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CEPHALOPODS IN THE TROPHIC RELATIONS OFF SOUTHERN BRAZIL

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ABSTRACT

Trophic relations of cephalopods in southern Brazil were investigated from predation on cephalopods by 71 species of potential predators, including two squids, 47 fishes, seven seabirds and 15 marine mammals from shelf, upper slope and oceanic adjacent waters. In all, 27 families and 41 species of cephalopods were identified from stomach contents. The number of families ranged from six, in the diet of shelf predators, to 27 families in those from upper slope and adjacent oceanic waters. The most frequent cephalopod prey on the shelf was *Loligo sanpaulensis*, particularly important in the diet of Franciscana dolphin *Pontoporia blainvillei*, occurring also in the diet of the penguin *Spheniscus magellanicus*, the fur seals *Arctocephalus australis*, *A. gazella*, *A. tropicalis*, and several benthic and demersal fishes. Ommastrephidae, mainly *Illex argentinus* and *Ornithoteuthis antillarum*, was the most frequent family in the diet of predators from upper slope and adjacent oceanic waters. *Illex argentinus* was an important prey for the wreckfish *Polyprion americanus*, the bigeye tuna *Thunnus obesus*, the swordfish *Xiphias gladius* and some marine mammals, especially in their winter and spring northward reproductive migration. *Ornithoteuthis antillarum* was frequent in the diet of the skipjack tuna *Katsuwonus pelamis*, the albacore *Thunnus alalunga*, the yellowfin tuna *T. albacares*, the Atlantic sailfish *Istiophorus albicans* and the white marlin *Tetrapturus albidus*. Ammoniacal squids, such as *Ancistrocheirus lesueurii*, *Histioteuthis spp*, *Chiroteuthis veranii* and *Octopoteuthis sp*, were mainly found in stomach contents of the blue shark, *Prionace glauca*, the pygmy sperm whale *Kogia breviceps*, the dwarf sperm whale *K. sima*, the long-finned pilot whale, *Globicephala melas* and oceanic seabirds. The relative importance, based on frequency of occurrence, of cephalopods as food resources seems to be higher in the food chains of the upper slope and adjacent oceanic waters, when compared to the continental shelf.

Cephalopods play an important role in the trophic relations of marine ecosystems. Many of them are active and efficient predators of a great variety of animals and also are prey of several marine species, mainly for those from oceanic waters, where the availability of food resources is lower than more productive regions, as continental shelves (Clarke, 1987, 1996a; Amaratunga, 1983). The cephalopods occupy several trophic levels and are considered to be mainly intermediaries in the energetic flux between the primary and secondary consumers and the predators of third and fourth level of the food webs. Due to their fast growth, the trophic interactions of muscular squids may be very complex, acting as predators, prey or competitor of some species of abundant fishes (Amaratunga, 1983; Angelescu and Prenski, 1987; Dawe and Brodziak, 1998).

In the marine ecosystems, the cephalopods generally occupy the role of subdominant predators and their importance in the food webs can be assessed from their relative importance in the diet of potential predators (Clarke, 1987). Among their predators are a large number of fishes, seabirds and marine mammals, many of them of commercial importance. For some large predators as sperm whales, pilot whales and zifids, cephalopods are the main source of food (Clarke, 1986a, 1996b). Tunas, billfishes and some pelagic sharks depends heavily on cephalopods (Smale, 1996), as well as several species of oceanic seabirds, as albatrosses and petrels (Croxall and Prince, 1996).

Many cephalopods, especially those inhabiting continental slopes and oceanic waters are difficult to catch with the fishing gears used in these environments. The stomach content analysis of the dominant predators, many of them target of commercial fishing, are the main source of data to assess the abundance and distribution of cephalopods. The identification of cephalopods in the stomach contents is difficult because these invertebrates are fleshy, easily digested, and with few structures that resist digestion. Usually beaks (or mandibles), eye lens, parts of gladius, sucker rings and hooks are the only remains found in the stomach contents. Among these hard structures, the chitinous beaks are the most useful for cephalopod identification due to their resistance to digestion and characteristic shape and pigmentation (Clarke, 1986b).

In this paper, the presence of cephalopods in the diet of fishes and cephalopods from commercial landings, cruise surveys and stranded or incidentally caught seabirds and marine mammals was analyzed to investigate their relative importance in the trophic relations of southern Brazilian shelf and adjacent oceanic waters.

The Study Area

The shelf and slope along southern Brazil are located in the western boundary of the Subtropical Convergence. Between late autumn and early spring, the shelf is dominated by cold waters of the coastal branch of the Malvinas (Falklands) Current, flowing northward, and the discharge of La Plata River and Patos Lagoon. From late spring to early autumn, warm coastal waters under the influence of the southward flowing Brazil Current are dominant (Castello et al., 1997; Garcia, 1997). The shelf waters productivity can be considered moderate to high, with the mean annual particulate primary production rates around 160 g C m^{-2} yr^{-1} (Odebrecht and Garcia, 1997). Upwelling processes of Subtropical Waters are common on the shelf in spring and summer, due to the strong influence of NE winds. This region sustains a multispecific demersal trawl fishery that, between 1990 and 1994, yielded in mean 50,000 t yr^{-1}, of which several species of the family Sciaenidae represented over 70% (Haimovici et al., 1997). The shelf cephalopod fauna of southern Brazil is relatively well known (Palacio, 1977; Juanicó, 1979; Haimovici and Perez, 1991).

