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TROPHIC RELATIONSHIPS OF THE LONG-FINNED SQUID *LOLIGO SANPAULENSIS* ON THE SOUTHERN BRAZILIAN SHELF

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The diet and predators of *Loligo sanpaulensis* (Cephalopoda: Loliginidae) on the southern Brazilian shelf were studied by examining the stomach contents of 668 long-finned squid (12–184 mm mantle length) caught by bottom trawl and the stomach contents of 47 potential predators, including stranded penguins and marine mammals as well as fish and cephalopods caught with diverse fishing gears in the region. Of 313 long-finned squid stomachs containing food, fish occurred in 36.4% of stomachs, crustaceans in 23.3% and cephalopods in 6.4%. Identified prey included demersal fish, shrimps and conspecifics. *Loligo sanpaulensis* was preyed on by 31 of the 47 potential predatory species examined. The frequency of occurrence (*FO*) was high (>20%) in the stomach contents of La Plata dolphins *Pontoporia blainvillei,* penguins *Spheniscus magellanicus*, fur seals *Arctocephalus* spp., the benthic shark *Mustelus canis* and the benthic finfish *Astroscopus sexpinosus* and *Percophis brasiliensis*. It was less important (5–20% *FO*) for the benthic and demersal fish *Helicolenus lahillei*, *Paralichthys isosceles*, *P. patagonicus*, *Merluccius hubbsi* and *Urophycis mystacea,* and of minor importance (2–5% *FO*) in the diet of the finfish *Trichiurus lepturus*, *Cynoscion guatucupa*, *Macrodon ancylodon*, *Pagrus pagrus* and *Pomatomus saltatrix*. *Loligo sanpaulensis* seems to be a link in the pelagic and benthic foodwebs of the southern Brazilian shelf, because it is preyed on by such high-level predators as marine mammals and penguins, and by several of the most abundant fish found in the region.

Squid are important components of foodwebs in most marine ecosystems (Amaratunga 1983, Clarke 1996). They are organisms with a fast metabolic rate and growth and they play an important role in the transfer of energy to higher trophic levels (Nixon 1987, O'Dor and Wells 1987). Their role in the system is reflected, in part, by their relative importance in the diet of their predators (Clarke 1987).

The common long-finned squid *Loligo sanpaulensis* Brakoniecki 1984 (Cephalopoda: Loliginidae) occurs along the east coast of South America between 21 and 40°S and is endemic to the region under the influence of the Subtropical Convergence. It seems to be adapted to a wider temperature range than the congenerics *L. gahi*, which never reach warm waters north of the subtropical front, and *L. plei*, which is always found north of the front (Roper *et al.* 1984, Haimovici and Perez 1991a).

Along the coast of southern Brazil between late autumn and early spring, the shelf is dominated by cold waters of the coastal branch of the Malvinas Current flowing northwards and, from late spring to early autumn, by warm coastal waters under the influence of the south-flowing Brazil Current (Garcia 1997). In this environment, the most abundant squid is *Loligo sanpaulensis*, whereas over the upper slope the dominant squid species is *Illex argentinus*, with little overlapping between the two (Haimovici and Perez 1991b). In the cooler season, the density of *L. sanpaulensis* is comparable with congeneric species from other shelves of the world (Andriguetto and Haimovici 1991) but, because of its relatively small size and widespread distribution on the shelf, it is not subject to a directed fishery and is only caught as by-catch by shrimp trawlers in coastal waters (Haimovici and Mendonça 1996).

In this paper, the importance of long-finned squid in the foodweb of the southern Brazilian shelf is assessed on the basis of an analysis of stomach contents of *L. sanpaulensis* collected in a series of demersal trawl surveys and commercial landings and the stomach contents of potential predators collected from diverse sources.

MATERIAL AND METHODS

Diet

Squid samples were obtained from bottom trawl surveys by the R.V. *Atlântico Sul* and from catches by commercial trawlers targeting flatfish and shrimp from the continental shelf of southern Brazil from 1987 to 1996, between 26°50′ and 34°31′S and 20 and 84 m (Fig. 1). Stomachs, either frozen or fixed in

