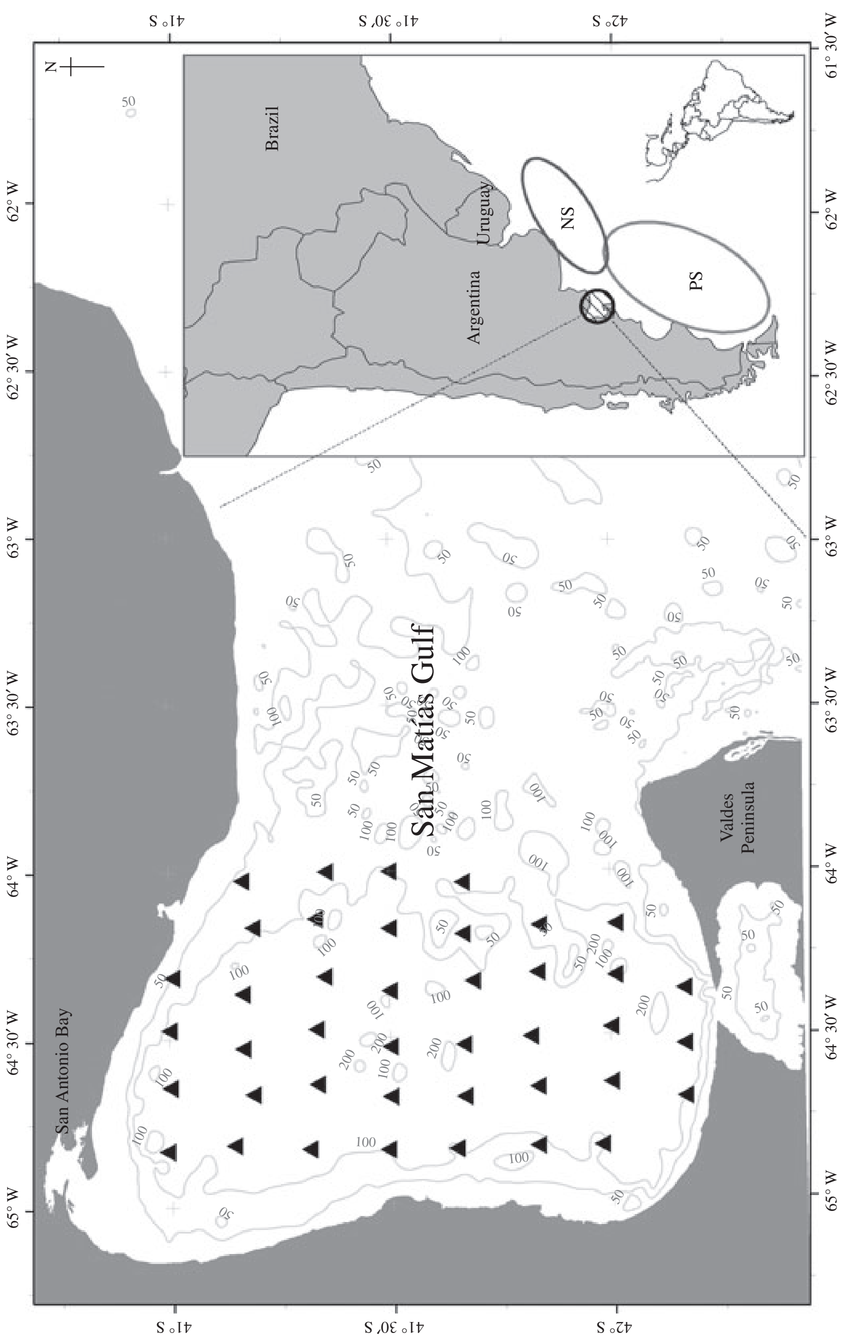

FIG. 1. Location of the three stocks of *Merluccius hubbsi* in Argentine waters. The greatest stock is known as Patagonic stock (PS), separated from the Northern stock (NS) shared by Argentina, Uruguay and Brazil. ▲, location of the hauls performed in the San Matías Gulf.

present work was to assess diet composition and feeding strategy of *M. hubbsi* in San Matías Gulf, in order to use this information for the sustainable management of the fishery. Also, the results are discussed in relation to other stocks in order to suggest potential impacts of fishing and cannibalism on the structure of the *M. hubbsi* population.

MATERIALS AND METHODS

STUDY AREA

The study area was the SMG (40° 50′ to 42° 15′ S; 63° 05′ to 65° 10′ W; Fig. 1), which is the second largest gulf in Argentina. The Gulf is *c*. 20 000 km^2 and 55% of its area is deeper than 100 m. The maximum depth is 180 m in the central area and the mouth is at the eastern side with a depth of 50–70 m (Williams *et al*., 2010). The Gulf is a semi-enclosed basin with relatively isolated waters (Piola & Scasso, 1988; Scasso & Piola, 1988; Rivas & Beier, 1990; Gagliardini & Rivas, 2004; Tonini *et al.,* 2006, 2007; Williams *et al.,* 2010).