The continental slope and oceanic adjacent waters are strongly influenced by the oligotrophic waters of Brazil Current. Especially in winter and spring, productivity may be increased along the shelf break associated to upwelling of the Subtropical Water due to frontal vortices of cyclonic circulation formed by the Brazil and Malvinas (Falklands) Currents (Castello et al., 1997; Garcia, 1997). The demersal fishery over the upper slope is undertaken mainly by bottom longliners for wreckfish (*Polyprion americanus*) that, in the early 90s, yielded around 2000 t yr^{-1} (Peres and Haimovici, 1998). In the outer shelf and upper slope, the skipjack tuna (*Katsuwonus pelamis*) is fished with live bait and yielded ca 3200 t yr^{-1} (1990–1994). Tunas, billfishes and pelagic sharks are fished by Brazilian longliners over the slope and oceanic adjacent waters (ca 3400 t yr^{-1} in 1990–1994) (Haimovici et al., 1997). The cephalopod fauna of these environments is less known than the one of the shelf (Perez and Haimovici, 1993).

Material and Methods

The presence of cephalopods was investigated in the diet of 71 nektonic potential predators of southern Brazil (26°S–34°S), including seven species of seabirds and 15 of marine mammals found stranded along beaches or incidentally caught in the gillnet coastal fishery, 36 species of pelagic and demersal fishes and two squids caught along the shelf (<200 m) and upper slope (200–500 m) and 11 species of oceanic pelagic fishes caught with surface longliners in oceanic waters adjacent to the upper slope (>500 m) (Fig. 1).

Most of data were obtained from stomachs collected between 1980 and 1998 and examined by the authors (Haimovici et al., 1989; Teixeira and Haimovici, 1989; Haimovici and Krug, 1992; Capitoli and Haimovici, 1993; Santos and Haimovici, 1997; 1998; in press; Santos, 1999). Part of the data were obtained from published papers, thesis and unpublished reports by other authors (Clarke et al., 1980; Lessa, 1982; Pinedo, 1982; Pinedo and Barros, 1983; Juras and Yamaguti, 1985; Queiroz, 1986; Pinedo, 1987; Rosas, 1989; Schwingel, 1991; Vaske, 1994; Vaske and Rincón, 1998).

The cephalopods were retrieved in various stages of digestion, ranging from whole individuals, in few stomach contents, to the presence of only beaks, as most cases. To estimate the size composition of the cephalopods found in the diet of predators, regression equations which relate mantle length (ML-mm) and total weight (TW-g) with the beak size were used (Clarke, 1986b; Santos, 1999). The rostral lengths of upper (URL) and lower (LRL) beaks of squids and sepiolids and hood lengths of upper (UHL) and lower (LHL) beaks of octopuses were measured in tenths of millimeters, following Clarke (1986b). The numbers of squids per stomach were estimated from undigested specimens and upper or lower beaks, whichever were the most numerous.

The relative importance of the cephalopods in the diet of their different predators was not easy to assess from the available data. For a considerable number of the predator species, particularly among marine mammals, birds and large pelagic fishes, the total number of stomach contents was known but not the number of weight of the other type of prey. Thus we were not able to estimate the importance of cephalopods in the diet in mass and the only information available for all the predators examined by the authors and most of the consulted papers was the number of stomachs with each cephalopod species (Nc) in relation to the total number of stomachs with food (Nt). This quantity was referred as 'frequency of occurrence' ($FO = Nc/Nt \times 100$) and used as a measure of relative importance.

The scientific names of cephalopods followed Sweeney and Roper (1998), fishes Eschmeyer (1998), seabirds Vooren and Fernandes (1989) and marine mammals Rice (1998).

Inferences on the diet of predators from stomach content analysis have inherent limitations. Oceanic seabirds could have fed on dead squids, mainly when referred to ammoniacal ones, that float when die, as well as these animals could eat remains of cephalopods taken out of cetacean regurgitation or fishery discards (Clarke et al., 1981; Lipinski and Jackson, 1989; Croxall and Prince, 1994). Seabirds, large pelagic fishes and marine mammals can have eaten their preys far from where they were caught or found stranded and the diet of unhealthy animals can differ of healthy ones. These limitations were taken into account as far as possible in the interpretation of the results.

Results

Twenty seven families and at least 41 species of cephalopods (Table 1, Fig. 1) were identified in the stomach contents of the 71 species of predators investigated (Table 2). The species of cephalopods eaten by shelf fishes and *Loligo sanpaulensis* are listed in Figure 2, those preyed upon by upper slope and oceanic adjacent waters fishes and *Illex*

Table 1. Taxonomic list of cephalopod species found in the diet of several predators of southern Brazil.

Class Cephalopoda	Family Histioteuthidae
Subclass Coleoidea	*Histioteuthis* sp. Orbigny, 1841
Superorder Decabrachia	Family Neoteuthidae
Order Spirulida	*Alluroteuthis antarctica* Odhner, 1923
Family Spirulidae	Family Brachioteuthidae
Spirula spirula (Linnaeus, 1758)	*Brachioteuthis* sp. Verrill, 1881
Order Sepiolida	Family Ommastrephidae
Family Sepiolidae	*Illex argentinus* (Castellanos, 1960)
Semirossia tenera (Verrill, 1880)	*Todarodes filippovae* Adam, 1975
Heteroteuthis dispar (Rüppell, 1844)	*Ommastrephes bartramii* (Lesueur, 1821)
Order Teuthida	*Ornithoteuthis antillarum* Adam, 1957
Suborder Myopsina	*Hyaloteuthis pelagica* (Bosc, 1802)
Family Loliginidae	Family Thysanoteuthidae
Loligo plei Blainville, 1823	*Thysanoteuthis rhombus* Troschel, 1857
Loligo sanpaulensis Brakoniecki, 1984	Family Chiroteuthidae
Suborder Oegopsina	*Chiroteuthis veranii* (Férussac, 1835)
Family Lycoteuthidae	Family Mastigoteuthidae
Lycoteuthis lorigera (Steenstrup, 1875)	*Mastigoteuthis* sp. Verrill, 1881
Family Enoploteuthidae	Family Cranchiidae
Enoploteuthis sp. Orbigny, 1844	Superorder Octobrachia
Abralia veranyi (Rüppell, 1844)	Order Octopodida
Abralia redfieldi Voss, 1955	Suborder Incirrina
Abraliopsis sp. Joubin, 1896	Family Bolitaenidae
Family Ancistrocheiridae	*Japetella diaphana* Hoyle, 1885
Ancistrocheirus lesueurii (Orbigny, 1842)	Family Octopodidae
Family Pyroteuthidae	*Octopus vulgaris* Cuvier, 1797
Pteryogioteuthis giardi Fischer, 1896	*Octopus tehuelchus* Orbigny, 1834

argentinus are in Figure 3 and those found in the stomach contents of different seabirds and marine mammals in Figure 4.

