The Argentine short-finned squid *Illex argentinus* in the food webs of southern Brazil

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Predation on *Illex argentinus* (Cephalopoda, Ommastrephidae) in southern Brazil (26°S to 34°S) was studied from its presence in contents of over 14 000 stomachs from 63 potential predator species including fishes, cephalopods, penguins and marine mammals. The size composition of *I. argentinus* in the diet of their main predators was estimated using regression equations that relate mantle length and body weight to beak size. The short-finned squid was found in the diet of 32 species and appears to play an important role in the trophic relations along the upper slope and adjacent oceanic waters, where it was found in the diet of the swordfish *Xiphias gladius*, the tunas *Thunnus obesus*, *T. alalunga* and *T. albacares*, and the wreckfish *Polyprion americanus*. These five species stand for more than half of the landings from the upper slope demersal and oceanic pelagic fisheries in the region. On the shelf, where the dominant squid was *Loligo sanpaulensis*, *Illex argentinus* was only occasionally found in the diet of a few neritic predators. In southern Brazil, overall predation was more intense on subadults and adults of the winter-spring spawning group on the upper slope and oceanic adjacent waters, differently from its southern range along Uruguay and Argentina waters where the short-finned squid is abundant on the shelf and is preyed upon mainly by the demersal fish assemblage.

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INTRODUCTION

Illex argentinus inhabits the Southwestern Atlantic Ocean from Rio de Janeiro (22°S) to the southern tip of South America (54°S) (Roper & al. 1984). Its biology, population dynamics and fishery have received special attention by the international scientific community in recent years, particularly in the southern part of its distribution, on Argentinean and Malvinas/Falkland Island waters, where it supports one of the most important squid fisheries of the world (FAO 1995). In southern Brazil, no commercial fisheries for the short-finned squid *Illex argentinus* have been developed, but occasional large catches have been taken in bottom trawl surveys. Juveniles were found predominantly on the shelf and subadults and adults on the upper slope, where the existence of a major spawning group was observed in winter and spring and a minor spawning group in summer (Haimovici & Perez 1990; Santos & Haimovici 1997a).

In the southern Brazil the shelf width ranges from 90 to 180 km and is characterised by the runoff of the La Plata River and the Patos Lagoon; the upper slope, by the alternating influence of the cold northward Malvinas/ Falkland Current and the warm southward Brazil Current in the western boundary of the Subtropical Convergence Zone (Garcia 1997). On the shelf the mean annual primary production rates are presumed to be moderate to high, around 160 g C m^{-2} y^{-1} (Castello & al. 1997) and over 68 % of the commercial landings for the period 1990-1994 were of demersal bony fishes, mostly of the family Sciaenidae (Haimovici & al. 1997). *Loligo sanpaulensis* was the most frequently caught squid in shelf bottom trawl surveys (Haimovici & Andriguetto 1986), forming part of the diet of diverse neritic predators (Santos & Haimovici 1998). The upper slope and adjacent oceanic waters are under the influence of the oligotrophic Brazil Current, but shelf break upwelling of Subantarctic Water in winter-spring and summer are cited as sources of increased productivity (Castello & al. 1997) and *Illex argentinus* was the most frequent cephalopod in upper slope bottom trawl surveys (Haimovici & Perez 1991).

The importance of a species in the food webs can be assessed from its relative importance in the diet of its potential predators (Clarke 1987). Cephalopods have few structures resistant to the digestive processes and beaks are the most frequently used for their identification as prey (Clarke 1986). In some cases, the beaks can be identified to the species level if a regional reference collection of beaks is available. Furthermore, if the relations between the sizes of the beaks and specimen size are calculated, the size composition of the cephalopod prey species can be reconstructed.

In the last two decades a large number of stomach contents of fishes and cephalopods were obtained from commercial landings, surveys and from stranded or incidentally caught marine birds and mammals from southern Brazil. In this paper, the presence of *Illex argentinus* in those stomach contents and published studies were analysed to investigate its relative importance in the food webs of southern Brazil.

MATERIAL AND METHODS

Predation on *Illex argentinus* was analysed from its presence in the stomach contents of 63 potential pelagic (living in the sea at middle or surface levels) and demersal (living on or near the bottom of sea) predators from the shelf (10-200 m), upper slope (200-500 m) and adjacent oceanic waters (> 500 m) between the latitudes of 26°S and 34°S (Fig. 1).

Examined material included the beaks or remains of cephalopods in the stomach contents of 3 shelf pelagic fishes, 30 species of demersal fishes, and 2 of squid caught with bottom trawls and other gears along the con-

Table 1. List of the fishes, cephalopods, penguins and marine mammals of southern Brazil that had their diet studied for predation on *Illex argentinus*. Region (shelf, upper slope and oceanic), habitat (demersal: dem and pelagic: pel), number of stomachs with food examined and mean annual commercial landings in tonnes (1990-1994 period) in southern Brazil (from Haimovici & al. 1997 and Peres & Haimovici, 1998) are indicated.