SAMPLING AND STOMACH CONTENTS ANALYSIS

Merluccius hubbsi (6471 individuals) were obtained from 82 hauls along the SMG during the springs of 2006 and 2007 (October to November, 41 hauls each year; Fig. 1). Catches were obtained by bottom trawler and the individuals were classified in three total length (L_T) groups: group 1, ≤23 cm [small, young-of-the-year recruits (Renzi & Pérez, 1992; Romero *et al*., 2010)], group 2, 24–53 cm (medium-sized) and group 3, >53 cm (large). The distinction between medium- and large-sized fish was defined according to the differential growth between sexes starting at *c*. 53 cm L_T (females reach larger sizes than males) (Renzi *et al*., 2009; Ocampo Reinaldo, 2010). Individuals were weighed (g), dissected and each stomach was removed and stored deep-frozen (−20° C) in polyethylene bags. Empty stomachs and stomachs with digested contents (without recognizable prey) were discarded from the analysis. To characterize diet by sex, stomachs of individuals of undetermined sex were also discarded. The rarely found intact prey were identified, measured and weighed. Diagnostic hard parts (otoliths, bones and cephalopod beaks) were retrieved and stored in 70% ethanol. Prey were identified to the lowest possible taxonomic level using the reference collections of the *Instituto de Biología Marina y Pesquera 'Almirante Storni'* and the *Laboratorio de Mamíferos Marinos* (www.cenpat.edu.ar), and published catalogues (Menni *et al.,* 1984; Clarke, 1986; Boschi *et al.,* 1992; Gosztonyi & Kuba, 1996; Volpedo & Echevarría, 2000; García-Godos, 2001).

The total number of fishes consumed was determined from counts of left, right and unassigned otoliths. The minimum number per fish species was obtained as the sum of half the number of otoliths rounded up to the nearest whole number. The number of cephalopods was estimated as the maximum number of lower or upper beaks (Pierce & Boyle, 1991). The size (L_T of fishes and dorsal mantle length of squid in cm) and wet mass (g) of each prey were estimated from hard parts by allometric regressions [for fishes and *I. argentinus*, Koen Alonso *et al.,* 2000; for Nichol's lanternfish *Gymnoscopelus nicholsi* (Gilbert 1911) in replacement for Silvery lightfish *Maurolicus muelleri* (Gmelin 1789), Ivanovic, 2000; for small squid *Loligo* spp., Rodríguez *et al.,* 2002; for *M. hubbsi*, Ocampo Reinaldo, 2010; Marine Mammal Laboratory, unpubl.data].

DATA ANALYSIS

The importance of each prey (or ecological groups of prey when necessary) was evaluated using the percentage frequency of occurrence (%F), the percentage by number (%N), the percentage of the wet mass estimated by regression (%M) and the index of relative importance (%I_{RI}) (Pinkas *et al.,* 1971; Cortés, 1997; Koen Alonso *et al.,* 2000, 2001, 2002). The I_{RI} is a commonly used measure that provides a summary of dietary composition and is calculated from: $I_{RI} = (\%M + \%N)\%F$.

To account for uncertainty due to sampling, non-parametric 95% C.I. for $\%N$ and $\%M$ were generated by bootstrapping (Efron, 1979). The basic bootstrap procedure was written in Microsoft QBasic. Random samples were drawn with replacement and the procedure was repeated 1000 times.

Spearman rank correlation (r_S) (Conover, 1999) was used to evaluate cannibalism, assessing the relationship between predator size (male and female) and prey size (*M. hubbsi* acting as prey). The variables considered were predator L_T and the regression-estimated L_T of the prey.

FEEDING STRATEGY

The feeding strategy was assessed by Levin's standardized index (Levin's I_S) (Krebs, 1989) following Labropoulou & Eleftheriou (1997) and the Costello graphical method (Costello, 1990) modified by Amundsen *et al.* (1996). Diet breadth was evaluated using Levin's I_S: $B_i = (n-1)^{-1}[(\Sigma_j\, p_{ij}^2)^{-1} - 1]$, where B_i = Levin's standardized index for predator i, p_{ij} = proportion of diet of predator i that is made up of prey j and n = number of prey categories. This index ranges from 0 to 1; low values indicating diets dominated by few prey items (specialist predators) and higher values indicating generalist diets.

The Amundsen's method is based on a two-dimensional representation where each point relates the $\%F$ of a prey to its specific abundance ($\%P_i$): $\%P_i = 100[(\Sigma_i S_i)(\Sigma_{ti} S_{ti})^{-1}]$, where $\Sigma_i S_i$ = total number of prey i and $\Sigma_{ti} S_{ti}$ = total number of prey in the stomachs with prey i.

The interpretation of Amundsen's diagram can be obtained by examining the distribution of points along the diagonals and axes of the graph. The upward diagonal from the left to the right corner provides a measure of prey importance, with dominant prey at the top and rare or unimportant prey at the lower end. The vertical axis represents the feeding strategy of the predator in terms of specialization or generalization. Predators are specialized on the prey positioned in the upper part of the graph, whereas prey positioned in the lower part were eaten only occasionally (generalization). Prey located in the upper left of the diagram would be indicative of specialization by individual predators and those in the upper right would represent specialization of the predator population.

RESULTS

A total of 2113 stomachs with contents present were used to analyse the diet and 4358 empty stomachs were discarded (no food present or evidence of regurgitation; Table I). The sizes of *M. hubbsi* ranged between 7 and 90 cm L_T (Table I), but fish that had stomach contents ranged between 9 and 82 cm. The prey identified in stomach contents belonged to different taxonomic groups (Osteichthyes, Echinodermata, Mollusca, Crustacea, Annelida and Cnidaria; Table II). Prey were grouped in 14 ecological categories for subsequent analysis. The percent contribution of each prey by *M. hubbsi* size is shown in Fig. 2.

The analysis of the I_{RI} was carried out only with females and males (869 individuals and undetermined fish were not considered) and showed that for group 1, the most important prey were planktonic crustaceans (Table III). For group 2 of both sexes, the most important prey were planktonic crustaceans, followed by *E. anchoita* and benthic crustaceans. Group 3 showed differences in their most important prey: females consumed *M. hubbsi* followed by benthic crustaceans, while males showed the opposite pattern.