Loliginid squids were the main cephalopods preyed on the shelf and among them *L. sanpaulensis* was by far the most important (Figs. 2,3,4). Small and large squids were found (Fig. 5), and were very frequent in the diet of *Pontoporia blainvillei* and relatively important for *Spheniscus magellanicus, Arctocephalus australis, A. gazella* and *A. tropicalis*. It occurred with *FO* over 5% in the stomach contents of benthic and demersal fishes as *Mustelus canis, Astroscopus sexpinosus, Percophis brasilianus, Helicolenus dactylopterus lahillei, Paralichthys isosceles, P. patagonicus* and *Merluccius hubbsi*. With a lower frequency (*FO* < 5%) in the diet of several pelagic and demersal shelf fishes, as *Pomatomus saltatrix, Trichiurus lepturus, Cynoscion guatucupa, Macrodon ancylodon* and *Pagrus pagrus*. *L. sanpaulensis* occurred also in the diet of predators from upper slope and oceanic waters. The other loliginid found was *Loligo plei*, in the diet of some shelf and upper slope predators, but with very lower frequency (Figs. 2,3,4).

Ommastrephid squids were important in the diet of upper slope and oceanic adjacent water predators. *I. argentinus* was found in the diet of many marine mammals and pelagic and demersal fishes, being frequent in the stomach contents of *Thunnus obesus, Xiphias gladius, Polyprion americanus, Globicephala melas* and *K. breviceps*. Although small individuals (< 100 mm ML) had been found, most of its predators fed on mature or maturing individuals (> 200 mm ML) (Fig. 5). Other frequent ommastrephids were *Ornithoteuthis antillarum*, the most frequent cephalopod in the diet of *Katsuwonus pelamis*,

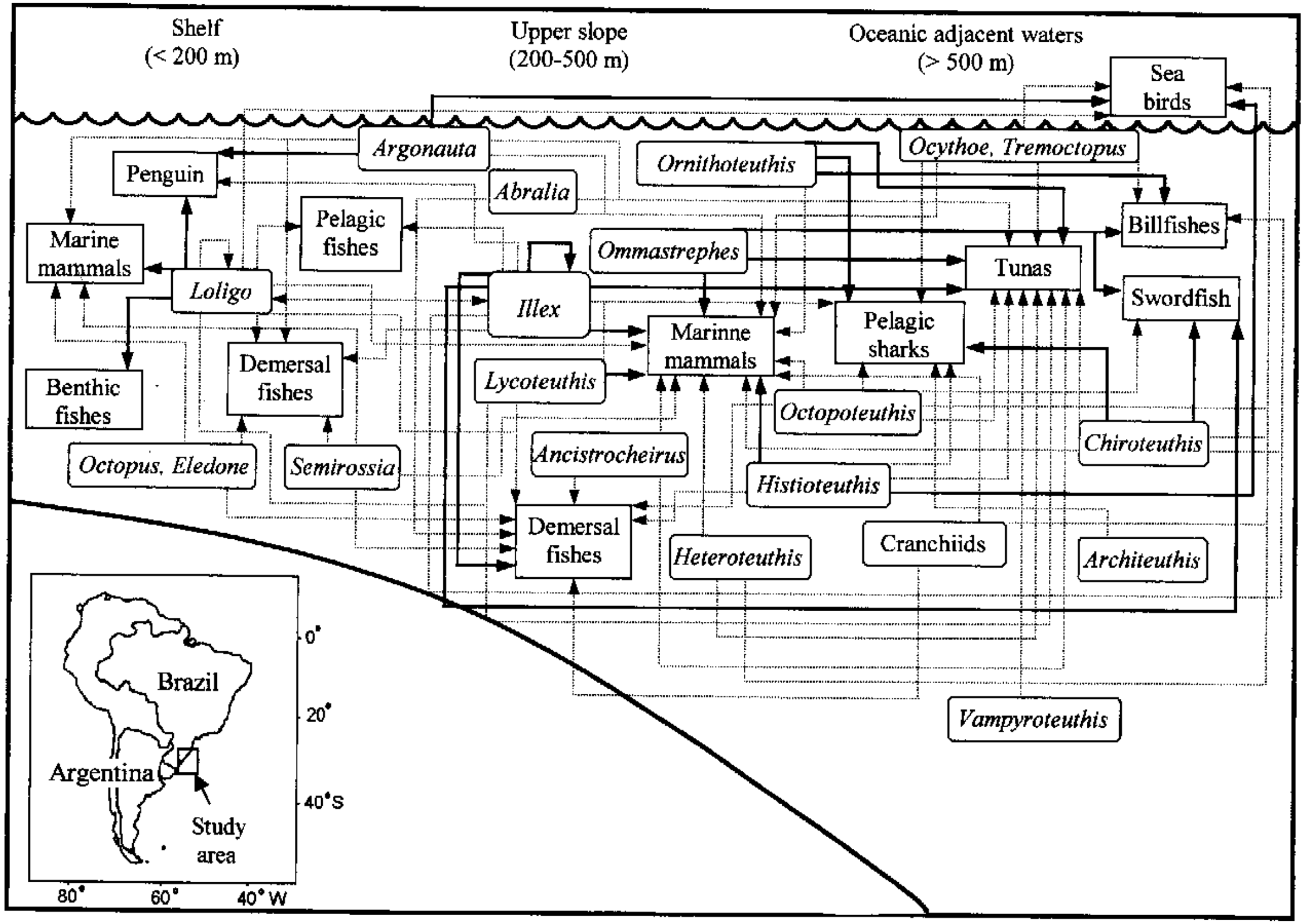

Figure 1. Diagrammatic summary of predation on cephalopods in southern Brazil. Full lines indicate frequent predation (cephalopod distributions based on Packard, 1972; Nesis, 1987).