Predator species	Common name	Mean annual commercial landings	Region and habitat	Stomachs with food	Source of data
FISHES					
Engraulis anchoita	anchoita	-	shelf-pel	512	2
Scomber japonicus	chub mackerel	969	shelf-pel	30	2
Trachurus lathami	rough scad	1555	shelf-pel	124	2
Conger orbignyanus	Argentine conger	-	shelf-dem	146	1
Cynoscion guatucupa	striped weakfish	8785	shelf-dem	220	1
Cynoscion jamaicensis	Jamaica weakfish	-	shelf-dem	73	1
Macrodon ancylodon	king weakfish	3966	shelf-dem	1402	3
Merluccius hubbsi	Argentine hake	129	shelf-dem	231	1
Micropogonias furnieri	white croaker	14709	shelf-dem	194	1
Mustelus canis	smooth dogfish	-	shelf-dem	54	1
Pagrus pagrus	red porgy	238	shelf-dem	362	1
Paralichthys isosceles	flounder	-	shelf-dem	304	1
Paralichthys orbignyanus	flounder	< 1000	shelf-dem	308	1
Paralichthys patagonicus	Patagonian flounder	< 1000	shelf-dem	290	1
Percophis brasiliensis	Brazilian flathead	-	shelf-dem	66	1
Pomatomus saltatrix	bluefish	3521	shelf-dem	164	1
Porichthys porosissimus	lantern midshipman	-	shelf-dem	114	1
Prionotus nudigula	red searobin	-	shelf-dem	244	1
Prionotus punctatus	bluewing searobin	988	shelf-dem	743	1
Rhinobatus horkeli	Brazilian guitarfish	460	shelf-dem	1000	1;4
Squatina argentina	Argentine angel shark	-	shelf-dem	56	1
Squatina guggenhein	angel shark	< 1000	shelf-dem	109	1
Squatina occulta	angel shark	< 1000	shelf-dem	58	1
Sympterigia acuta	skate	-	shelf-dem	1510	5
Sympterigia bonapartei	skate	-	shelf-dem	809	5
Trichiurus lepturus	cutlassfish	441	shelf-dem	490	1
Umbrina canosai	Argentine croaker	9629	shelf-dem	726	1
Urophycis brasiliensis	squirrel codling	1186	shelf-dem	663	1
Evoxymetopon taeniatus	channel seabbarfish	-	upper slope-dem	14	1
Galeorhinus galeus	school shark	-	upper slope-dem	101	1
Helicolenus lahillei	blackbelly rosefish	-	upper slope-dem	33	1
Polyprion americanus	wreckfish	2036	upper slope-dem	> 100	1
Scyliorhinus besnardi	polkadot catshark	-	upper slope-dem	8	1
Billfishes [(b)]		-	oceanic-pel	151	1
Coryphaena hippurus	common dolphinfish	-	oceanic-pel	71	1

tinental shelf and upper slope, 12 species of oceanic pelagic fishes caught by longliners between the isobaths of 500 and 3000 m, over 100 stranded penguins (*Spheniscus magellanicus*) and 15 species of marine mammals incidentally caught by gill nets or stranded in beaches (Table 1).

Besides the cephalopod remains and beaks examined and identified by the authors, relevant published data on the food habits of some potential predators of the region were also included in the analysis (Clarke & al. 1980; Lessa 1982; Pinedo 1982; Juras & Yamaguti 1985; Queiroz 1986; Pinedo 1987; Rosas 1989; Schwingel 1991; Vaske 1994; Vaske & Rincón 1998).

The frequency of occurrence of *Illex argentinus* in each species of predator was calculated as

$$\%FO = \frac{Ni}{Nt} \times 100$$

where Ni is the number of stomachs containing the short-finned squid and Nt is the total number of stomachs with food. The numbers of squid per stomach were estimated from undigested specimens and 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 composition of the short-finned squid in the diet of preda-

Table 1. (continued)

Predator species	Common name	Mean annual commercial landings	Region and habitat	Stomachs with food	Source of data
Istiophorus albicans	Atlantic sailfish	-	oceanic-pel	35	1
Isurus oxyrinchus	shortfin mako	< 500	oceanic-pel	19	1
Katsuwonus pelamis	skipjack tuna	2402	oceanic-pel	600	1
Naucrates ductor	pilotfish	-	oceanic-pel	39	6
Prionace glauca	blue shark	< 500	oceanic-pel	40	1;7
Sphyrna lewini	hammerhead shark	< 500	oceanic-pel	13	1
Tetrapturus albidus	white marlin	-	oceanic-pel	34	1
Thunnus alalunga	albacore	1075	oceanic-pel	101	1
Thunnus albacares	yellowfin tuna	684	oceanic-pel	343	1
Thunnus obesus	bigeye tuna	500	oceanic-pel	73	1
Xiphias gladius	swordfish	601	oceanic-pel	195	1
CEPHALOPODS					
Loligo sanpaulensis	common long-finned squid	100	shelf-dem	313	1
Illex argentinus	Argentine short-finned squid	-	shelf-dem	151	1
Illex argentinus	Argentine short-finned squid	-	upper slope-dem	212	1
PENGUINS					
Spheniscus magellanicus	Magellanic penguin		shelf	120	1
MARINE MAMMALS					
Otaria flavescens	South American sea lion		shelf	(a)	8
Pontoporia blainvillei	franciscana		shelf	361	1;9
Tursiops truncatus	bottlenose dolphin		shelf	13	1;9
Arctocephalus australis	South American fur seal		upper slope	15	1
Arctocephalus gazzella	Antarctic fur seal		upper slope	3	1
Arctocephalus tropicalis	Subantarctic fur seal		upper slope	12	1
Mirounga leonina	Southern elephant seal		upper slope	1	1
Delphinus sp.	common dolphin		oceanic	3	1
Globicephala melas	long-finned pilot whale		oceanic	4	1
Lagenodelphis hosei	Fraser's dolphin		oceanic	4	1
Kogia breviceps	pigmy sperm whale		oceanic	2	1
Kogia simus	dwarf sperm whale		oceanic	1	10
Orcinus orca	killer whale		oceanic	2	1
Physeter macrocephalus	sperm whale		oceanic	1	11
Pseudorca crassidens	false killer whale		oceanic	3	1