The analysis of the Levin's I_S indicated that the diets of all groups were dominated by few prey items (Fig. 3). According to Amundsen's criterion, small hake of both sexes were specialized pelagic crustacean feeders (Fig. 3). Although all individuals

TABLE I. Number and categories of the stomachs sampled. The numbers in parenthesis indicate stomachs with *Merluccius hubbsi* (number of cannibals)

Sex/stomach content	Small				Medium				Large				L_T (cm)		
	Full	Everted	Empty	Digested	Full	Everted	Empty	Digested	Full	Everted	Empty	Digested	Total	Minimum	Maximum
Female	250 (2)	78	295	16	435 (33)	128	601	56	69 (29)	30	98	5	2061	10	90
Male	227 (2)	69	235	9	383 (17)	164	668	70	31 (11)	19	52	4	1931	9	76
Undetermined	688 (1)	191	1355	171	30 (2)	2	34	10	—	—	—	—	2480	7	47
Sub-total	1165	338	1884	196	848	294	1302	136	100	49	150	9			
Total		3583				2580				308			6471		

L_T, total length.

TABLE II. Species and taxonomic groups found in stomach contents of hake. Items found in low frequency: occasional (∗), ≤10 individuals in total; rare (∗∗), ≤2 individuals in total are indicated

	Prey	Habitat	Ecological category
Mollusca	*Illex argentinus*	DP	Squid
	Small squid *Loligo* spp.	DP	
	Cuttlefish *Semirrosia* sp.*	B	
Crustacea	*Alpheus puapeba*	B	Benthic crustacean
	White shrimp *Peisos petrunkevitchi*	B	
	*Pontocaris boschii**	B	
	Gammaridae*	B	
	Hyperidae	B	
	Isopoda*	B	
	Mysidacea	B	
	Cumacea	B	
	Schizopoda	B	
	Unidentified shrimp*	B	
	Euphausiidae	P	Planktonic crustaceans
	Argentine red shrimp *Pleoticus muelleri*	BD	Argentine red shrimp
	Digested Crustacea Decapoda	B	Other crustaceans
	Unidentified crustacean	B	
Fish	*Engraulis anchoita*	P	Anchovy
	Maurolicus muelleri	BP	Silvery lightfish
	Merluccius hubbsi	DP	Hake
	South-west Atlantic Ocean butterfish *Stromateus brasiliensis*	P	Pelagic medium fishes
	Rough scad *Trachurus lathami***	P	Other pelagic small fishes
	Pink cusk-eel *Genypterus blacodes***	D	Benthic-demersal small fish
	Snail fish *Agonopsis chiloensis***	B	
	Patagonian hoki *Macruronus magellanicus***	D	
	Cocherito *Serranus auriga***	B	
	Banded cusk-eel *Raneya brasiliensis**	B	
	Silver porgy *Diplodus argenteus***	B	
	Red searobin *Prionotus nudigula***	B	
	Unidentified fishes		Unidentified fish
Others	Polychaeta body parts*	IB	Polychaeta
	Sea urchin *Pseudechinus* sp.	EB	Other benthic organisms
	Cnidaria body parts	EB	

P, pelagic; D, demersal; B, benthic, IB, infaunal-benthic; EB, epibenthic.

consumed the dominant prey, small proportions of different prey were occasionally consumed by some individuals. Medium and large hake took many different types of prey (each prey was consumed by a few individuals), but planktonic crustaceans were also an important prey for medium hake. The r_s between the size of cannibal

