ELSEVIER

Fisheries Research 33 (1997) 139–147

FISHERIES RESEARCH

Food and feeding of the short-finned squid *Illex argentinus* (Cephalopoda: Ommastrephidae) off southern Brazil

Roberta Aguiar Santos [*,1], Manuel Haimovici [2]

Fundação Universidade do Rio Grande, Depto. de Oceanografia, Cx.P. 474, Rio Grande 96201-900, RS, Brazil

Accepted 28 July 1997

Abstract

Diet and feeding habits of the short-finned squid *Illex argentinus* were studied from the analysis of 729 stomachs of juveniles, subadults and adults caught with trawls on the continental shelf and slope off southern Brazil (26°35′S–34°31′S) from 1981 to 1992. Food, in different degrees of digestion, was found in 363 stomachs (49.8%). Feeding activity occurred at day and night and seemed to be most intense at dusk and early night. The proportion of stomachs with food increased with size and sexual maturity. Fish occurred in 43.8%, cephalopods in 27.5% and crustaceans in 18.7% of the stomachs with food. Identified prey included the fish *Diaphus dumerilii*, *Maurolicus muelleri* and *Merluccius hubbsi*, the cephalopods *I. argentinus*, *Loligo sanpaulensis*, *Spirula spirula*, *Semirossia tenera* and *Eledone gaucha* and the crustaceans *Oncaea media* and *Euphausia* sp. The occurrence of fish increased with squid size, but both cephalopods and crustaceans were equally important for all sizes. Cannibalism was observed at all sizes. The overall low proportion of stomachs with food, the high rate of cannibalism and the low frequency of occurrence of crustaceans for the juveniles and subadults in all seasons, but particularly in the summer and autumn, may reflect a limited availability of food in the region. If this is true, the main nursery grounds for the spawners off southern Brazil are likely to be off the Rio de La Plata Front or in the offshore confluence between the Brazil and Malvinas Currents, where primary and secondary production is higher than off southern Brazil. © 1997 Elsevier Science B.V.

Keywords: Cephalopoda; Squids; *Illex argentinus*; Feeding; Brazil; Southwestern Atlantic

1. Introduction

The short-finned squid *Illex argentinus* is distributed in the southwestern Atlantic Ocean (Roper et al., 1984) (Fig. 1) and has supported the most important squid fishery in the world in recent years (FAO, 1995). Most of the information available on this species refers to the southern range of its distribution, where this squid is exploited (reviewed by Haimovici et al., in press). In southern Brazil, no commercial fishery for the short-finned squid has developed, but this species is frequently found in the stomach contents of both demersal and pelagic fishes of the upper slope and adjacent oceanic waters (Zavala-Camin, 1981; Santos, 1992) and large catches have been taken occasionally in bottom trawl surveys (Yesaki et al., 1976; Haimovici and Perez, 1990).

* Corresponding author. Pós-graduação em Ocenografia biológica; e-mail: posras@super.furg.br

[1] Tel.: +55 532 30 1900 (r. 242); fax: +55 532 30 2126.

[2] Tel.: +55 532 30 2000 (r. 142); fax: +55 532 30 2126.