1 examined by the authors; 2 Schwingel, 1991; 3 Juras & Yamaguti, 1985; 4 Lessa, 1982; 5 Queiroz, 1986; 6 Vaske, 1994; 7 Vaske & Rincón, 1998; 8 Rosas, 1989; 9 Pinedo, 1982; 10 Pinedo, 1987; 11 Clarke & al. 1980

(a) numbers not reported
(b) Included both *Istiophorus albicans* and *Tetrapturus albidus* not identified to species level

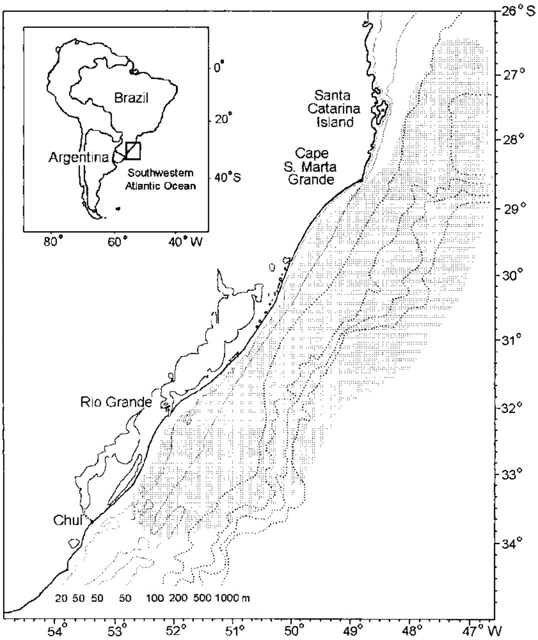

Fig. 1. Map of southern Brazil showing the region from where the stomach contents of 63 species of potential predators of *Illex argentinus* were collected.

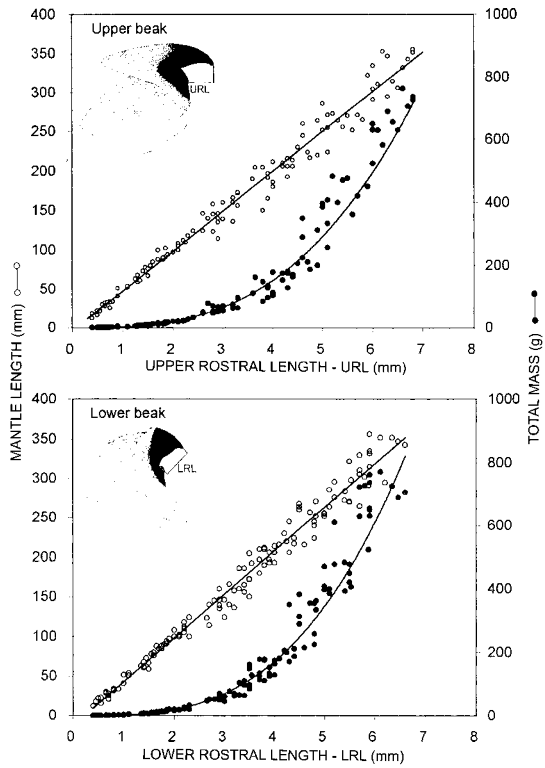

Fig. 2. Mantle length vs. beak rostral length and body weight vs. beak rostral length relationships of *Illex argentinus* off southern Brazil. (The corresponding equations are given in the text).

tors, regression equations that relate mantle length/body weight and beak size were used.

We referred to short-finned squid under 100 mm ML as juveniles, over 100 and under 200 mm as subadults and over 200 mm as adults. The cutting points corresponded approximately to the upper limit of maturity stage 1 (immature) and the lower limit of stage 5 (mature) following Santos & Haimovici (1997a).

The importance of *Illex argentinus* in the food webs of the shelf, upper slope and adjacent oceanic waters was assessed from its frequency in the diet of different potential predators and estimates of their abundance. No estimates of the absolute abundance of the marine fishes were available, but commercial landing statistics of the fisheries along southern Brazil in the 1990-1994 period, obtained from Haimovici & al. (1997) and Peres & Haimovici (1998), provided indices of their abundance in the region. Relative abundance estimates of upper slope demersal fishes were also available from a winter bottom trawl survey in 1986 (Vooren & al. 1988).

RESULTS

ILLEX ARGENTINUS BEAKS CHARACTERISATION AND SIZE RELATIONSHIPS

Whole cephalopods were rarely found in the stomach contents, and the identification and estimation of the mantle lengths of the short-finned squid prey was mostly based on beaks. The beaks of *Illex argentinus* were described by Santos (1992) and Ivanovic & Brunetti (1997). Both beaks of larger individuals have yellowish brown lateral walls, crests and hoods and become darker, nearly black, around the rostrum. The lower beak has broad lateral walls without folds and has a very conspicuous tooth; the transparent strip below the jaw angle, characteristic of ommastrephids, is not clearly apparent in the larger beaks. The upper beak has a broad medially curved hood, with the insertion of the wing in the middle of the anterior edge of the lateral wall and has a moderately acute rostrum. The beaks of *I. argentinus* could be distinguished from those of other ommastrephids occurring in the region (Santos 1992), but identification became increasingly difficult with decreasing sizes of the beaks. The smaller beaks (rostral length < 1.5 mm) are less pigmented, have moderately acute and dark rostrum and the transparent strip below the jaw angle is conspicuous; the lower has broad lateral walls and the upper a pigmented elongated patch on each wing.