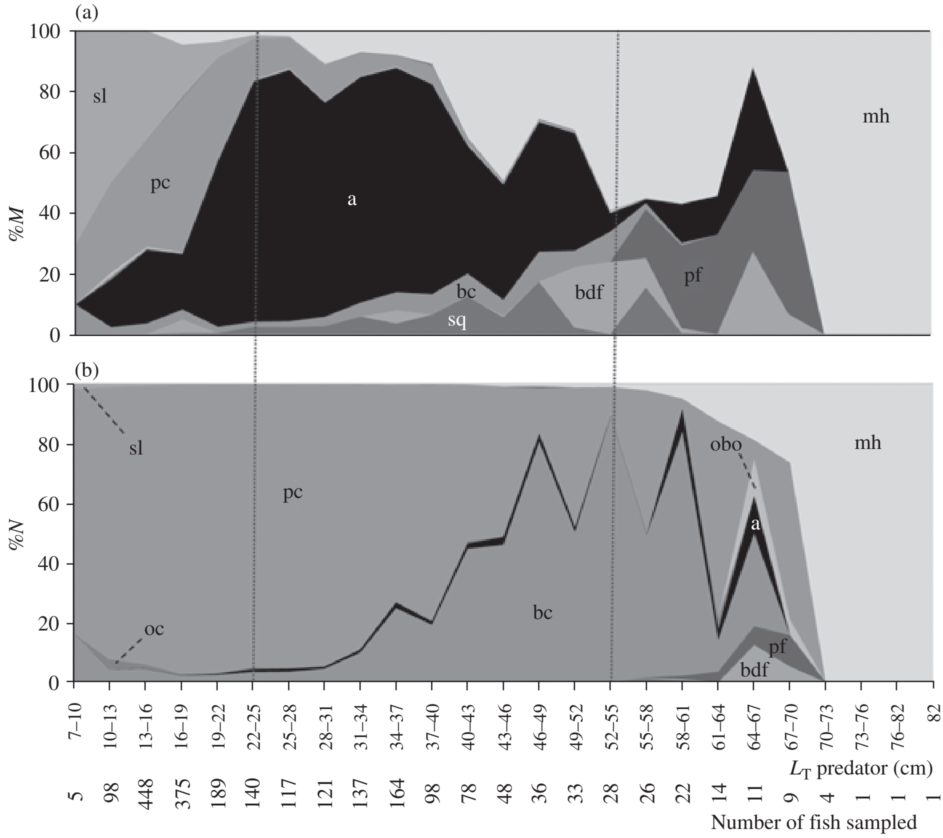

FIG. 2. Mean (a) wet mass percentage (%M) and (b) number percentage (%N) of prey of *Merluccius hubbsi* grouped by total length (L_T, 3 cm intervals) (sq, squid; bdf, benthic-demersal fishes; pf, pelagic medium fishes; bc, benthic crustaceans; a, *Engraulis anchoita*; oc, other crustaceans; obo, other benthic organisms; pc, planktonic crustaceans; sl, *Maurolicus muelleri*; mh, *M. hubbsi*). *Merluccius hubbsi* is divided into small, medium and large.

hake and the estimated size of their prey were significant for both sexes ($P < 0{\cdot}01$; Fig. 4 and Table IV).

Small cannibals consumed *M. hubbsi* accounting for 24% of their own mass, while the consumption by mass for medium and large cannibals did not exceed 7% (Fig. 5). The numerical relationships show that cannibals of all sizes consumed *M. hubbsi* between 100 and 110% of their own number. Small cannibals consumed their own size group (intracohort cannibalism, young-of-the-year hake), medium-sized cannibals consumed mainly small *M. hubbsi* and large cannibals consumed both small and medium *M. hubbsi* (Fig. 5).

DISCUSSION

Merluccius hubbsi is one of the most important and most studied fishery species in Argentina, but little has been published on their diet or feeding strategy (Ruiz &

TABLE III. (a) Diet composition of *Merluccius hubbsi* by total length (L_T) (group 1: 9–23 cm, group 2: 24–53 cm and group 3: 54–82 cm) and (b) 95% C.I. obtained by bootstrapping

(a)	Group 1 %F	Group 2 %F	Group 3 %F	Group 1 %N	Group 2 %N	Group 3 %N	Group 1 %M	Group 2 %M	Group 3 %M	Group 1 %I_{RI}	Group 2 %I_{RI}	Group 3 %I_{RI}
Females												
Squid	1·20	3·33	2·90	0·03	0·09	0·32	3·38	6·66	0·58	0·04	0·36	0·05
Benthic-demersal small fishes	0·00	0·89	8·70	0·00	0·02	0·95	0·00	3·79	9·55	0·00	0·05	1·86
Unidentified fishes	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00
Pelagic medium fishes	0·00	0·00	10·14	0·00	0·00	1·11	0·00	0·00	27·27	0·00	0·00	5·85
Benthic crustaceans	40·00	35·70	31·88	5·01	23·36	42·97	3·29	6·24	0·42	3·30	16·84	28·14
Engraulis anchoita	7·20	28·82	4·35	0·23	1·44	1·42	39·15	55·99	4·47	2·82	26·33	0·52
Other crustaceans	10·80	3·99	2·90	0·52	0·28	0·47	0·13	0·04	0·01	0·07	0·02	0·03
Other benthic organisms	1·20	1·33	7·25	0·03	0·04	0·95	0·85	0·20	0·20	0·01	0·01	0·17
Planktonic crustaceans	73·60	43·02	10·14	93·75	74·47	45·97	31·50	4·05	0·09	91·56	53·74	9·50
Argentine red shrimp	0·00	1·11	0·00	0·00	0·06	0·00	0·00	0·16	0·00	0·00	0·039	0·00
Maurolicus muelleri	11·20	0·44	0·00	0·41	0·01	0·00	19·22	0·11	0·00	2·18	0·01	0·00
M. hubbsi	0·80	7·32	42·03	0·02	0·23	5·69	2·49	22·75	57·33	0·02	2·67	53·87
Polychaeta	0·00	0·00	1·45	0·00	0·00	0·16	0·00	0·00	0·10	0·00	0·00	0·07
Other pelagic small fishes	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00
Males												
Squid	0·36	3·47	9·68	0·01	0·08	1·42	0·49	4·63	9·17	0·01	0·24	1·90
Benthic-demersal small fishes	0·72	0·25	0·00	0·01	0·01	0·00	4·33	0·46	0·00	0·03	0·01	0·00
Unidentified fishes	0·36	0·25	0·00	0·01	0·01	0·00	0·06	0·01	0·00	0·01	0·01	0·00
Pelagic medium fishes	0·00	0·00	3·23	0·00	0·00	0·28	0·00	0·00	10·11	0·00	0·00	0·62
Benthic crustaceans	33·57	30·02	32·26	2·25	16·91	83·29	2·02	6·20	1·85	1·48	10·01	50·83
E. anchoita	11·91	34·24	9·68	0·23	1·20	3·12	46·81	70·59	22·94	5·80	35·48	4·67