PII S0165-7836(97)00071-4

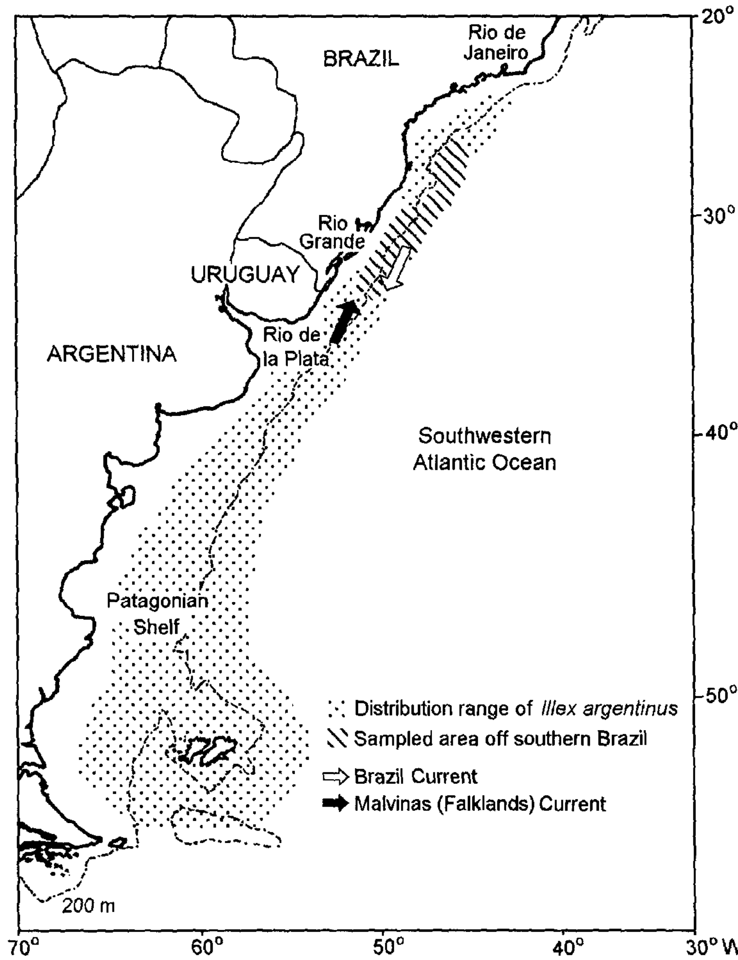

Fig. 1. Map showing the distribution range of *I. argentinus* and the area where the short-finned squids were sampled off southern Brazil.

Despite the lack of a commercial fishery targeting *I. argentinus* in southern Brazil, samples of juveniles and adults from incidental catches were obtained from bottom and midwater trawl surveys and plankton surveys, between 1980 and 1992. These samples allowed the study of the distribution and feeding of paralarvae (Haimovici et al., 1995; Vidal and Haimovici, in press), distribution of juveniles to adults (Haimovici and Perez, 1990), reproduction (Santos and Haimovici, 1997), predation and helminth parasites of the digestive tract (Santos and Haimovici, unpublished data). The comparison of several aspects of the life cycle and population dynamics of *I. argentinus* from different regions suggested that offspring produced off southern Brazil contribute to recruitment to the south off Uruguay and Argentina. *I. argentinus* is known to spawn in winter and spring along the western boundary of the Brazil–Malvinas (Falklands) Currents confluence (Haimovici et al., in press). Despite the presence of spawners and the large number of rhynchoteuthion paralarvae caught in plankton surveys in winter and spring off southern Brazil, juveniles were not correspondingly abundant in the following months. We hypothesise that the availability of food in the warm waters of the Brazil Current in southern Brazil is insufficient to sustain large numbers of fast growing organisms, such as ommastrephid squids, and may force young squids to migrate to colder waters of higher productivity. A similar pattern is found in the northwestern Atlantic with *I. illecebrosus*, for which highest abundance occurs at highest latitudes associated with highly productive cold water Currents (Hatanaka et al., 1985; O'Dor and Balch, 1985; Dawe and Brodziak, in press). To test this hypothesis, the diet and feeding of juveniles to adults short-finned squids in different seasons from southern Brazil were studied and compared with those from Argentina investigated by Koronkiewicz (1986) and Ivanovic and Brunetti (1994). Thus, this paper is aimed at improving our understanding of the trophic relations of *I. argentinus* in southern Brazil and explains some aspects of its distribution pattern.

2. Materials and methods

Squids were caught on the shelf and upper slope off southern Brazil between the latitudes of 26°35′S and 34°31′S (Fig. 1) in bottom and pelagic trawl surveys by the R/V 'Atlântico Sul' and from occasional catches by commercial trawlers off Rio Grande do Sul, from 1981 to 1992. The samples were either frozen or fixed in saline solution of formalin (10%) neutralised with borax and then preserved in ethanol (70%).

Analysis of squid specimens included determination of dorsal mantle length (ML, mm) and total weight (TW, g). Sex and maturity stage were assigned following the 8 stage scale of Brunetti (1990). Stages were subsequently grouped into immature, maturing, fully mature and spent.

Stomachs were examined for food content and the degree of digestion was recorded based on a four stage scale varying from undigested (1) to milky, fully digested food (4). Bony fishes were recognised from scales, vertebrae, spines, other bony fragments and otoliths and identified to the lower possible taxon. Total lengths (TL) of fishes identified to species were estimated from otolith length–total length relationships from a regional reference collection of otoliths available at our laboratory. Recognisable remains of cephalopods in stomachs included beaks, gladii, lenses, suckers, hooks, remains of mantle, arms and tentacles. Identification to species was usually based on beaks, and when possible, mantle lengths (ML) of cephalopod prey were estimated from beak rostral length–mantle length relationships from a regional reference collection of beaks available also at our laboratory. Crustaceans were recognised from remains of exoskeletons, appendages and eyes.

Diel changes in feeding intensity were analysed by comparing the rates between the numbers of stomachs with relatively undigested versus digested food and the occurrence of empty stomachs versus stomachs containing food. The samples were grouped into 4 h intervals between 0600 h and 0200 h.