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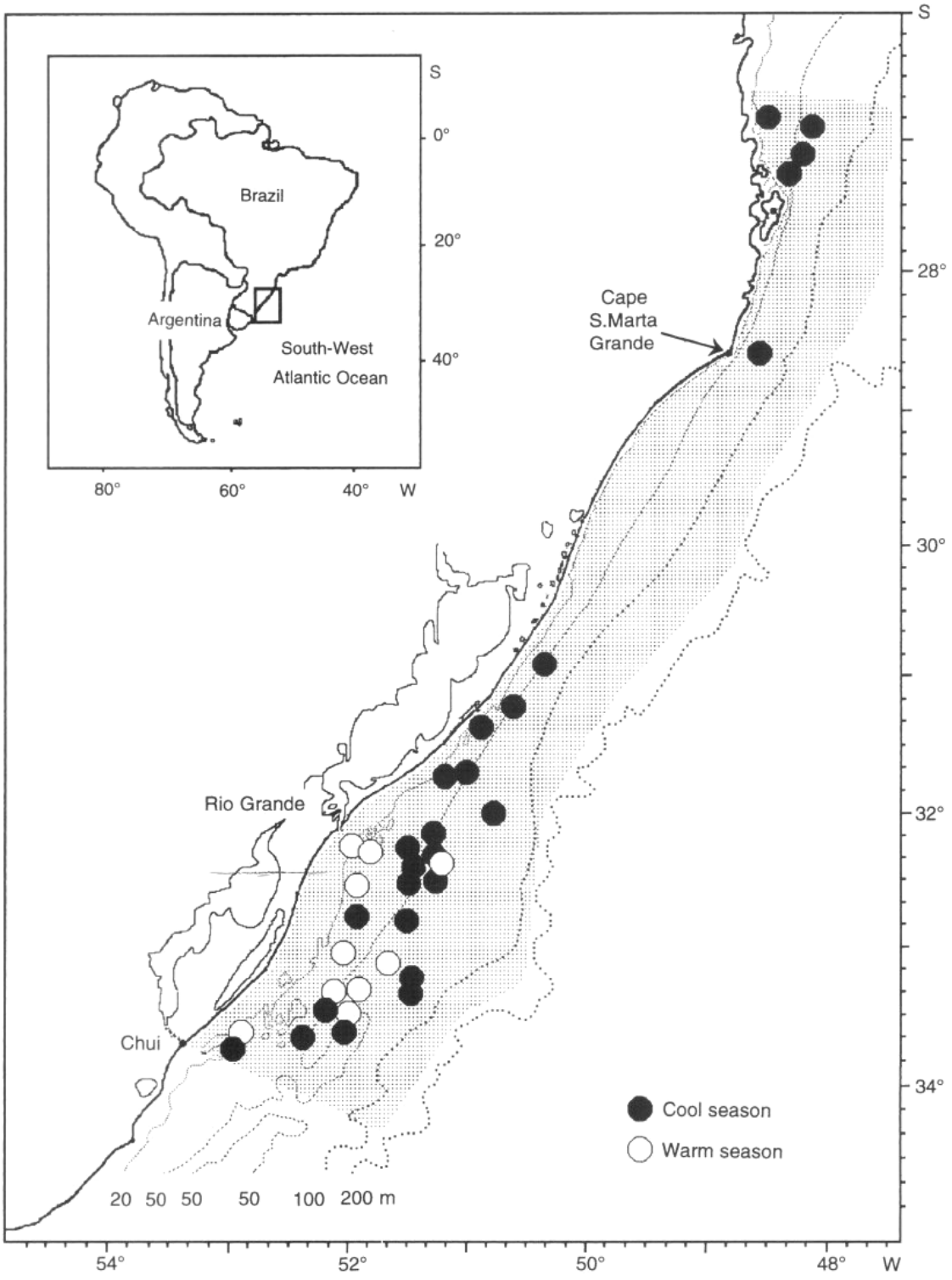

Fig. 1: The southern Brazilian shelf. Circles indicate where sampled *Loligo sanpaulensis* were collected. Stippled area indicates where the sampled potential predators were collected

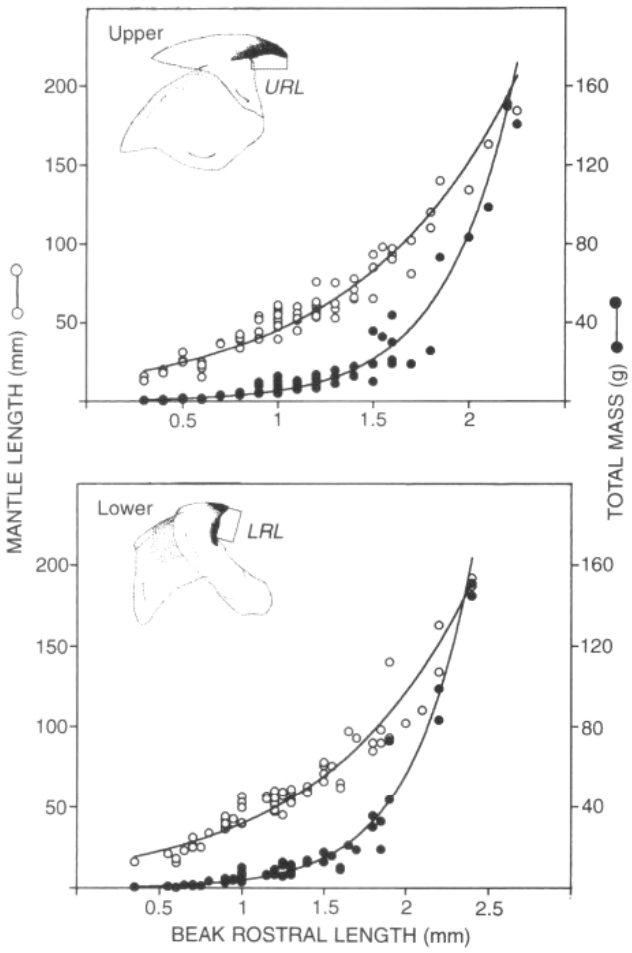

Fig. 2: Exponential relationships between mantle length and beak rostral length and between total mass and beak rostral length for *Loligo sanpaulensis* from the southern Brazilian shelf (the relevant equations are given in text)

10% saline solution of formalin, were examined for food content. Fish were recognized from skin, scales, vertebrae, eye lenses, otoliths, spines, rays and bony fragments. Identification to genus or species and estimation of total length (*TL*) was mainly from otoliths by comparison with a reference collection available at the laboratory ashore. Cephalopods were recognized from beaks, gladii, suckers, arms, tentacles and the remains of the mantle. Identification to species was usually based on beaks and, when possible, dorsal mantle lengths (*ML*) of prey were estimated from relationships between beak rostral length and mantle length, also based on a reference collection. Crustacean remains were mainly parts of the exoskeletons, appendages and eyes.