TABLE III. Continued

(a)	Group 1 %F	Group 2 %F	Group 3 %F	Group 1 %N	Group 2 %N	Group 3 %N	Group 1 %M	Group 2 %M	Group 3 %M	Group 1 %I_{RI}	Group 2 %I_{RI}	Group 3 %I_{RI}
Other crustaceans	11·55	4·47	0·00	0·61	0·27	0·00	0·18	0·10	0·00	0·09	0·02	0·00
Other benthic organisms	0·00	2·73	0·00	0·00	0·08	0·00	0·00	0·54	0·00	0·00	0·02	0·00
Planktonic crustaceans	69·31	42·68	19·35	96·57	81·30	8·50	30·27	5·74	0·04	90·95	53·61	3·06
Argentine red shrimp	0·00	0·25	0·00	0·00	0·01	0·00	0·00	0·05	0·00	0·00	0·01	0·00
M. muelleri	11·55	0·74	0·00	0·30	0·04	0·00	13·32	0·26	0·00	1·63	0·01	0·00
M. hubbsi	0·72	4·22	35·48	0·02	0·10	3·40	2·53	9·93	55·90	0·02	0·61	38·94
Polychaeta	0·00	0·25	0·00	0·00	0·01	0·00	0·00	0·03	0·00	0·00	0·01	0·00
Other pelagic small fishes	0·00	0·25	0·00	0·00	0·01	0·00	0·00	1·46	0·00	0·00	0·01	0·00

(b)	Group 1 %N	Group 2 %N	Group 3 %N	Group 1 %M	Group 2 %M	Group 3 %M
Females						
Squid	0·00–0·07	0·05–0·15	0·00–1·34	0·26–10·84	3·18–11·28	0·00–2·35
Benthic-demersal small fishes	—	0·01–0·06	0·23–3·45	—	0·35–10·55	2·59–20·76
Unidentified fishes	—	—	—	—	—	—
Pelagic medium fishes	—	—	0·26–3·39	—	—	11·51–48·83
Benthic crustaceans	3·09–8·00	15·27–32·52	19·72–78·02	2·07–5·03	3·92–9·64	0·16–1·06
Engraulis anchoita	0·12–0·43	1·08–1·99	0·00–6·90	25·69–51·89	45·4–65·54	0·00–12·72
Other crustaceans	0·27–1·02	0·11–0·61	0·00–2·28	0·06–0·25	0·02–0·11	0·00–0·02
Other benthic organisms	0·00–0·07	0·02–0·08	0·34–4·01	0·00–2·29	0·06–0·39	0·09–0·55
Planktonic crustaceans	90·81–96·02	65·05–82·58	4·36–73·88	23·43–40·65	2·95–5·52	0·01–0·28
Argentine red shrimp	—	0·01–0·13	—	—	0·03–0·39	—

TABLE III. Continued

(b)	Group 1 %*N*	Group 2 %*N*	Group 3 %*N*	Group 1 %*M*	Group 2 %*M*	Group 3 %*M*
Maurolicus muelleri	0·25–0·64	0·00–0·04	—	12·14–27·4	0·00–0·33	—
M. hubbsi	0·00–0·06	0·15–0·34	2·26–16·08	0·00–7·57	13·3–35·1	33·17–74·28
Polychaeta	—	—	0·00–0·94	—	—	0·00–0·36
Other pelagic small fishes	—	—	—	—	—	—
Males						
Squid	0·00–0·05	0·04–0·14	0·00–4·25	0·00–1·73	1·85–8·4	0·00–33·68
Benthic-demersal small fishes	0·00–0·04	0·00–0·02	—	0·00–16·77	0·00–1·75	—
Unidentified fishes	0·00–0·03	0·00–0·02	—	0·00–0·21	0·00–0·03	—
Pelagic medium fishes	—	—	0·00–1·40	—	—	0·00–33·51
Benthic crustaceans	1·36–3·79	9·51–25·91	73·73–95·32	1·13–3·79	3·56–9·79	0·93–5·45
E. anchoita	0·13–0·34	0·86–1·64	0·00–10·69	34·28–60·45	62·94–77·53	0·00–56·75
Other crustaceans	0·27–1·36	0·10–0·73	—	0·09–0·33	0·02–0·27	—
Other benthic organisms	—	0·04–0·14	—	—	0·22–0·95	—
Planktonic crustaceans	94·57–97·77	72·32–88·59	0·00–17·51	21·43–40·21	4·21–7·66	0·01–0·11
Argentine red shrimp	—	0·00–0·02	—	—	0·00–0·19	—
M. muelleri	0·19–0·50	0·00–0·11	—	8·98–20·18	0·00–0·64	—
M. hubbsi	0·00–0·07	0·06–0·17	1·42–5·45	0·00–7·46	4·88–17·64	22·28–87·43
Polychaeta	—	0·00–0·02	—	—	0·00–0·12	—
Other pelagic small fishes	—	0·00–0·02	—	—	0·00–5·17	—

%*F*, per cent frequency of occurrence; %*N*, percentage by number; %*M*, percentage of the wet mass estimated by regression; $\%I_{RI}$ index of relative importance.