Table 2. List of the predators that had their diet studied for predation on cephalopods. Region (shelf, slope and oceanic), habitat (demersal and pelagic), number of stomachs with food and mean annual commercial landings (1990–1994 period) in southern Brazil (from Haimovici et al., 1997 and Peres and Haimovici, 1998) are indicated.

Predator species	Common name	Region	Habitat	Mean annual commercial landings	Stomachs with food	Source of data
CEPHALOPODS						
Illex argentinus	Argentine long-finned	shelf, slope	demersal	-	363	1
Loligo sanpaulensis	common long-finned	shelf	demersal	100	313	1
FISHES						
Astroscopus sexpinosus	Brazilian stargazer	shelf	demersal	-	6	1
Conger orbignyanus	Argentine conger	shelf	demersal	-	146	1
Coryphaena hippurus	common dolphinfish	oceanic	pelagic	-	811	1
Cynoscion guatucupa	striped weakfish	shelf	demersal	8,785	220	1
Cynoscion jamaicensis	Jamaica weakfish	shelf	demersal	-	73	1
Engraulis anchoita	anchoita	shelf	pelagic	-	512	2
Evoxymetopon taeniatus	channel seabbarfish	slope	demersal	-	14	1
Galeorhinus galeus	school shark	slope	demersal	-	101	1
Helicolenus dactylopterus lahillei	blackbelly rosefish	slope	demersal	-	33	1
Istiophorus albicans	Atlantic sailfish	oceanic	pelagic	-	35	1
Isurus oxyrinchus	shortfin mako	oceanic	pelagic	<500	19	1
Katsuwonus pelamis	skipjack tuna	shelf, slope	pelagic	2,402	295	1
Macrodon ancylodon	king weakfish	shelf	demersal	3,966	1,402	3
Merluccius hubbsi	Argentine hake	shelf	demersal	129	231	1
Micropogonias furnieri	white croaker	shelf	demersal	14,709	194	1
Mustelus canis	smooth dogfish	shelf	demersal	-	54	1
Naucrates ductor	pilotfish	oceanic	pelagic	-	39	4
Pagrus pagrus	red porgy	shelf	demersal	238	362	1
Paralichthys isosceles	flounder	shelf	demersal	-	304	1
Paralichthys orbignyanus	flounder	shelf	demersal	<1,000	308	1

Table 2. Continued.

Predator species	Common name	Region	Habitat	Mean annual commercial landings	Stomachs with food	Source of data
Paralichthys patagonicus	Patagonian flounder	shelf	demersal	<1,000	290	1
Percophis brasilianus	Brazilian flathead	shelf	demersal	-	66	1
Polyprion americanus	wreckfish	slope	demersal	2,036	>100	1
Pomatomus saltatrix	bluefish	shelf	pelagic	3,521	164	1
Porichthys porosissimus	lantern midshipman	shelf	demersal	-	114	1
Prionace glauca	blue shark	oceanic	pelagic	<500	19; 40	1;5
Prionotus nudigula	red searobin	shelf	demersal	-	244	1
Prionotus punctatus	bluewing	shelf	demersal	988	743	1
Rhinobatus horkeli	Brazilian guitarfish	shelf	demersal	460	82; 918	1;6
Scomber japonicus	chub mackerel	shelf	pelagic	969	30	2
Scyliorhinus besnardi	polkadot catshark	slope	demersal	-	8	1
Sphyrna lewini	hammerhead shark	oceanic	pelagic	<500	13	1
Squatina argentina	Argentine angel shark	shelf	demersal	-	56	1
Squatina guggenhein	angel shark	shelf	demersal	<1,000	109	1
Squatina occulta	angel shark	shelf	demersal	<1,000	58	1
Sympterigia acuta	skate	shelf	demersal	-	1,510	7
Sympterigia bonapartei	skate	shelf	demersal	-	809	7
Tetrapturus albidus	white marlin	oceanic	pelagic	-	52	1
Thunnus alalunga	albacore	oceanic	pelagic	1,075	110	1
Thunnus albacares	yellow-fin tuna	oceanic	pelagic	684	418	1
Thunnus obesus	bigeye tuna	oceanic	pelagic	500	104	1
Trachurus lathami	rough scad	shelf	pelagic	1,555	124	2
Trichiurus lepturus	cutlassfish	shelf, slope	demersal	441	490	1
Umbrina canosai	Argentine croaker	shelf	demersal	9,629	726	1
Urophycis brasiliensis	squirrel codling	shelf	demersal	1,186	663	1
Urophycis cirrata	gulf hake	slope	demersal		58	1

Table 2. Continued.