Stomach content analysis included the determination of relative frequency of occurrence of prey types ($FO = N_p/N_t$), where N_p is the number of stomachs containing a prey type and N_t is the total number of stomachs with food. These frequencies of grouped prey types were compared by Chi-squared test. Although comparisons of frequencies of occurrence of prey items or stomachs with and without food have inherent limitations (Hyslop 1980), this method is the usual choice in feeding studies in nature, especially for cephalopods, which mince their prey (Breiby and Jobling 1985, Collins *et al.* 1994, Ivanovic and Brunetti 1994, Rocha *et al.* 1994).

Potential predators

Predation on *Loligo sanpaulensis* was studied from the presence of beaks or partly digested specimens in the stomach contents of potential predators from the study area (Fig. 1). Besides observations by the current authors, data were obtained from the literature. Predators included fish and cephalopods caught over the shelf in fishing surveys with diverse gears, more than 100 penguins (*Spheniscus magellanicus*) found dead along the coast, and marine mammals stranded on beaches along the southern Brazilian coast or from incidental catches by gillnets in the coastal fishery.

The percentage frequency of occurrence of *L. sanpaulensis* was calculated for each predator as $\%FO = (N_l/N_c) \times 100$, where N_l is the number of stomachs containing long-finned squid and N_c is the total number of stomachs with food. The numbers of squid in individual stomachs were estimated from undigested specimens and from counts of the upper or lower beaks, whichever were the most numerous. The rostral lengths of upper (*URL*) and lower (*LRL*) beaks were measured in mm, following Clarke (1986).

To estimate the size of long-finned squid in the stomach contents, exponential relationships of the *URL* and *LRL* to dorsal mantle length *ML* and total mass (*TM*) were calculated from 75 reference specimens measuring from 13 to 192 mm and 0.3 to 151.0 g (Fig. 2). The relevant equations were

$$ML = 13.546e^{1.211URL} \ (r = 0.959);$$

$$ML = 13.173e^{1.109LRL} \ (r = 0.958);$$

$$TM = 0.3408e^{2.766URL} \ (r = 0.952);$$

$$TM = 0.2768e^{2.659LRL} \ (r = 0.953).$$

Estimates of the abundance of the main predators of

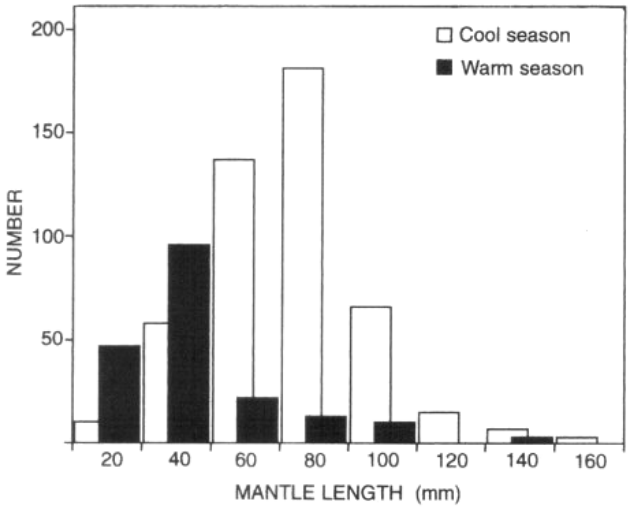

Fig. 3: Mantle length distribution of all *Loligo sanpaulensis* sampled

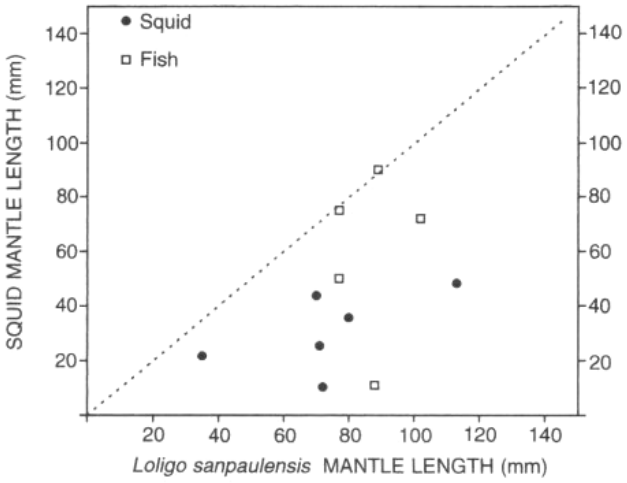

Fig. 4: Relationships between the size of *Loligo sanpaulensis* and the size of prey found in their stomachs

L. sanpaulensis in southern Brazil were obtained from two sources: catch per unit effort (*cpue*) and biomass estimates from six bottom trawl surveys performed between 1981 and 1983 (Haimovici *et al.* 1996) and commercial landing statistics in the period 1990–1994 (Haimovici *et al.* 1997).