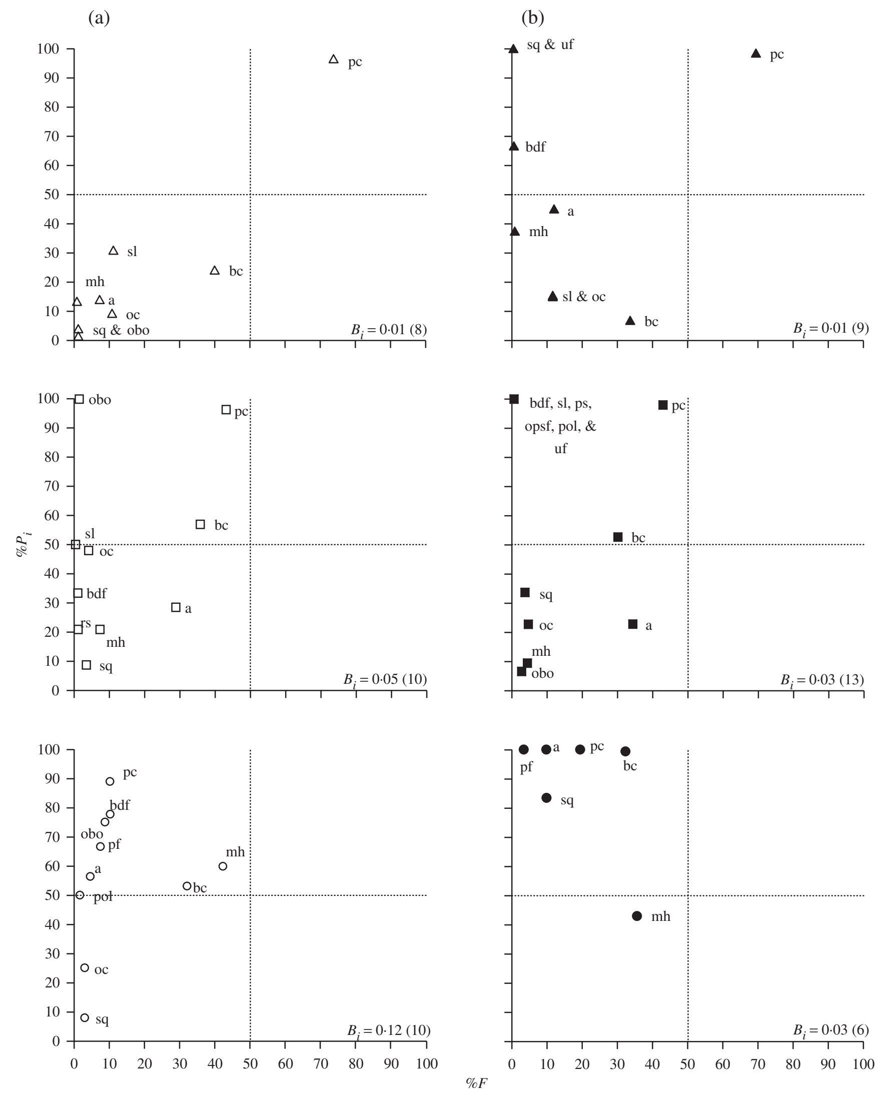

FIG. 3. Amundsen's graphics relating per cent frequency of occurrence (%F) of a prey to its specific abundance (%P_i) by and size of *Merluccius hubbsi*. (a) Females and (b) males (△, ▲, small *M. hubbsi*; □, ■, medium *M. hubbsi*; ○, ●, large *M. hubbsi*). B_i, Levin's standard index. Numbers in parenthesis indicate the number of prey items (sq, squid; bdf, benthic-demersal fishes; uf, unidentified fishes; pf, pelagic medium fishes; bc, benthic crustaceans; a, *Engraulis anchoita*; oc, other crustaceans; obo, other benthic organisms; pc, planktonic crustaceans; rs, Argentine red shrimp; sl, *Maurolicus muelleri*; mh, *M. hubbsi*; pol, Polychaeta; opsf, other pelagic small fishes).

Fondacaro, 1997). Although traditional techniques to assess feeding habits, such as stomach contents studies, are widely used, they have the potential disadvantage of either over- or underestimating some prey species due to differential digestion of the body structures. These techniques are, however, very useful in species where direct observation of trophic behaviour in nature is not possible.

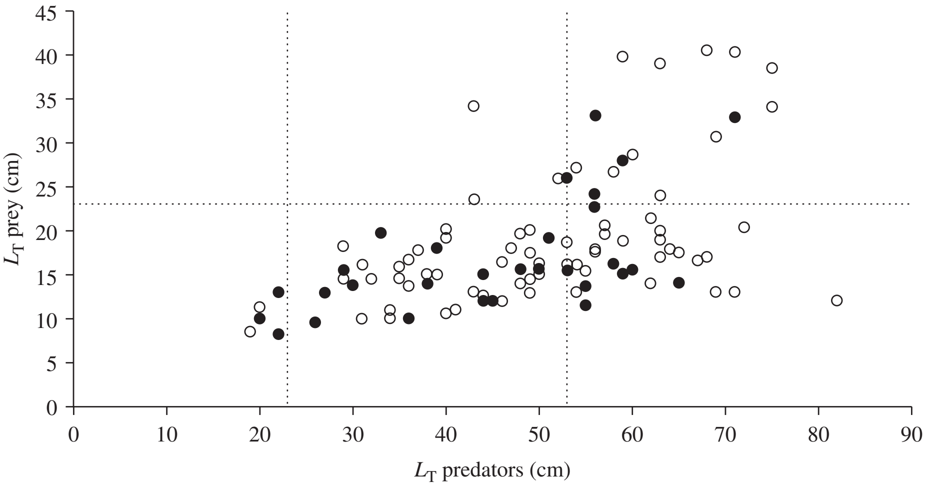

FIG. 4. Total length (L_T) of cannibal *Merluccius hubbsi* and estimated L_T of prey *M. hubbsi*. The L_T of the different groups of *M. hubbsi* (small, medium and large) are indicated (○, females; ●, males).

TABLE IV. Results of Spearman rank correlation (r_s) used to evaluate the relationship between cannibal *Merluccius hubbsi* total length (L_T) and prey L_T ($P < 0{\cdot}01$). Individuals with undetermined sex were not used in the correlation

Sex	r_s	n (prey)	L_T range of predators (cm)	L_T range of prey (cm)
Females	00·49	72	19–82	8–40
Males	00·57	31	20–71	8–33
Undetermined	—	4	16–42	15–37

n, sample size.