Predator species	Common name	Region	Habitat	Mean annual commercial landings	Stomachs with food	Source of data
Xiphias gladius	swordfish	oceanic	pelagic	601	218	1
SEA BIRDS						
Spheniscus magellanicus	Magellanic penguin	shelf			120	1
Diomedea exulans	wandering albatross	oceanic			3	1
Diomedea melanophris	black-browed albatross	oceanic			8	1
Phoebetria palpebrata	light-mantled sooty albatross	oceanic			1	1
Fulmarus glacialoides	Antarctic fulmar	oceanic			13	1
Puffinus gravis	great shearwater	oceanic			47	1
Puffinus puffinus	manx shearwater	oceanic			34	1
MARINE MAMMALS						
Arctocephalus australis	South American fur seal	shelf, slope			15; 26	1; 8
Arctocephalus gazella	Antarctic fur seal	oceanic			3	1
Arctocephalus tropicalis	Subantarctic fur seal	oceanic			12	1
Mirounga leonina	southern elephant seal	oceanic			1	1
Otaria flavescens	South American sea lion	shelf, slope			56; (a)	8; 9
Delphinus sp	common dolphin	shelf, slope, oceanic			3	1
Globicephala melas	longfinned pilot whale	shelf, slope, oceanic			4	1
Lagenodelphis hosei	Fraser's dolphin	slope, oceanic			4	1
Kogia breviceps	pygmy sperm whale	slope, oceanic			2	1
Kogia sima	dwarf sperm whale	shelf, slope			1	10
Orcinus orca	orca	shelf, slope, oceanic			2	1
Pontoporia blainvillei	Franciscana	shelf			111; 257	1;11
Physeter macrocephalus	sperm whale	slope, oceanic			1	12
Pseudorca crassidens	false killer whale	oceanic			3	1
Tursiops truncatus	bottlenose dolphin	shelf, oceanic			1;12	1;11

1 examined by RAS or MH	5 Vaske and Rincón, 1998	9 Rosas, 1989	(a) number not indicated
2 Schwingel, 1991	6 Lessa, 1982	10 Pinedo, 1987	
3 Juras and Yamaguti, 1985	7 Queiroz, 1986	11 Pinedo, 1982	
4 Vaske, 1994	8 Pinedo and Barros, 1983	12 Clarke et al., 1980	

Predators	*Loligo sanpaulensis*	*Astroscopus sexpinosus*	*Conger orbignyanus*	*Cynoscion guatucupa*	*Cynoscion jamaicensis*	*Macrodon ancylodon*	*Merluccius hubbsi*	*Micropogonias furnieri*	*Mustelus canis*	*Pagrus pagrus*	*Paralichthys isosceles*	*Paralichthys orbignyanus*	*Paralichthys patagonicus*	*Percophis brasilianus*	*Pomatomus saltatrix*	*Porichthys porosissimus*	*Squatina argentina*	*Squatina occulta*	*Sympterigia acuta*	*Sympterigia bonapartei*	*Trichiurus lepturus*	*Umbrina canosai*
Stomach with contents	313	6	156	220	73	1402	231	194	54	362	90	308	290	66	164	114	56	58	1510	809	490	726
Preys																						
Spirula spirula																						
Heteroteuthis dispar																						
Semirossia tenera									○	○											○	
Loligo plei											○		○									
Loligo sanpaulensis	○	●	○	○	○	○	○	○	●	○	○	○	○	●	○	○			○	○	○	○
Lycoteuthis lorigera							○														○	
Enoploteuthis sp																						
Abralia veranyi																						
Abralia redfieldi																						
Abralia sp																						
Abraliopsis sp																						
Ancistrocheirus lesueurii																						
Pterygioteuthis giardi																						
Octopoteuthis sp																						
Taningia danae																						
Moroteuthis ingens																						
Moroteuthis robsoni																						
Kondakovia longimana																						
Gonatus antarcticus																						
Pholidoteuthis boschmai																						
Architeuthis sp																						
Histioteuthis spp																						
Alluroteuthis antarctica																						
Brachioteuthis sp																						
Illex argentinus	○						○			○					○		○	○			○	
Todarodes filippovae																						
Ommastrephes bartramii																					○	
Ornithoteuthis antillarum																						
Hyaloteuthis pelagica																						
Thysanoteuthis rhombus																						
Chiroteuthis veranii																						
Mastigoteuthis sp																						
Cranchiidae																						
Japetella diaphana																						
Octopus vulgaris																						
Octopus tehuelchus										○												
Eledone gaucha																						
Eledone massyae										○	○											
Tremoctopus violaceus																						
Ocythoe tuberculata																						
Argonauta nodosa				○	○					○											○	
Haliphron atlanticus																						
Vampyroteuthis infernalis																						

Figure 2. Cephalopods preyed upon by *Loligo sanpaulensis* and pelagic and demersal fishes caught on the southern Brazilian shelf. (Circles indicate the presence in the diet; black circles indicate a frequency of occurrence (*FO*) over 10%).