RESULTS

Diet

From a total of 668 squid of 12–184 mm *ML* examined, 313 (46.8%) had food in their stomachs. In the warmer season (January–early June), most of the specimens were <60 mm *ML* ($\overline{ML}$ = 54.1 mm, Fig. 3). In the cooler season (July–October), specimens up to 120 mm were common ($\overline{ML}$ = 83.1, Fig. 3). Females had food in their stomachs more frequently (51.2%) than males (40.8%, $\chi^2_{\upsilon=1} = 6.93$, $p = 0.0085$). Fish occurred in 36.4% of stomachs with food, crustaceans in 23.3%, cephalopods in 6.4% and unidentified digested food in 38.3% (Table I). A single type of prey (fish, cephalopod or crustacean) was found in 92.2% of the stomachs with identifiable remains and a mixed diet of only two prey types in the remaining 7.8%. No significant differences were found in the percentages of prey categories between the sexes ($\chi^2_{\upsilon=2} = 5.84$, $p = 0.0587$), so data were pooled over sexes for further analysis.

The observed high occurrence of empty stomachs and unidentified digested food was probably attributable to the very high digestion rate (Bidder 1966, Lipiński 1987). Prey identification was very difficult because squid macerate prey during ingestion. Identified bony fish included only *Urophycis brasiliensis*, *Raneya fluminensis* and *Symphurus* The cephalopod prey items were all squid, and included *Loligo sanpaulensis* with *ML* of 21.8–48.6 mm and a single specimen of *Illex argentinus* of 10 mm *ML*. Recognizable crusta-ceans were the shrimps *Artemesia longinaris* and *Pleoticus muelleri* (Table I). The *ML* and *TL* respectively of squid and fish eaten ranged from 12.5 to 101.1% of the predator's mantle length (Fig. 4).

The proportions of fish, cephalopods and crustaceans in the stomach contents and empty stomachs of different size groups of long-finned squid in the warm and cool seasons are shown in Figure 5. In the warm season the sizes of fish, cephalopods and crustaceans did not differ significantly with predator size (respectively $\chi^2_{\upsilon=3} = 0.389$, $p = 0.4367$; $\chi^2_{\upsilon=3} = 0.389$, $p = 0.9943$; $\chi^2_{\upsilon=3} = 6.673$, $p = 0.97475$). Crustaceans were the main prey of the squid *ML* range 20–80 mm, with *%FO* of 54.5–70, whereas fish and crustaceans were equally important for large squid (*%FO* = 44.4). In the cooler season, fish were the most frequent prey for all sizes of squid, increasing significantly with size from 16.7 to 46.1% ($\chi^2_{\upsilon=3} = 23.6$, $p = 0.0001$). The proportion of empty stomachs was not significantly different among sizes in the cooler season, but there was a significant difference in the warm season ($\chi^2_{\upsilon=4} = 24.2$, $p = 0.0001$).

Table I: Number of stomachs containing a given prey (*n*), percentage frequency of occurrence (*%FO*) and the length range of prey items in 313 *Loligo sanpaulensis* stomachs with food from the southern Brazilian shelf

Prey item	*n*	*%FO*	Length range (mm)
Osteichthyes	114	36.4	
Symphurus sp.	1	0.3	50–75
Urophycis brasiliensis	3	1.0	72
Raneya fluminensis	1	0.3	11–90
Unidentified Osteichthyes	109	34.8	
Crustacea	73	23.3	
Artemesia longinaris	11	3.5	
Pleoticus muelleri	10	3.2	
Unidentified Dendrobranchiata	24	7.7	
Unidentified Brachyura	1	0.3	
Unidentified Crustacea	27	8.6	
Cephalopoda	20	6.4	
Illex argentinus	1	0.3	10
Loligo sanpaulensis	10	3.2	22–49
Loligo sp.	2	0.6	
Unidentified Teuthoidea	7	2.2	
Digested, unidentified	120	38.3	

Predators

The presence of *Loligo sanpaulensis* in the diet of 47 potential predators was investigated, 35 of them stomach contents examined by the authors. The diet of 31 of the potential predator species included *Loligo sanpaulensis* to some extent (Table II).

The *%FO* of *Loligo sanpaulensis* was highest (>20%) in the stomach contents of the La Plata dolphin *Pontoporia blainvillei*, the common dolphin *Delphinus delphis*, the fur seals *Arctocephalus australis*, *A. gazzella* and *A. tropicalis*, the penguin *Spheniscus magellanicus*, the benthic shark *Mustelus canis* and the benthic fish *Astroscopus sexpinosus* and *Percophis brasiliensis*. Frequencies between 5 and 20% were found in stomach contents of the benthic finfish *Helicolenus lahillei*, *Paralichthys isosceles*, *P. patagonicus* and *Urophycis mystacea*, and the demersal-pelagic fish *Merluccius hubbsi*. *%FO* was between 2 and 5% in the diet of the finfish *Cynoscion guatucupa*, *Macrodon ancylodon*, *Pagrus pagrus*, *Pomatomus saltatrix* and *Trichiurus lepturus*, species that feed at different levels of the water column. Cannibalism was rare, cephalopods identified as *Loligo sanpaulensis* being found in just 3.2% of the stomachs examined.

The size distribution of the long-finned squid in the diet of six predators for which data were available are shown in Figure 6: La Plata dolphin, found year-round, preyed on small to large long-finned squid with $\overline{ML}$ of 92.7, 98.2, 104.0 and 115.9 mm respectively in winter, spring, autumn and summer. *Arctocephalus australis*, sampled only in winter and spring, also preyed on small and large squid, but with a dominance of large ones ($\overline{ML}$ = 96.4 mm). The penguin, which appears over the southern Brazilian shelf only in the cooler season, also preyed on small and large squid, with $\overline{ML}$ in winter of 71.5 mm and in spring of 86.1 mm. The common dolphin *Delphinus delphis*, collected only in winter, preyed on small specimens ($\overline{ML}$ = 57.5 mm) as did the demersal fish *Trichiurus lepturus* ($\overline{ML}$ = 54.7 mm) and *Paralichthys patagonicus* ($\overline{ML}$ = 55.1 mm).