Several authors have indicated that *M. hubbsi* may be seasonally distributed in space, depending on environmental conditions (Podestá, 1990; Ocampo Reinaldo, 2010; Williams *et al*., 2010) and its reproductive behaviour (Di Giácomo *et al.,* 1993; Pájaro *et al.,* 2005). This causes seasonal variations in its feeding habits. Moreover, some prey may also show seasonal variations (*e.g. S. porosa*; Perier & Di Giácomo, 2002; Romero *et al.,* 2008) or interannual variations in their abundance (*e.g. I. argentinus*, Morsan & Crespi, 2005; Romero *et al.,* 2007), so diet characterization may vary between seasons and years. The samples for this study were obtained in a short temporal window (spawning season, spring 2006 and 2007), which is the season of maximum aggregation of schools of *M. hubbsi* and allowed a first approximation of the diet of *M. hubbsi* in San Matías Gulf.

The results following Amundsen's criterion indicate that, within SMG, *M. hubbsi* behaves as a generalist predator, although small *M. hubbsi* seem to specialize in feeding on planktonic crustaceans (Euphausiidae). This was not observed in medium and large *M. hubbsi* of either sex, since they showed numerous prey groups with low frequency of occurrence and variable specific abundance. On the other hand,

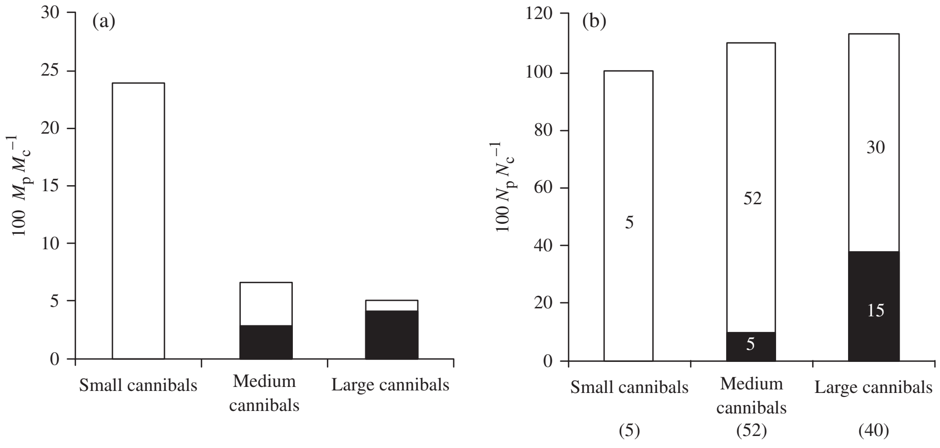

FIG. 5. Percentage of (a) mass prey per mass cannibals ($100\ M_p M_c^{-1}$) and (b) number prey per number cannibals ($100\ N_p N_c^{-1}$) by size of cannibals in *Merluccius hubbsi* (the numbers on bars indicate the total number of prey found). □, small prey; ■, medium prey. The numbers in parenthesis indicate the number of cannibals analysed.

according to the Levin's I_S the diets of all groups of *M. hubbsi* were dominated by few prey items, indicating that they are specialist predators. Amundsen *et al.* (1996) suggested that in a population with a high between-phenotype component, different individuals specialize in different resources and that this contributes to the global width of the trophic niche of the species. Therefore, medium and large *M. hubbsi* would have a generalist feeding strategy characterized by specialized individuals that capture different prey. This may be due to different causes: (1) old *M. hubbsi* have more 'individual experience', increased swimming and sensory skills and increase their feeding efficiency consuming specific prey items (Hart, 1986) or (2) each *M. hubbsi* is a generalist predator and the individual variations observed are casual and related to the local abundance of different prey at a specific moment. Prenski & Angelescu (1993) pointed out that the diet of *M. hubbsi* in the ACS shows variations related to depth, latitude, day hours and relative abundance of the prey.

In general, crustaceans were important in all stages of the life cycle of *M. hubbsi*, although larger fish consumed fewer pelagic crustaceans and more benthic groups and fishes. In the silver hake *Merluccius bilinearis* (Mitchill 1814), the change from copepods to euphausiids as prey items in smaller *M. bilinearis* is also gradual and is not completed when *M. bilinearis* are large (Koeller *et al.*, 1989). Medium-sized *M. hubbsi* of both sexes seemed to be typically generalist, while large *M. hubbsi* had differences between sexes. Large females consumed more fishes in general (smaller *M. hubbsi* in particular) than males, while large males consumed more crustaceans than fishes. These changes in the composition of the diets are not detected in a one-dimensional index like Levin's I_S and the use of complementary descriptive methods becomes necessary. This study agrees with Sánchez & García de la Rosa (1999), who reported that small *M. hubbsi* make the largest vertical migrations, following the daily migrations of the zooplankton, so the latter always constitute the available prey. A similar behaviour was observed in recruits of the European hake *Merluccius merluccius* (L. 1758) in the Balearic Islands which follow the oblique nocturnal migrations of its prey (mainly euphausiids and myctophids) (Cartes *et al.,* 2009). Koeller *et al*. (1989) found that juveniles of *M. bilinearis* are opportunistic, adapting to the available zooplankton population. On the other hand, large *M. hubbsi* stay longer near the bottom, which, combined with an increase in body length and mouth size and an increase in swimming and sensory capabilities, would explain the change in the relevance of different trophic groups in relation to the size of the predator. Also, fishes are a better source of energy (1·12–1·7 kcal g^{-1}) than crustaceans (0·9 kcal g^{-1}) (Elías & Rajoy, 1992), which may also influence prey selectivity. Differences between large females and males may be due to differences in growth [*i.e.* females reach larger sizes than males of the same age (Ocampo Reinaldo, 2010)] which may influence the observed results of diet composition of this group.