Predators	*Illex argentinus*	*Evoxymetopon taeniatus*	*Galeorhinus galeus*	*Helicolenus d. lahillei*	*Polyprion americanus*	*Scyliorhinus besnardi*	*Urophycis cirrata*	*Coryphaena hyppurus*	*Istiophorus albicans*	*Isurus oxyrinchus*	*Katsuwonus pelamis*	*Naucrates ductor*	*Prionace glauca*	*Sphyrna lewini*	*Tetrapturus albidus*	*Thunnus alalunga*	*Thunnus albacares*	*Thunnus obesus*	*Xiphias gladius*
Stomach with contents	363	14	101	33	>100	8	58	81	35	19	295	39	40	13	52	110	418	101	218
Preys																			
Spirula spirula	○																		
Heteroteuthis dispar														○		●	○	○	○
Semirossia tenera	○					●	○												
Loligo plei							○										○		
Loligo sanpaulensis	○		○	○			○										○		
Lycoteuthis lorigera					○					●	○		○	●		●	○	●	○
Enoploteuthis sp																	○		○
Abralia veranyi																	○	○	
Abralia redfieldi						●										○	○		
Abralia sp																○	○	○	○
Abraliopsis sp																	○		
Ancistrocheirus lesueurii					○				○				●				○	○	○
Pterygioteuthis giardi					○														
Octopoteuthis sp		○			○			○					○			○	○	○	○
Taningia danae																			
Moroteuthis ingens													○						○
Moroteuthis robsoni																			
Kondakovia longimana																			
Gonatus antarcticus																			
Pholidoteuthis boschmai																		○	
Architeuthis sp													○						
Histioteuthis spp		○						○		●			●			○	○	○	○
Alluroteuthis antarctica																			
Brachioteuthis sp																			
Illex argentinus	○	○	●	●	●	●		○	○	○	○	○	○	○	○	●	●	●	●
Todarodes filippovae					○														○
Ommastrephes bartramii					○			○	●				○		●	○	○	●	●
Ornithoteuthis antillarum								○	●		○				●	●	●	●	○
Hyaloteuthis pelagica																			
Thysanoteuthis rhombus											○						○	○	○
Chiroteuthis veranii								○					●		○	○	○	●	●
Mastigoteuthis sp																			
Cranchiidae																			
Japetella diaphana																	○	○	○
Octopus vulgaris					○	●										○			
Octopus tehuelchus																			
Eledone gaucha	○																		
Eledone massyae																			
Tremoctopus violaceus								○					○			○	○	○	○
Ocythoe tuberculata								○								○	○	○	
Argonauta nodosa							○	○	○		○	○	●		○	○	○	○	○
Haliphron atlanticus													○	○		○	○		
Vampyroteuthis infernalis																	○		

Figure 3. Cephalopods preyed upon by *Illex argentinus* and pelagic and demersal fishes caught on upper slope and oceanic adjacent waters of southern Brazil. (Circles indicate the presence in the diet; black circles indicate a frequency of occurrence (*FO*) over 10%).

Predators	*Diomedea exulans*	*Diomedea melanophris*	*Fulmarus glacialoides*	*Phoebetria palpebrata*	*Puffinus gravis*	*Puffinus puffinus*	*Spheniscus magellanicus*	*Arctocephalus australis*	*Arctocephalus gazella*	*Arctocephalus tropicalis*	*Mirounga leonina*	*Delphinus sp*	*Globicephala melas*	*Kogia breviceps*	*Kogia sima*	*Lagenodelphis hosei*	*Orcinus orca*	*Physeter macrocephalus*	*Pontoporia blainvillei*	*Pseudorca crassidens*	*Tursiops truncatus*
Stomachs with contents	**3**	**8**	**13**	**1**	**47**	**34**	**120**	**41**	**1**	**8**	**1**	**3**	**5**	**2**	**1**	**4**	**3**	**1**	**368**	**3**	**1**
Preys																					
Spirula spirula																					
Heteroteuthis dispar			○											○							
Semirossia tenera												●		○					○		
Loligo plei							○										○		○		○
Loligo sanpaulensis					○	○	●	●	○	●		●				○	○		●		
Lycoteuthis lorigera											○		●	●	○		○				
Enoploteuthis sp																					
Abralia veranyi																					
Abralia redfieldi														●							
Abralia sp														○							
Abraliopsis sp																					
Ancistrocheirus lesueurii													○								
Pterygioteuthis giardi																					
Octopoteuthis sp	●												○	○			○	○			
Taningia danae																		○			
Moroteuthis ingens														○							
Moroteuthis robsoni										○				○			○	○			
Kondakovia longimana																		○			
Gonatus antarcticus							○										○	○			
Pholidoteuthis boschmai																		○			
Architeuthis sp																		○			
Histioteuthis spp	●	●	●								○		●	●	●		○	○			
Alluroteuthis antarctica	●	●				○			○												
Brachioteuthis sp															○						
Illex argentinus							○			○	○	●	○	●							
Todarodes filippovae																		○			
Ommastrephes bartramii										●							○			○	
Ornithoteuthis antillarum														○			○				
Hyaloteuthis pelagica												○									
Thysanoteuthis rhombus																					
Chiroteuthis veranii				●									○	○	○						
Mastigoteuthis sp															○			○			
Cranchiidae												○	●	●	○		○	○			
Japetella diaphana														○							
Octopus vulgaris																					
Octopus tehuelchus																			○		
Eledone gaucha																			○		
Eledone massyae																					
Tremoctopus violaceus					○																
Ocythoe tuberculata										○							○				
Argonauta nodosa		●			●	○	●	○		○									○		
Haliphron atlanticus																					
Vampyroteuthis infernalis																					

Figure 4. Cephalopods preyed upon by seabirds and marine mammals found dead in beaches or incidentally caught by coastal gillnet fishery of southern Brazil. (Circles indicate the presence in the diet; black circles indicate the main species in the diet).