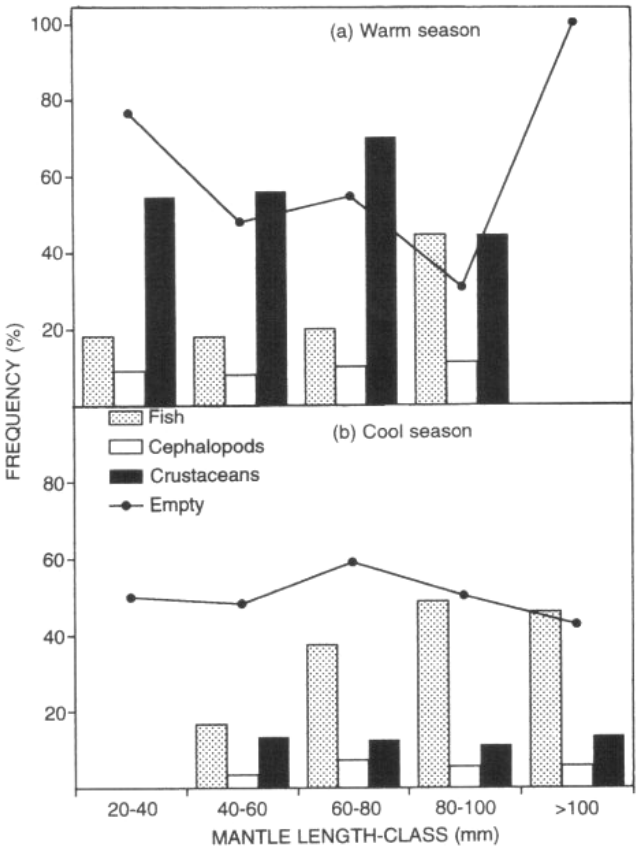

Fig. 5: Relative frequency of occcurrence of fish, cephalopods and crustaceans in different *ML* classes of *Loligo sanpaulensis* from (a) the warm (*n* = 80) and (b) the cool (*n* = 233) seasons on the southern Brazilian shelf. The percentage frequency of occurrence of empty stomachs is also indicated

Mean commercial landings, *cpue*s and estimated abundance of the main fish on the southern Brazilian shelf that preyed upon *L. sanpaulensis* are shown in Table III. Species representing 83.7% of commercial landings and 70.6% of total catches in bottom trawl surveys fed to some degree on *L. sanpaulensis*, but only 9.4% of commercial landings and 10.7% of total

Table II: List of fish, cephalopods, penguins and marine mammals found on the southern Brazilian shelf that preyed on *Loligo sanpaulensis*. Number of stomachs with food examined and the source of data, the percentage of stomachs with *Loligo sanpaulensis* (*%FO*), numbers of squid per stomach, and their mantle length (*ML*) and total mass (*TM*) mean and range are indicated

Predator species	Number of stomachs examined and source of feeding data	*Loligo sanpaulensis* as prey			
		%FO	Number	Mean and range	
				ML (mm)	*TM* (g)
FISH					
Astroscopus sexpinosus	6[1]	33.3	4–5	67.5 (37–93)	15.4 (3.6–30.3)
Conger orbignyanus	156[1]	0.6	1	30	2.2
Cynoscion guatucupa	220[1]	2.7	1	61.5 (40–72)	12.2 (4.3–16.7)
Cynoscion jamaicensis	78[1]	1.3	1	33	2.7
Galeorhinus galeus	166[1]	*	–	–	–
Helicolenus lahillei	33[1]	6.1	1	44.0 (43–45)	5.3 (5.0–5.6)
Macrodon ancylodon	1 402[2]	3.8	–	–	–
Merluccius hubbsi	231[1]	6.1	–	–	–
Micropogonias furnieri	194[1]	1.0	1	26.4 (25–27)	1.6 (1.2–1.8)
Mustelus canis	51[1]	27.5	1–2	61.9 (30–100)	14.0 (2.2–35.9)
Pagrus pagrus	362[1]	*	1–4	47.2 (13–134)	6.2 (0.3–70.9)
Paralichthys isosceles	90[1]	8.9	1–2	49.9 (32–73)	7.1 (2.5–17.3)
Paralichthys orbignyanus	308[1]	0.6	3–4	16.2 (9–25)	0.5 (0.1–1.4)
Paralichthys patagonicus	290[1]	8.6	1–2	55.1 (38–193)	8.9 (3.8–165.6)
Percophis brasiliensis	63[1]	36.5	1–2	62.9 (20–140)	9.9 (0.8–78.5)
Pomatomus saltatrix	164[1]	3.7	–	–	–
Porichthys porosissimus	133[1]	0.8	1	70.7	16.0
Sympterigia acuta	1 510[3]	*	–	–	–
Sympterigia bonapartei	809[3]	*	–	–	–
Trichiurus lepturus	490[1]	4.9	1–4	54.7 (20–182)	8.8 (0.8–144.5)
Umbrina canosai	726[1]	0.1	–	–	–
Urophycis brasiliensis	663[1]	1.4	1	49.0 (23–85)	8.6 (1.3–22.4)
Urophycis mystacea	58[1]	5.2	1–2	69.4 (51–83)	15.0 (7.1–21
CEPHALOPODS					
Loligo sanpaulensis	313[1]	3.2	1	35.0 (22–49)	3.1 (1.1–6.8)
Illex argentinus	363[1]	1.7	1–2	40.5 (36–46)	3.8 (3.3–5.9)
PENGUINS					
Spheniscus magellanicus	120[1]	66.7	1–220	74.4 (25–190)	18.0 (1.4–159.7)
MARINE MAMMALS					
Pontoporia blainvillei	361[4,1]	51.0	1–180	98.7 (33–188.5)	34.8 (2.5–163.6)
Arctocephalus australis	15[1]	93.3	1–6	96.4 (45–171)	32.9 (5.6–125.0)
Arctocephalus gazzella	3[1]	33.3	1	105	40.2
Arctocephalus tropicalis	12[1]	33.3	1–4	83.9 (58–134)	23.8 (10.1–70.9)
Delphinus delphis	3[1]	100.0	13–30	57.5 (36–113)	9.9 (3.3–47.7)