Stomach content analysis was based in the relative frequency of occurrence (FO = Ni/Nt), where Ni is the number of stomachs with one type of prey and Nt is the total number of stomachs with any kind of content and compared between size groups or seasons using χ^2 test. Comparisons of occurrence of prey items in stomachs or of stomachs with and without food have inherent limitations (Hyshop, 1980), particularly for cephalopods which mince their prey and frequently discard hard parts useful for identification. This approach may lead to an underestimate of fish because the volume of ingested food is not considered and because small pieces of hard parts of squid and crustaceans are more likely to be recognised for longer time after ingestion than muscular tissue of fish. Unfortunately there are no simple alternative approaches and this method is the usual choice for squid feeding studies in nature (Breiby and Jobling, 1985; Ivanovic and Brunetti, 1994; Collins et al., 1994; Rocha et al., 1994).

3. Results

3.1. Feeding intensity and diet

From a total of 729 squids of 37 to 356 mm ML examined, 363 (49.8%) had food in their stomachs. The percentage of stomachs with food was significantly higher for females (58.2%) than for males (49.4%) ($\chi^2_{\nu=1} = 5.41$; $P = 0.020$).The prey categories found were fishes, which occurred in 43.8% of stomachs, cephalopods in 27.5%, crustaceans in 18.7% and unidentified digested food in 27.8% of the stomachs with food (Table 1). A single type of prey (fish, cephalopod or crustacean) was present in 78.6% of the stomachs with identifiable contents, 17.9% contained two and in 3.4% there were the

Table 1
Number of occurrence (N), percentage of occurrence (FO%) and length range of prey items in 363 stomach with food of *I. argentinus* (ML 34 to 356 mm)

Prey item	N	FO%	Prey length range (mm)
Osteichthyes	159	43.80	
Diaphus dumerilii	6	1.65	47–81
Maurolicus muelleri	7	1.93	34–58
Merluccius hubbsi	7	1.93	39–108
Unidentified osteichthyes	142	39.12	
Crustacea	68	18.73	
Unidentified calanoid Copepoda	3	0.83	
Oncaea media	1	0.28	
Mysidacea	1	0.28	
Euphausia sp.	9	2.48	
Unidentified Decapoda	8	2.20	
Unidentified Crustacea	46	12.67	
Cephalopoda	100	27.55	
Unidentified Teuthoidae	58	15.98	
Enoploteuthidea	3	0.83	
I. argentinus	28	7.71	17–131
Loligo sanpaulensis	6	1.65	36–46
Semirossia tenera	1	0.28	20
Spirula spirula	1	0.28	
Eledone gaucha	1	0.28	43–48
Eledone sp.	2	0.55	
Digested food	101	27.82	

three recognisable types. No significant differences in mixture of diet was found between the sexes ($\chi^2_{\nu=2}=1.83$; $P=0.401$) thus, data of both sexes were pooled for further analysis.

Otoliths were rare, probably because when squid fed on fishes, except small ones, they discarded the head (Breiby and Jobling, 1985). Otolith from only three fish prey species were found and identified as: *Merluccius hubbsi*, *Maurilicus muelleri* and *Diaphus dumerilii* (Table 1).

Unidentified Teuthoidea was the most frequently occurring category of cephalopod. Cannibalism was difficult to quantify because many cephalopods could not be identified to species, but among those identified, 67% were *I. argentinus* with ML ranging from 17 to 131 mm (Table 1).

Crustaceans in most cases, could not be further identified. Calanoid copepods, one species of cyclopoid, *Oncaea media* and the euphausiid *Euphausia* sp. were recognised. Uropods of mysids and remains of decapods were found in several stomachs (Table 1).

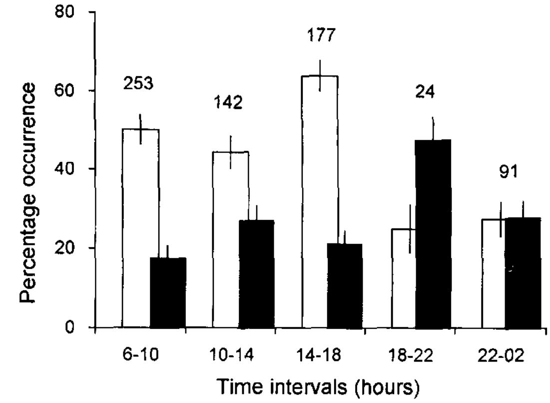

Fig. 2. Diel variation in the feeding of *I. argentinus*. White: empty stomachs; Black: stomachs with relatively undigested food. Lines indicate 95% confidence intervals and the numbers above the bars the number of specimens in each time interval.