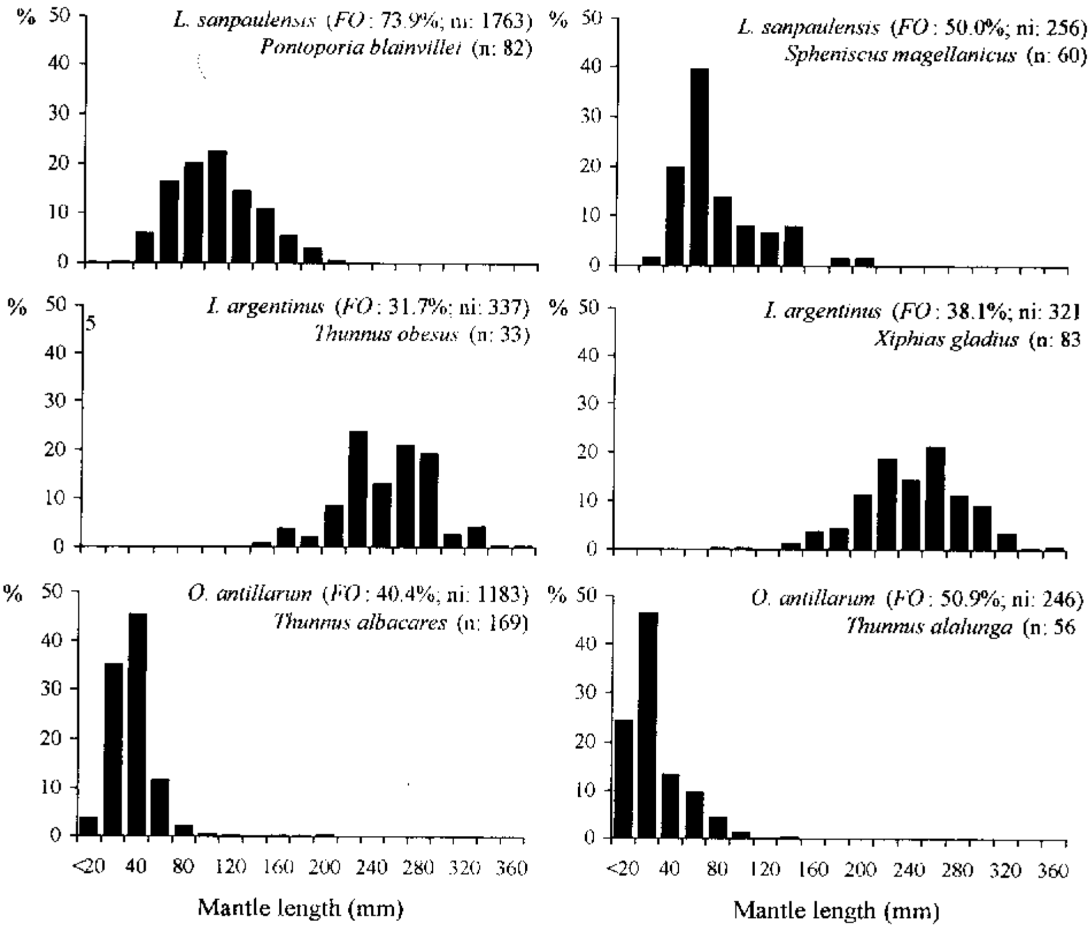

Figure 5. Mantle length distribution of *Loligo sanpaulensis*, *Illex argentinus* and *Ornithoteuthis antillarum* in the stomach contents of some of their main predators. (*FO*: frequency of occurrence; ni: number of squids measured and n: number of predators with each species of squid).

Thunnus alalunga, *T. albacares*, *Istiophorus albicans* and *Tetrapturus albidus*, generally with small sizes (Fig. 5) and *Ommastrephes bartramii* frequent in the diet of *Thunnus obesus*, *X. gladius* and marine mammals, such as *Orcinus orca* and *Kogia breviceps* (Figs. 2,3,4). *Todarodes filippovae* and *Hyaloteuthis pelagica*, were far less frequent, found in the diet of marine mammals and pelagic and demersal fishes from upper slope and of oceanic adjacent waters. Other relatively frequent oceanic muscular squids were *Lycoteuthis lorigera* and *Abralia spp*, mainly in the diet of *T. alalunga*, *T. obesus*, *Isurus oxyrinchus*, *Sphyrna lewini*, *Globicephala melas* and *K. breviceps* (Figs. 2,3,4).

Ammoniacal squids occurred with relatively frequency in the diet of upper slope and oceanic predators. The more frequent species were *Ancistrocheirus lesueurii*, *Octopoteuthis* sp, *Histioteuthis* spp and *Chiroteuthis veranii*, mainly in the diet of *Prionace glauca*, *Kogia sima*, *K. breviceps*, *G. melas* and oceanic seabirds (Figs. 3,4).

With very low frequencies were observed other oceanic squids such as *Enoploteuthis* sp, *Abraliopsis* sp, *Moroteuthis robsoni*, *Pholidoteuthis boschmai*, as well as cranchiids and onychoteuthids not identified to specific level (Figs. 3,4).

The presence of the benthic octopuses *Eledone gaucha*, *E. massyae*, *Octopus tehuelchus* and *Octopus vulgaris* was observed with low frequency in the diet of demersal fishes and marine mammals of shelf and upper slope, although the presence of a small *O. vulgaris* (ML < 20 mm) was recorded in a stomach content of *T. alalunga* (Figs. 2–4).

The pelagic octopus *Argonauta nodosa* was found mainly in the diet of species of shelf and upper slope, being frequent, sometimes in large number of very small individuals, in stomach contents of *Spheniscus magellanicus* and, to a lesser degree, in *Katsuwonus pelamis* (Figs. 2–4). Other pelagic octopuses, as *Tremoctopus violaceus* and *Ocythoe tuberculata*, were found in the stomach contents of large pelagic fishes and marine mammals of upper slope and oceanic adjacent waters. With small frequency occurred *Japetella diaphana*, *Haliphron atlanticus* and the bathypelagic vampyromorphid *Vampyroteuthis infernalis* (Figs. 3,4).

Sepiolids were infrequent, *Semirossia tenera* was found mainly in stomach contents of shelf and upper slope predators, and *Heteroteuthis dispar* in predators from upper slope and oceanic adjacent waters (Figs. 2–4).

The sizes of cephalopod prey were mostly small, with ML under 100 mm. The larger were *Ommastrephes bartramii*, *I. argentinus*, *Thysanoteuthis rhombus*, *Ancistrocheirus lesueurii*, *Pholidoteuthis boschmai* and *Octopoteuthis* sp, reaching ML over 250 mm, preyed upon mainly by *P. americanus*, *T. alalunga*, *T. albacares*, *T. obesus*, *Xiphias gladius* and by marine mammals from upper slope and of oceanic adjacent waters. The presence of remains of a buccal mass and arms remains of an *Architeuthis* sp, with estimated mantle length of 1012 mm and total weight of 92 Kg, was observed in the stomach content of a blue shark.