To estimate the size of *Illex argentinus* in the stomach contents, linear relationships of the upper rostral length (URL) and lower rostral length (LRL) to dorsal mantle

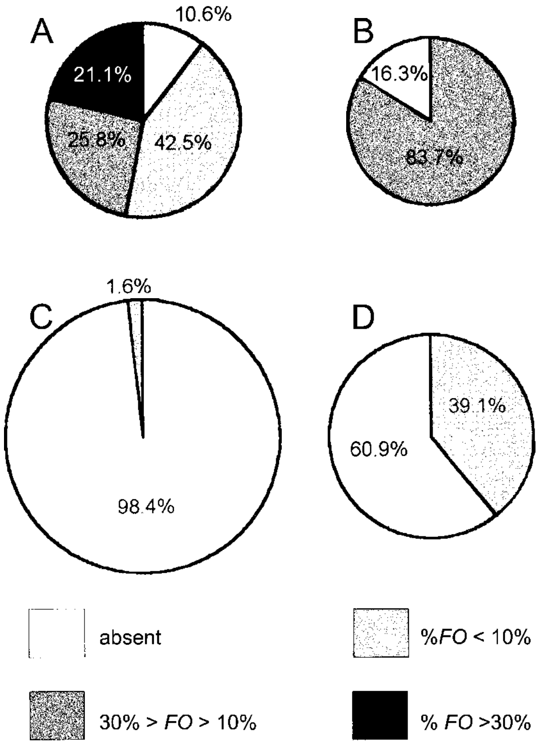

Fig. 3. Percentages of the mean annual landings of the oceanic pelagic (A), upper slope demersal (B), shelf demersal (C), and shelf pelagic (D) fisheries along southern Brazil (1990-1994) of the fish species that fed very frequently (*%FO* > 30 %), frequently (30 % > *%FO* > 10 %) and occasionally (*%FO* < 10 %) on the short-finned squid *Illex argentinus*. Mean annual landings 1990-1994 (Haimovici & al. 1997; Peres & Haimovici 1998): A, 6096 t; B 2431 t; C, 49 251 t; D, 8882 t.

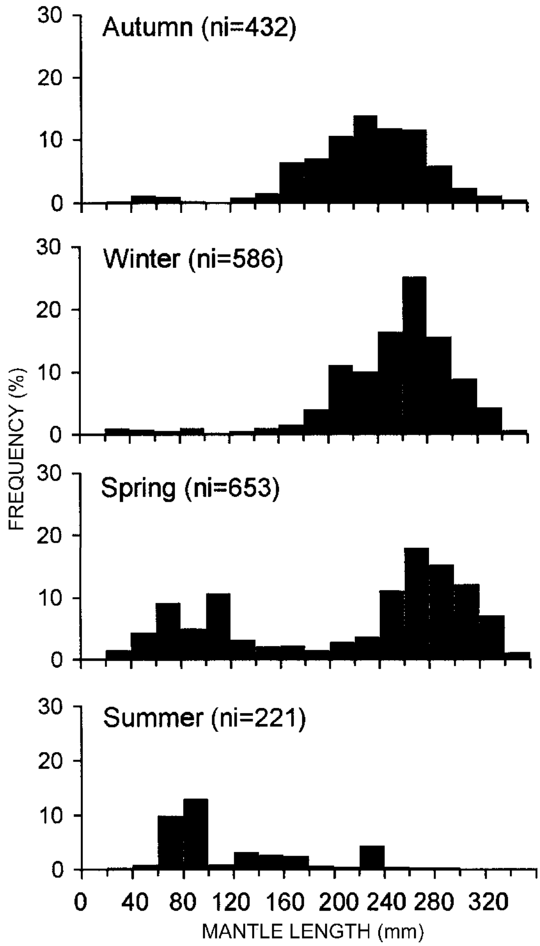

Fig. 4. Mantle length distributions of *Illex argentinus* in the stomach contents of all predators pooled by seasons off southern Brazil (ni = number of specimens of *I. argentinus*).

length (ML) and potential relationships of the URL and LRL to body weight (BW) were calculated from 131 reference specimens of 12 to 356 mm ML and 0.15 to 772.0 g BW (Fig. 2). The corresponding equations were:

$$ML = -3.563 + 50.883URL \quad (r = 0.989)$$
$$ML = -12.228 + 55.187LRL \quad (r = 0.989)$$
$$BW = 2.7204URL^{2.9068} \quad (r = 0.995)$$
$$BW = 2.2750LRL^{3.1210} \quad (r = 0.996)$$

Predation on *Illex argentinus*

Data from over 14 000 stomach contents of 63 species of potential predators were analysed (Table 1) and *Illex argentinus* occurred to some degree in the diet of 32 of those species (Table 2). The short-finned squid occurred in 23.5 % of the investigated species of predators from the shelf and 80.0 % of those from the upper slope and oceanic adjacent waters. The frequencies of occurrence in the stomach contents were respectively 0.2 %, 7.7 % and 10.1 %.

The relative abundance of *Illex argentinus* predators in the landings or surveys and the frequency of occurrence of the short-finned squid in their stomach contents follows:

Oceanic pelagic fisheries yielded annually 6096 t (1990-1994) from which species that fed on *Illex argentinus* amounted to 89.4 % of the landings (Fig. 3A). The swordfish *Xiphias gladius* and the tuna *Thunnus obesus* represented 21.1 % of the landings and fed very frequently (*%FO* > 30 %) on the short-finned squid. *Thunnus alalunga* and *T. albacares* (25.8 % of the landings) fed frequently (30 % > *%FO* > 10 %) on *I. argentinus*. The dolphinfish *Coryphaena hippurus*, skipjack tuna *Katsuwonus pelamis*, billfishes *Tetrapturus albidus* and *Istiophorus albicans*, and pelagic sharks *Isurus oxyrinchus*, *Prionace glauca* and *Sphyrna lewini*

(42.5 % of the landings) fed occasionally (*%FO* < 10 %) on *I. argentinus*.