* Numbers not reported
[1] Present study
[2] Juras and Yamaguti (1985)
[3] Queiroz (1986)
[4] Pinedo (1982)

survey catches had long-finned squid at a value >5% *FO* in their stomach contents (Fig. 7).

DISCUSSION

The diet of *Loligo sanpaulensis*, consisting mainly of fish and crustaceans, and to a lesser extent squid, was basically similar to the diet of other loliginids (Karpov and Cailliet 1979, Lipiński 1987, Collins *et al.* 1994, Rocha *et al.* 1994, Coelho *et al.* 1997). The present results are consistent with those obtained by Andriguetto (1989) for the same species in the region, although there were some differences, e.g. the relatively greater importance of crustaceans in the warmer season than found by Andriguetto. This difference should be interpreted with caution, because most of the current summer samples were obtained from a shrimp-directed fishery.

Only three fish species preyed on by long-finned squid could be identified from their otoliths: *Symphu-*

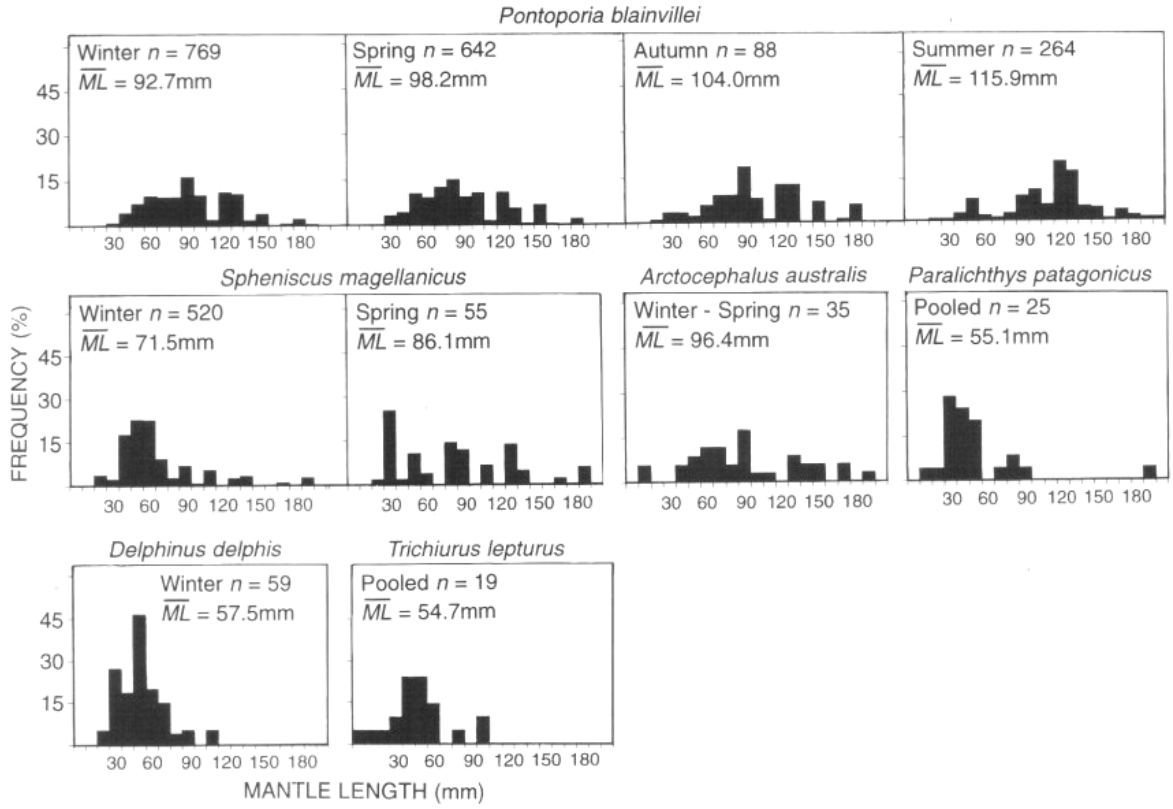

Fig. 6: Mantle length (*ML*) distribution of *Loligo sanpaulensis* in the stomach contents of *Pontoporia blainvillei*, *Spheniscus magellanicus*, *Delphinus delphis*, *Arctocephalus australis*, *Trichiurus lepturus* and *Paralichthys patagonicus* from the southern Brazilian shelf (*n* = number of specimens of *Loligo sanpaulensis*)