Angelescu *et al*. (1958) reported that the most important trophic-fishing relationships around *M. hubbsi* include *E. anchoita*, squid and cannibalism. Similarly, Muto & Soares (2011) investigated the feeding ecology of *M. hubbsi* in two regions with high primary production in south-east Brazil, and found that the major food sources of *M. hubbsi* were fishes, crustaceans and squid (at least four species of Cephalopoda), with seasonal changes and depth variations. In this study, *E. anchoita* was important only for medium *M. hubbsi* of both sexes ($\%I_{RI} > 26$) and squid were not an important prey in any group of *M. hubbsi* ($\%I_{RI} < 2$). In SMG, exceptional abundances of *I. argentinus* were recorded during autumn and winter of 1995, 1997, 2001 and 2003, which favoured their capture by a jigger fleet, but the interannual variation in abundance was evidenced by low catches and landings of trawlers and jiggers during the remaining years (Romero *et al.,* 2007). Crespi Abril (2010) analysed also the diet of squid during 2005–2008 and did not find evidence that *M. hubbsi* was an important prey. This may indicate that within SMG there are no important and direct trophic relationships between *M. hubbsi* and squid, at least when squid are in low abundance.

Cannibalism is a special form of predation which poses intriguing evolutionary questions, and has the potential to regulate the population abundance in a density-dependent manner (Smith & Reay, 1991). In this study, cannibalism was detected in small- and medium-sized *M. hubbsi* and was important in large *M. hubbsi* ($\%I_{RI}$ >39). Although there seems to be an increase in prey size in relation to predator size, most prey *M. hubbsi* were small (<23 cm L_T). These results are similar to those obtained in other studies carried out in the ACS (Sánchez & García de la Rosa, 1999), which reported inter- and intracohort cannibalism. Cannibalism was also reported in other species of *Merluccius*. Large Cape hake *Merluccius capensis* Castelnau 1861 show a preference (>70% of the diet) for small and medium conspecifics (Macpherson & Gordoa, 1994). In *M. bilinearis* intracohort cannibalism occurs at the early juvenile stage, at times exceeding 40% by mass of the gut contents (Koeller *et al.,* 1989). Ruiz & Fondacaro (1997) analysed the diet of the *M. hubbsi* in the spawning area of the Patagonian stock in spring and observed that *Peisos petrunkevitchi* was the principal prey, followed by *E. anchoita*. Although these authors did not classify *M. hubbsi* by size, they seldom detected cannibalism and thus suggested that cannibalism occurs in areas where food is scarce. Similarly, Muto & Soares (2011) pointed out that cannibalism was rarely detected near Cabo Frío ($\%F = 0{\cdot}5$, $\%N = 0{\cdot}1$) and not at all near Ubatuba in Brazil, and suggested that *M. hubbsi* is a generalist and opportunist predator feeding on the most available prey. The dietary preference of *M. capensis* for small *M. capensis* was not related to the distribution and density of conspecifics nor to the density of alternative prey (Macpherson & Gordoa, 1994), but it has been suggested that cannibalism could be the main cause of natural mortality in this species (Lleonart *et al*., 1985). Likewise, intracohort cannibalism in *M. bilinearis* seems to be an important factor in establishing year class size (Koeller *et al*., 1989). In a semi-enclosed and relatively shallow ecosystem like SMG, there may be an enhanced availability of smaller *M. hubbsi* for larger cannibals. Hence, the trawl fishing fleet very frequently obtains mixed catches in SMG with *M. hubbsi* of all sizes (Romero *et al*., 2010) and the same pattern was observed in research surveys (pers. obs.).

A large number of empty stomachs were detected in medium (>200% more than those with contents) and large *M. hubbsi* (*c*. 150%). Females in both groups showed a higher incidence of cannibalism and a lower proportion of empty stomachs than males, which could indicate a preference for their conspecifics. This may be related to an active search for food during the post-spawning period and may indicate an opportunistic behaviour.

With respect to relative biomass contribution, small *M. hubbsi* did not represent the most important item for large *M. hubbsi*. On the contrary, medium-sized *M. hubbsi*, although in a lower numerical proportion, provided a larger biomass contribution. Considering only numerical consumption and that the trawl fishing fleet in SMG targets medium and large *M. hubbsi* (Romero *et al.,* 2010) and the longline fleet targets mostly large *M. hubbsi* (González *et al.,* 2007), the results may indicate that a decrease in large *M. hubbsi*, due to an hypothetical scenario of increasing fishing pressure, may favour medium-sized *M. hubbsi*, and thus increase cannibalistic pressure on small *M. hubbsi*. On the other hand, given that larger female *M. hubbsi* show an extended reproductive season, produce more eggs per unit of mass, and these eggs have better nutritional quality (Macchi *et al*., 2004, 2006; Pájaro *et al.,* 2005), excessive fishing on this group would increase the risk of overfishing through two combined effects: a direct effect of recruitment-overfishing and an indirect one of growth-overfishing, the latter through enhanced cannibalism of medium *M. hubbsi* on small *M. hubbsi*. These topics may lead to new hypotheses to explore and may promote the incorporation of trophic interactions in quantitative statistical models that could potentially improve the fisheries resources management in the San Matías Gulf.

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