On the upper slope demersal environment, the short-finned squid appeared very frequently (*%FO* > 30 %) in the diet of *Scyliorhinus besnardi*, although a low number of stomachs were examined. *Illex argentinus* was frequent in the diet of the school shark *Galeorhinus galeus*, the rosefish *Helicolenus lahillei* and the wreckfish *Polyprion americanus* (30 % > *%FO* > 10 %) and occurred occasionally in the stomach contents of the seabbarfish *Evoxymetopon taeniatus* (*%FO* < 10 %). Two of these predators, *Galeorhinus galeus* and *Polyprion americanus*, amounted to more than half of the total fish catch in a bottom trawl survey in the upper slope of southern Brazil in winter of 1986 (Vooren & al. 1988). *Galeorhinus galeus* was intensely fished, mainly with gill nets and longliners on the shelf and upper slope until 1990 (Haimovici & al. 1997). *Polyprion*

Table 2. List of the fishes, cephalopods, penguins and marine mammals of southern Brazil that preyed on *Illex argentinus*. Percent of stomachs with *Illex argentinus* (*%FO*), numbers of squid per stomach, their mantle length (*ML*) and body weight (*BW*) mean and range are indicated.

Predator species	*%FO*	Numbers per stomach	*Illex argentinus* Mean and range *ML*(mm)	*Illex argentinus* Mean and range *BW* (g)
FISHES				
Merluccius hubbsi[(a)]	-	-	-	-
Pagrus pagrus[(a)]	-	-	-	-
Pomatomus saltatrix	1.8	-	-	-
Squatina argentina[(a)]	5.4	-	-	-
Squatina occulta	1.7	1	265.0	351.0
Trichiurus lepturus	3.1	1 - 4	65.5 (20 - 200)	20.1 (0.2 - 156)
Evoxymetopon taeniatus	7.1	3	36.7 (30 - 40)	1.4 (0.8 - 2)
Galeorhinus galeus [(a)]	18.8	-	- -	
Helicolenus lahillei	18.2	1	127.7 (60 - 280)	88.6 (5 - 415)
Polyprion americanus [(c)]	26.7	1 - 4	230.6 (80 - 332)	274.0 (12 - 693)
Scyliorhinus besnardi	62.5	1 - 2	194.9 (108 - 293)	182.7 (277 - 476)
Billfishes [(b)]	4.0	1 - 12	163.1 (93 - 293)	121.3 (18 - 476)
Coryphaena hippurus	7.0	1-2	222.7 (125 - 281)	241.8 (41 - 413)
Istiophorus albicans	8.6	4 - 80	97.9 (57 - 192)	25.9 (25 - 140)
Isurus oxyrinchus	5.3	1	319.2	614.1
Katsuwonus pelamis	1.0	1 - 6	81.5 (54 - 131)	10.6 (4 - 45)
Naucrates ductor[(a)]	-	-	-	-
Prionace glauca[(a)]	5.0	-	-	-
Sphyrna lewini	7.7	2	278.7 (261 - 297)	408.8 (335 - 483)
Tetrapturus albidus	5.9	1 - 40	113.0 (62 - 166)	119.5 (72 - 163)
Thunnus alalunga	11.9	1 - 5	239.4 (130 - 312)	285.2 (46 - 559)
Thunnus albacares	12.5	1 - 47	173.7 (40 - 345)	176.4 (2 - 778)
Thunnus obesus	49.3	1 - 55	261.7 (144 - 378)	360.6 (59 - 802)
Xiphias gladius	31.3	1 - 61	256.5 (92 - 345)	347.5 (17 - 778)
CEPHALOPODS				
Loligo sanpaulensis	0.3	1	13.7	0.3
Illex argentinus (shelf)	6.0	1 - 2	37.0 (19 - 49)	3.0 (0.2 - 9)
Illex argentinus (upper slope)	9.0	1	70.9 (44 - 130)	12.0 (2 - 47)
PENGUINS				
Spheniscus magellanicus	3.0	1 - 3	160.7 41 - 248)	133.8 (2 - 288)
MARINE MAMMALS				
Arctocephalus tropicalis	9.1	5	325.9 (18 - 333)	632.6 (586 - 673)
Mirounga leonina	100.0	3	279.4 (260 - 313)	419.7 (331 - 577)
Delphinus sp.	100.0	4 - 9	59.0 (21 - 326)	24.7 (0.4 - 652)
Globicephala melas	75.0	1 - 4	220.6 (150 - 332)	246.0 (67 - 693)
Kogia breviceps	100.0	1 - 31	280.4 (151 - 339)	459.3 (105 - 734)
Physeter macrocephalus	100.0	75	(237 - 378)	(251 - 935)

(a) *%FO* and/or squid numbers and size not reported. (b) Included both *Istiophorus albicans* and *Tetrapturus albidus* not identified to species level. (c) From 15 samples of over hundred stomachs pooled