rus sp., *Urophycis brasiliensis* and *Raneya fluminensis*, all of which are uncommon benthic fish (Haimovici *et al.* 1996). They cannot be assumed to be representative of the diet of long-finned squid, because only seven otolith pairs recovered from 5 of the 114 stomachs containing fish remains could be identified to that level. However, their occurrence is an indication that *Loligo sanpaulensis* feeds near the bottom. The two shrimps identified in the stomach contents, *Artemesia longinaris* and *Pleoticus muelleri*, are also benthic organisms and are abundant from spring to summer in coastal waters (Ruffino 1991). Squid were not frequently found in the diet of *Loligo sanpaulensis* and cannibalism did not appear to be important off southern Brazil. Cannibalism in loliginids is usually associated with limited food resources or crowded conditions, such as on spawning grounds, and its frequency of occurrence increases with size and maturation (Fields 1965, Karpov and Cailliet 1979, Amaratunga 1983, Lipiński 1987). *Loligo sanpaulensis* does not form dense aggregations (Andriguetto and Haimovici 1991), probably explaining the low incidence of cannibalism observed.

Illex argentinus only preyed occasionally on *Loligo sanpaulensis* (*%FO* = 1.7), because the overlapping distribution of the two species is restricted to larger juveniles over the outer shelf in winter and spring (Haimovici and Perez 1991b). Predation by *Loligo sanpaulensis* on *Illex argentinus* was even less important (*%FO* = 0.3). Therefore, it is concluded that trophic interactions between the two dominant squid of southern Brazil waters are not important. A different picture can be drawn for the northern and southern shelf of Argentina, where the distribution of *Illex argentinus* overlaps respectively with *Loligo sanpaulensis* and *Loligo gahi* and predation on these species reaches 5.2 and 13.1% *FO* respectively (Table I in Ivanovic and Brunetti 1994).

Although few data on prey size were obtained, the finding of predation on fish species with a *TL* as large as the predator's *ML* is in agreement with that described for other *Loligo* species (Rocha *et al.* 1994).

Table III: Mean landings from the shelf fisheries, 1990–1994, and the mean *cpue* and biomass range estimates from botton trawl surveys, 1981–1983, for some of the most important fish of the southern Brazilian shelf that preyed on *Loligo sanpaulensis* and their main prey

Predator species	Mean landings ('000 tons)*	Mean *cpue* ($kg \cdot h^{-1}$)*	Estimated biomass ('000 tons)†	Main prey	Source of feeding data
Loligo sanpaulensis	0.1	(4.4)‡	(1.2–3.5)‡	Benthic fish and crustaceans	This study
Cynoscion guatucupa	8.8	183.6	36.7–325.2	Benthic and pelagic fish, crustaceans	Vieira (1990)
Macrodon ancylodon	4.0	25.17	1.8–20.7	Shrimps, benthic fish and *L. sanpaulensis*	Juras and Yamaguti (1985)
Pagrus pagrus	0.3	0.83	–	Demersal fish, benthic invertebrates, cephalopods	Capitoli and Haimovici (1993)
Mustelus canis	Not recorded	9.0	–	Benthic crustaceans, *L. sanpaulensis* and fish	Unpublished data
Paralichthys isosceles	Not recorded	0.5	–	Benthic crustaceans, fish and cephalopods	Unpublished data
Paralichthys spp.	1.4	3.3	–	Benthic crustaceans, fish and cephalopods	Carneiro (1995)
Percophis brasiliensis	0.2	0.7	–	Benthic fish, *L. sanpaulensis* and crustaceans	Unpublished data
Pomatomus saltatrix	3.5	0.2	–	Pelagic fish and crustaceans	Haimovici and Krug (1992)
Trichiurus lepturus	0.4	43.9	3.1–37.8	Benthic and pelagic crustaceans, fish and cephalopods	Martins (1992)
Total demersal shelf fisheries	49.2				
Total pelagic shelf fisheries	8.9				

* From Haimovici *et al.* (1997)
† From Haimovici *et al.* (1996)
‡ From Andriguetto and Haimovici (1991)

Among the predators of *Loligo sanpaulensis*, the La Plata dolphin *Pontoporia blainvillei* is probably the one that relies on it extensively. This small dolphin lives in coastal waters of Argentina, Uruguay and Brazil and, in all three regions, *L. sanpaulensis* is part of its diet (Brownell 1975, Pinedo 1982, Perez *et al.* 1996). It also appears to select the larger squid, because the average size of squid preyed on by this dolphin was bigger than those found during surveys, especially in summer, where the $\overline{ML}$ found by Andriguetto and Haimovici (1991) was 58.4 mm. The impact of the La Plata dolphin on the long-finned squid along southern Brazil must be considerable, because recent aerial surveys have estimated the dolphin population at about 4 400 animals between 29 and 34°S (E. Secchi, Museu Oceanográfico de Rio Grande, Brazil, pers. comm.).

The penguin *Spheniscus magellanicus* includes this squid among its main prey in the study area (Azevedo and Schieller 1991). Considerable numbers of one-year-old juvenile penguins from breeding grounds along the Patagonian coast reach the continental shelf of southern Brazil during winter and spring and frequently are found dead along the coast after storms (Vooren 1997). Penguins do not appear to be size-selective for the long-finned squid, because the size distribution in the stomach contents did not differ from that found by Andriguetto and Haimovici (1991) for winter and spring.