Discussion

Six families and seven species of cephalopods were recorded in the diet of the shelf predators. Haimovici and Perez (1991) recorded the same number of families and one more species, in the review of the coastal cephalopod fauna of southern Brazil. The similarity in the numbers of shelf species recorded from predator's diet and surveys shows that a fairly precise list of cephalopods can be obtained analysing stomach contents.

In the upper slope and oceanic adjacent waters, 27 families were registered in the diet of predators, far more than the 12 families formerly recorded from bottom trawl surveys in the area (Perez and Haimovici, 1993). Furthermore, the higher number of *taxa* in the stomach contents compared with the survey from the slope and oceanic waters, confirms the utility of dietary studies to survey the cephalopod fauna composition.

The low number of cephalopod *taxa* in the southern Brazilian shelf can be attributed to the low diversity of substrates, mostly soft bottoms, and to the influence of cold waters (<15°C) during part of the year that prevent the occurrence of tropical cephalopods. The higher diversity in upper slope and oceanic adjacent warm waters is reflected in the large number of widely distributed species of epi, meso and bathypelagic cephalopods in the Southwestern Atlantic (Nesis, 1999).

The assessment of the importance of cephalopods in the food webs is made more difficult because we lack estimates of abundance of the predators and also ignore the amount of energy represented by the cephalopods in their diets. A first approximation can be obtained assuming that landings represent the relative abundance of the fishes and the frequency of occurrence of cephalopods in the stomach contents are an index of their relative importance in the diets of their predators.

Following this approach, according to commercial landings reported by Haimovici et al. (1997), we estimated that the shelf fishes that preyed more heavily on cephalopods were of little importance in the catches, less than 1000 t yr^{-1}. Those that fed occasionally on them (*FO* < 5%) yielded around 15,000 t yr^{-1}, less than a third of the demersal trawl fishery landings. In contrast tunas, billfishes and wreckfish, which feed intensely on cephalopods (FO 10% – 80%), yielded over 5000 t yr^{-1} to Brazilian fishers, besides the catches by foreign longliners. Comparing this numbers we concluded that cephalopods have a larger relative importance in the upper slope and oceanic adjacent waters than in shelf waters.

On the shelf *Loligo sanpaulensis* occurs year round and is the most abundant cephalopod (Haimovici and Andriguetto, 1986). The only estimates of its abundance are around 3000 t in the early 80s by Andriguetto and Haimovici (1991). It is part of the incidental catch of bottom trawlers, but no specific fishery is developed for it in southern Brazil. This squid seems to occupy an intermediary level in the energy transference, feeding in midwater and being a prey of both pelagic and benthic fishes (Santos and Haimovici, 1998). One of the species that fed more heavily on *L. sanpaulensis* was the Franciscana dolphin, that also feed on this species in all its distribution range, from coastal waters of Argentina to Rio de Janeiro (Brownell, 1975; Pinedo, 1982; Santos and Haimovici, 2001). Other seasonally important predators were juvenile Magellanic penguins that arrive in southern Brazilian coast from Patagonia, in some years, in large numbers (Vooren, 1997). All other cephalopod species were far less frequent and *Loligo plei,* octopuses and sepiolids were rare in bottom trawl survey catches and absent in commercial landings (Haimovici and Andriguetto, 1986).

On the upper slope and oceanic adjacent waters two ommastrephids seems to be the most important links in the trophic relations: *I. argentinus* and *O. antillarum.* The first performs diel vertical migrations (Moiseev, 1991) and was found to be an important prey for large pelagic fishes, as the swordfish and bigeye tuna, that have the ability to prey in midwater up to 600 m (Carey and Robison 1981; Colette and Nauen 1983; Holland et al., 1990). It was also a prey for the near bottom dwelling wreckfish and the school shark, emphasising its role in the transference of energy between the pelagic and demersal environment (Santos and Haimovici, 2000). Tunas, billfishes and the swordfish, migrate from the tropics to southern Brazil from May to October, when the influence of cold waters of Malvinas (Falklands) Current is stronger in the region (Weidner and Arocha, 1999). Their permanence in the region is probably associated to the northward reproductive migration of adults and subadults *I. argentinus* from Uruguayan and northern Argentinean waters that occurs in the same time of the year (Santos and Haimovici, 2000).

The other important ommastrephid was the smaller-sized and more epipelagic *O. antillarum.* Its major occurrence in the diet of the smaller tunas *T. alalunga* and *T. albacares* and billfishes, can be explained by the association of these predators with more superficial waters and also because its small size. Juveniles *O. antillarum* (ml < 50 mm) were fairly frequent and mid water trawls in the EEZ of southern Brazil (REVIZEE Program–Avaliação do Potencial Sustentável dos Recursos Vivos na Zona Econômica Exclusiva do Brasil, unpubl. data).

The neutrally buoyant and slow swimming ammoniacal squids were found in the diet of diverse predators from upper slope and oceanic adjacent waters, being more frequent in the stomach contents of blue shark, *Prionace glauca,* a slower swimmer with a broad trophic range, and some marine mammals, as *Kogia sima*, *K. breviceps* and *G. melas*, teuthophagous species adapted to feed in deeper waters (Clarke, 1986a).

From the analysis of the stomach contents of potential predators off southern Brazil, it was concluded that the cephalopod fauna is far more diverse and has a higher relative importance in the offshore food webs when compared to the neritic environment. The loliginid *L. sanpaulensis* was the dominant cephalopod on the shelf, whilst two ommastrephids dominated more oceanic waters, one of them *I. argentinus*, that may have some fishery potential, was important in the food web of the slope and the other, *O. antillarum*, appears as an important component of the pelagial food webs of oceanic adjacent waters.

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