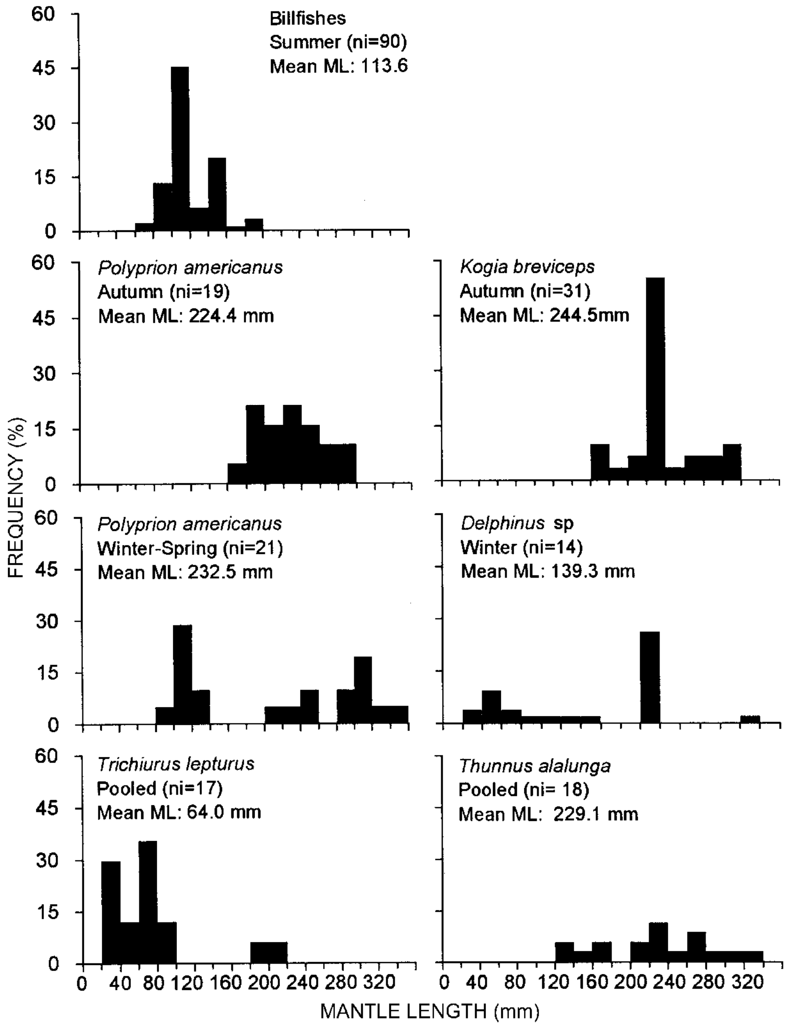

Fig. 5. Mantle length distributions of *Illex argentinus* in the stomach contents of billfishes, (*Istiophorus albicans* and *Tetrapturus albidus*), *Polyprion americanus*, *Trichiurus lepturus*, *Kogia breviceps*, *Delphinus* sp. and *Thunnus alalunga* off southern Brazil (ni = number of specimens of *I. argentinus*).

americanus, fished with longliners, represented 83.7 % of the 2431 t demersal fish landings from upper slope in the early 1990s (Fig. 3B)(Peres & Haimovici 1998).Other potential predators of the short-finned squid from the upper slope were the tilefish *Lopholatilus villari*, the hake *Urophycis cirratus* and the small sized sharks of the genus *Squalus* but for which no data were available.

On the shelf the short-finned squid was occasionally preyed (*%FO* < 10 %) by the bony fishes *Merluccius hubbsi*, *Pagrus pagrus*, *Pomatomus saltatrix*, *Trichiurus lepturus*, and the angel sharks *Squatina argentina* and *S. occulta* (Table 2). The neritic species that fed on *Illex argentinus* represented only 1.6 % of the 49 251 t of demersal fish landings and 39.1 % of the 8882 t of pelagic fish landings from 1990-1994 period in southern Brazil (Fig. 3C, 3D).

Beaks of *Illex argentinus* occurred in the stomachs of diverse incidentally caught or stranded marine mammals and birds: *Arctocephalus tropicalis*, *Mirounga leonina*, *Delphinus* sp., *Globicephala melas*, *Kogia breviceps*, *Physeter macrocephalus* and the penguin *Spheniscus magellanicus* (Table 2). All these species fed frequently on cephalopods and despite the small number of stomach contents analysed, most of the specimens fed on *I. argentinus*.