Young fur seals *Arctocephalus australis*, from breeding grounds off Uruguay, as well as vagrant adult males of *A. gazzella* and *A. tropicalis* from the Antarctic Convergence, reach southern Brazil in winter (Pinedo *et al.* 1992). All three species prey on *Loligo sanpaulensis*, with preference for larger specimens. These fur seals do not occur in large numbers in the region and their impact on the long-finned squid is therefore probably small.

Among fish that prey on long-finned squid, the benthic shark *Mustelus canis* and the ambushing finfish *Paralichthys* spp., *Percophis brasiliensis* and *Astroscopus sexpinosus* always feed near the bottom, whereas other bony fish that prey on *Loligo sanpaulensis* feed both near the bottom and in the water column (Juras and Yamaguti 1985, Vieira 1990, Haimovici and Krug 1992, Martins 1992, Carneiro 1995).

The long-finned squid appears to be more important in the diet of the bottom-feeding fish but, except for the flatfish, these are not abundant: <9.4% of commercial landings and 10.7% of the total catches in bottom trawl surveys. In contrast, it was only of secondary

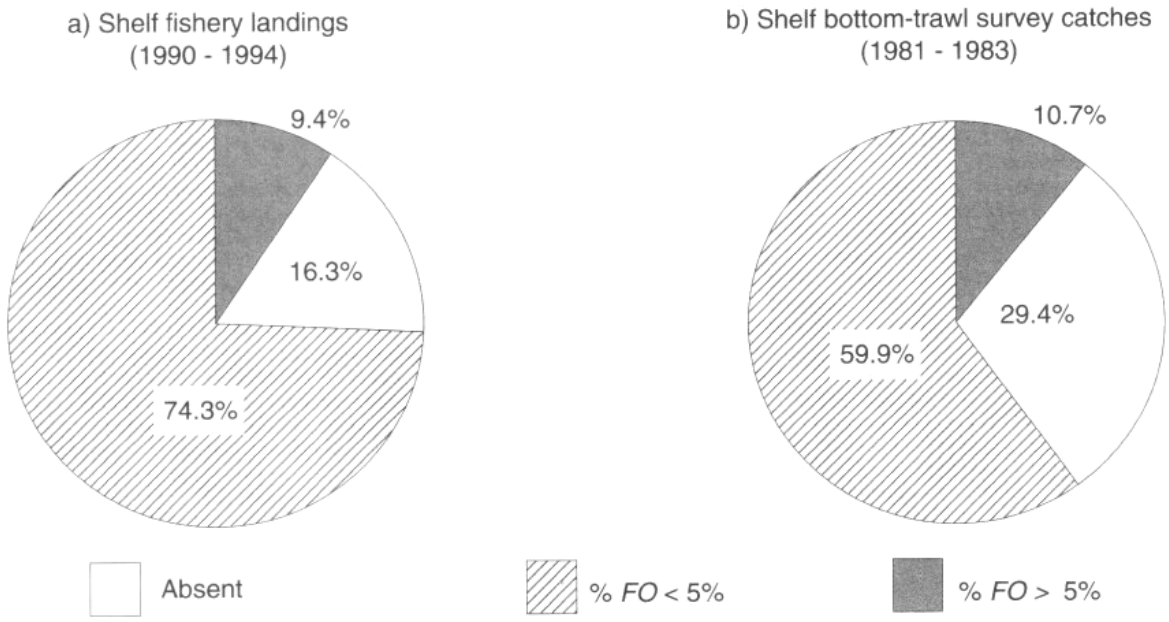

Fig. 7: Percentage distribution of predatory fish sampled from each of two time-period-specific sources by intensity of predation on *Loligo sanpaulensis*, as reflected by percentage frequency of occurrence (%*FO*) in predator stomachs – (a) commercial landings (after Haimovici *et al.* 1997), (b) bottom trawl survey catches (after Haimovici *et al.* 1996)

importance to demersal-pelagic species, including the cutlassfish *Trichiurus lepturus* and the weakfish *Cynoscion guatucupa* and *Macrodon ancylodon*, that represent 74.3% of commercial landings and 59.5% of the total catch in bottom trawl surveys. Therefore, despite the fact that *Loligo sanpaulensis* was a prey of secondary importance for demersal and pelagic finfish that feed in the water column, the total predation on long-finned squid by these species may be more important than the total predation by bottom-feeding fish, marine mammals and penguins combined, because the former group is far more abundant.

An analysis of midwater trawl surveys by Mello *et al.* (1992) found that *Loligo sanpaulensis*, *Trichiurus lepturus* and *Cynoscion guatucupa* form part of the main nektonic assemblages of the region. This association suggests that *Loligo sanpaulensis* ascends in the water column, probably at night, where it probably feeds and is preyed upon (Mello *et al.* 1992). On the other hand, the occurrence of demersal-benthic species in the stomach contents of long-finned squid and its presence in the stomach contents of several benthic predators indicates a strong connection of this squid with the sea bed, as also observed by other authors for this species off Argentina (Castellanos 1967) and also other species of the genus (Karpov and Cailliet 1979, Lipiński 1987).

It can be concluded that *L. sanpaulensis* over the southern Brazilian shelf occupies an intermediary level in the pelagic and benthic foodwebs, because it feeds and is eaten in the water column and on the sea bed. It also seems to play an important role in those foodwebs because it is preyed upon by high-level predators such as marine mammals and penguins and by several of the most abundant fish species found there.

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