Illex argentinus was insignificant in the diet of *Loligo*

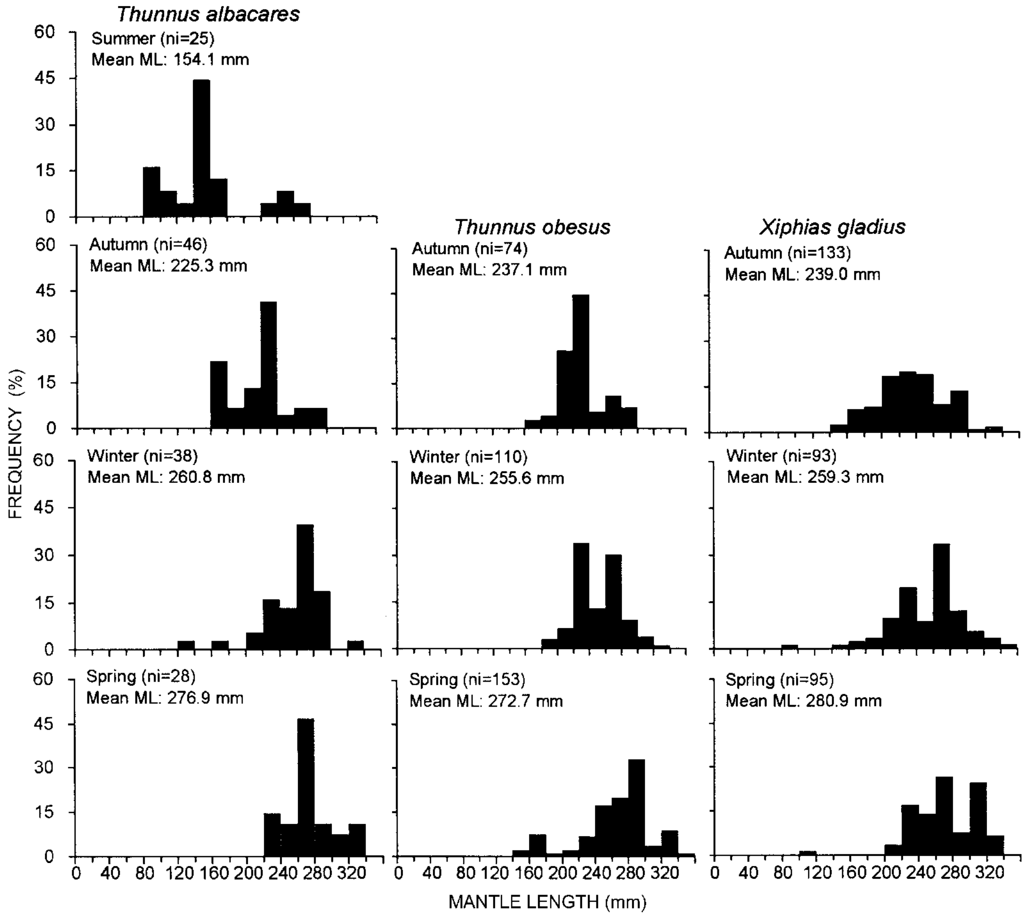

Fig. 6. Mantle length distributions of *Illex argentinus* in the stomach contents of *Thunnus albacares*, *T. obesus* and *Xiphias gladius* off southern Brazil (ni = number of specimens of *I. argentinus*).

sanpaulensis (*%FO* = 0.3 %). Cannibalism was recorded in 6.0 % of the stomachs from shelf and 9.0 % in those from the upper slope (Table 2). It is believed that these percentages underestimated cannibalism as a large proportion of stomach contents of *I. argentinus* had only scant remains of squid that could not be further identified (Santos & Haimovici 1997b).

Size ranges of preyed *Illex argentinus*

Small and large *Illex argentinus* were preyed upon year round (Fig. 4). The mantle length distributions of *I. argentinus* in the stomach contents of those predators with sufficient seasonal or year round pooled data are shown in Figs 5 and 6. In summer, smaller *I. argentinus* (20-180 mm ML) were found in the diet of billfishes, *Thunnus albacares* and the cutlassfish *Trichiurus lepturus*. In the same season, larger squid (220-280 mm ML) were found in stomach contents of *T. albacares*. In winter and spring the oceanic dolphin *Delphinus* sp. and the wreckfish *Polyprion americanus* fed on both, small and large short-finned squid (20-300 mm ML), and *Xiphias gladius* and all three *Thunnus* species fed only on large specimens (mostly 200-340 mm ML).

Mantle length composition of the *Illex argentinus* preyed upon by shelf, upper slope and oceanic predators in the warm (summer and early autumn) and in the cold (winter and early spring) seasons are shown in Fig. 7. In both seasons, short-finned squid eaten by shelf predators were mainly juveniles and subadults (15-240 mm ML) and those eaten by upper slope predators were juveniles to adults (15-340 mm ML). Oceanic predators fed on juvenile, subadult and adult squid in the warm season (20-320 mm ML) and mostly on large individuals in cold season (200-320 mm ML).

DISCUSSION

A general picture extracted from our results is that large oceanic pelagic fishes, and to a lesser degree demersal upper slope fishes are the most important source of mortality of short-finned squid in southern Brazil.

Tunas and the swordfish are known to migrate from the north to southern Brazil where they are fished mainly from May to October (Antero da Silva 1994). This southward migration coincides with the enhanced winter-spring biological production in this last region (Castello & al. 1997). It also coincides with the northward winter and spring reproductive migration of subadult and adult *Illex argentinus* from Uruguayan and Argentinean waters (Haimovici & Perez 1990; Santos & Haimovici 1997a). The strong association of tunas and xiphoid fishes with *I. argentinus* in this region was also evidenced by the presence of the larvae of didymozoid parasites in the digestive tract of the juvenile and subadult short-finned squid (Santos 1992) as these parasites have tunas and xiphoid fishes as final hosts (Hochberg 1990).

Not all the large oceanic pelagic predators fed to the same extent on *Illex argentinus* as it was more frequent in the diet of *Xiphias gladius* and *Thunnus obesus*. Tunas and billfishes are visual feeders that prey mostly at daytime (Longhurst & Pauly 1987). *Illex* genus squid are known to perform diel migrations moving to deeper water layers during daytime (Roper & Young 1975; Nigmatullin 1989). The higher occurrence of short-finned squid in the stomach contents of *Thunnus obesus* and *Xiphias gladius* may be related to their affinity for greater depths (up to 600 m) compared with other tunas that are known to be near-surface species (Carey & Robison 1981; Colette & Nauen 1983; Holland & al. 1990). In fact *Thunnus albacares* and *T. alalunga* had as the most frequent cephalopod in their diet *Ornithoteuthis antillarum* (Santos 1992) a smaller and more epipelagic squid.

The role of *Illex argentinus* in upper slope demersal food web is difficult to assess quantitatively because of regurgitation of demersal fishes when hauled to surface, but it appears to be fairly important as the short-finned squid was eaten by *Polyprion americanus* and *Galeorhinus galeus*, two of the most abundant large predators of this environment.

In the shelf food web the short-finned squid appears to be unimportant, as mostly small *Illex argentinus* were found with low frequency in the stomach contents of only a few neritic fishes that, in turn, represents a small fraction of the commercial landings. These observations are in agreement with the low relative abundance of *I. argentinus* found in bottom trawl surveys on the shelf (Haimovici & Andriguetto 1986).

Contrasting with southern Brazil, where *Illex argentinus* occurred mostly along the upper slope, off

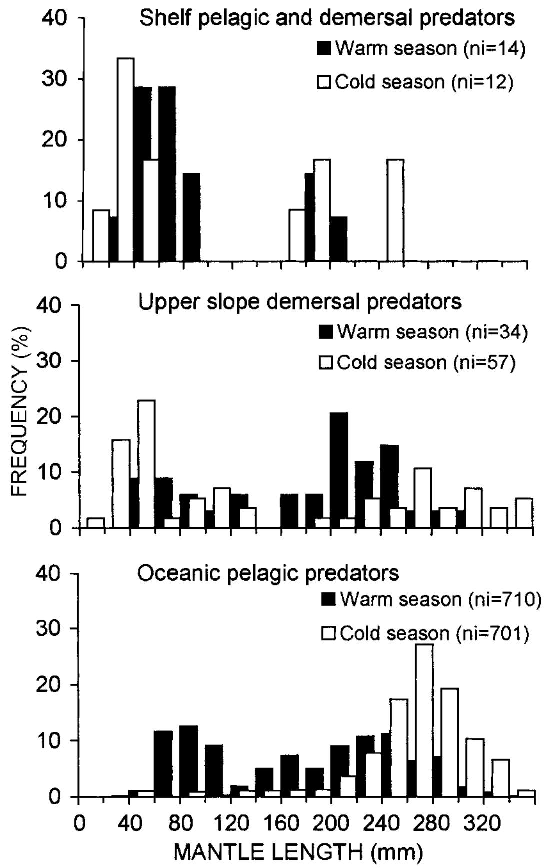

Fig. 7. Mantle length distributions of *Illex argentinus* in the stomach contents of shelf demersal and pelagic, upper slope demersal and oceanic pelagic predators in cold (winter and early spring) and warm (summer and early autumn) seasons off southern Brazil (ni = number of specimens of *I. argentinus*).

Uruguay and northern Argentina juvenile and subadult *I. argentinus* occur mostly on the shelf (Hatanaka & al. 1985; Nigmatullin 1989; Brunetti & al. 1991) and is an important prey for the common hake *Merluccius hubbsi* that is the most abundant demersal fish in the region with biomass estimates of around two million tonnes (Angelescu & Prenski 1987). Juvenile and subadult short-finned squid are also important components of the food webs on the southern Argentinean shelf, and the species estimated biomass was over two million tonnes (Prenski & al. 1991; Prenski & Angelescu 1993).

Two spawning groups are postulated to occur in southern Brazil, a minor summer spawning small-sized group that mature between 140 to 250 mm ML and a major group that matures between 188 to 356 mm ML (Haimovici & Perez 1990; Santos & Haimovici 1997a). The size distribution of the *Illex argentinus* found in the stomach contents fits into that pattern (Fig. 4). The

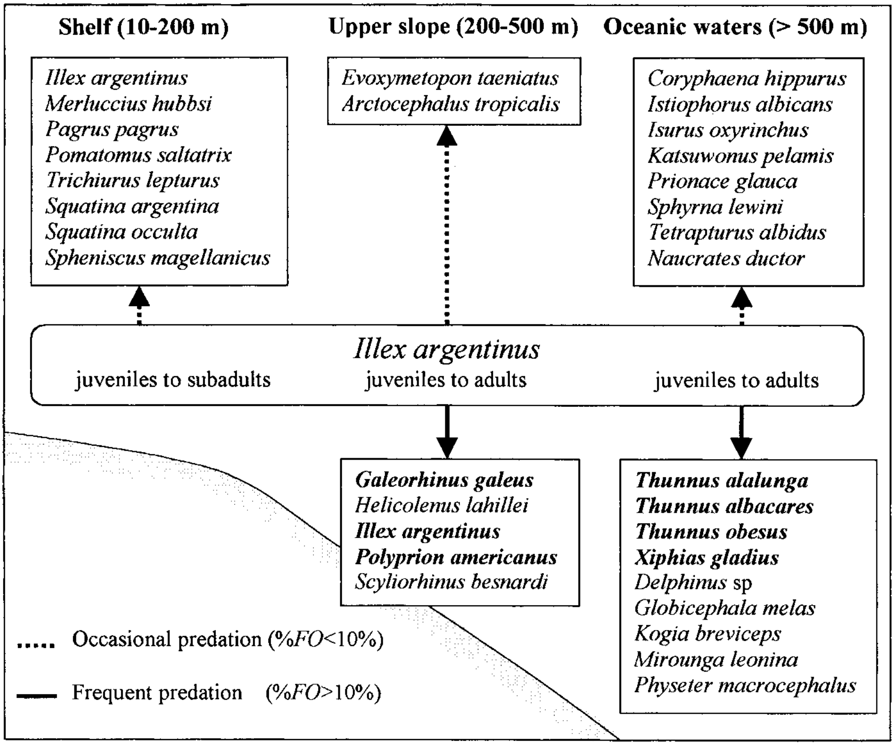

Fig. 8. Diagrammatic summary of predation on *Illex argentinus* off southern Brazil. In bold abundant species that preyed frequently (*%FO* > 10 %) on the short-finned squid.

smaller specimens preyed in winter and spring and the larger specimens preyed in summer correspond to summer spawning group and the small short-finned squid preyed in summer and autumn and the larger ones preyed from autumn to spring correspond to the winter-spring spawning group.

Fig. 8 summarises the main trophic relations of *Illex argentinus* in southern Brazil. We were not able to find any species that preyed heavily on juvenile *I. argentinus*, particularly in shelf waters. This reflects the low abundance of juvenile *I. argentinus* in the region and supports the hypothesis that the major nursery grounds of the southern Brazil spawners occur further south in Uruguayan and Argentinean waters. Predation was more intense by demersal and pelagic predators of the upper slope and adjacent oceanic waters, mainly in the cold season.

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