The highest rate of relatively undigested food was observed at dusk and early night (1800–2200 h) but the differences among time intervals were not significant ($\chi^2_{\nu=4}=6.79$; $P=0.147$) (Fig. 2). The highest proportion of empty stomachs occurred from the early morning to the afternoon (0600–1800 h) and

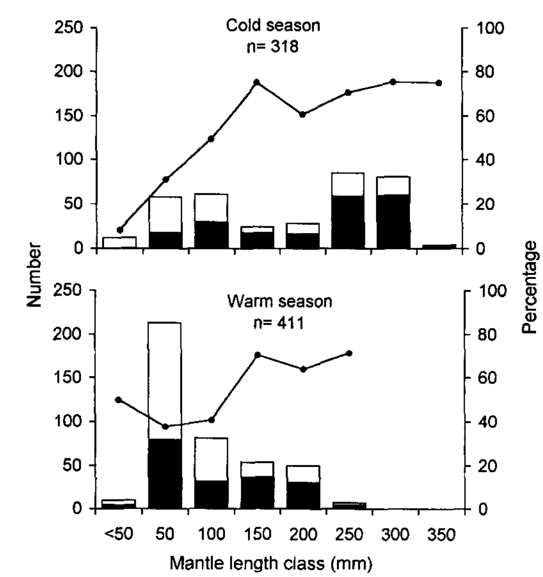

Fig. 3. Mantle length distribution of all *I. argentinus* sampled in the cold season (above) and in the warm season (below). White: total number; Black: number with stomachs containing food. Lines indicate the percentage of stomachs with food.

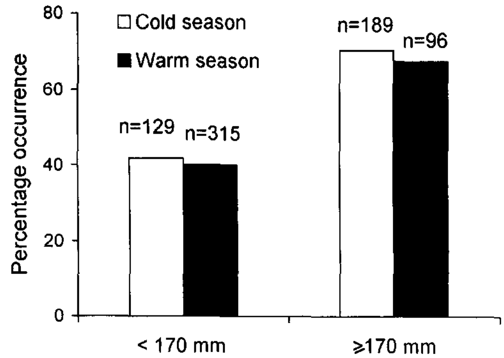

Fig. 4. Percentage occurrence of stomachs with food for *I. argentinus* assigned to size groups smaller vs. larger than 170 mm ML, in the cold and in the warm seasons.

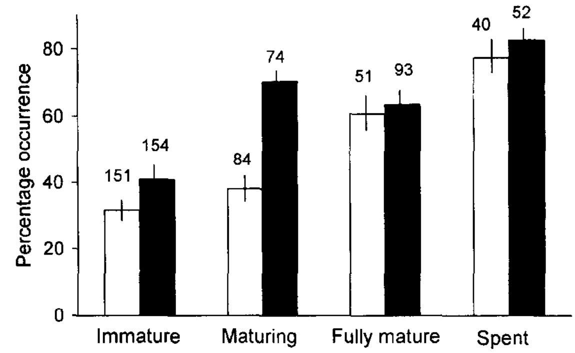

Fig. 6. Percentage of males (white) and females (black) *I. argentinus* at different maturity stages, with food in their stomachs. Lines indicate 95% confidence intervals, the numbers above the bars indicate the number of squids analysed.

the lowest at dusk and night (1800–0200 h) with significant differences among time interval ($\chi^2_{\upsilon=1}$ = 28.23; $P < 0.001$). It was concluded that feeding occurs at all times but most frequently at dusk and early night.

3.2. Effect of predator size, maturity and season

The mantle length composition and the numbers of squids with food in their stomachs in the cold season (late autumn to early spring) and warm season (late spring to early autumn) are shown in Fig. 3. Note that smallest squid (< 150 mm ML) were most prevalent in the sample from the warm season whereas largest squid ($\geq$ 250 mm ML) were most prevalent in the sample from the cold season when large spawners are present in the region. Frequency of occurrence of stomachs with food was compared between squids smaller vs. larger than 170 mm ML, in the cold and warm seasons (Fig. 4). Squids smaller than 170 mm ML had food in 30.4% of stomachs with no significant differences between seasons in their percentages ($\chi^2_{\upsilon=1} = 1.908$; $P = 0.167$). Squid larger than 170 mm ML had food in 69.6% of stomachs and also did not show differences between seasons ($\chi^2_{\upsilon=1} = 1.936$; $P = 0.164$). The percentage of stomachs with food in the larger size group was significantly higher in both the cold and warm seasons ($\chi^2_{\upsilon=1} = 28.58$; $P < 0.001$ and $\chi^2_{\upsilon=1} = 22.57$; $P < 0.001$, respectively).

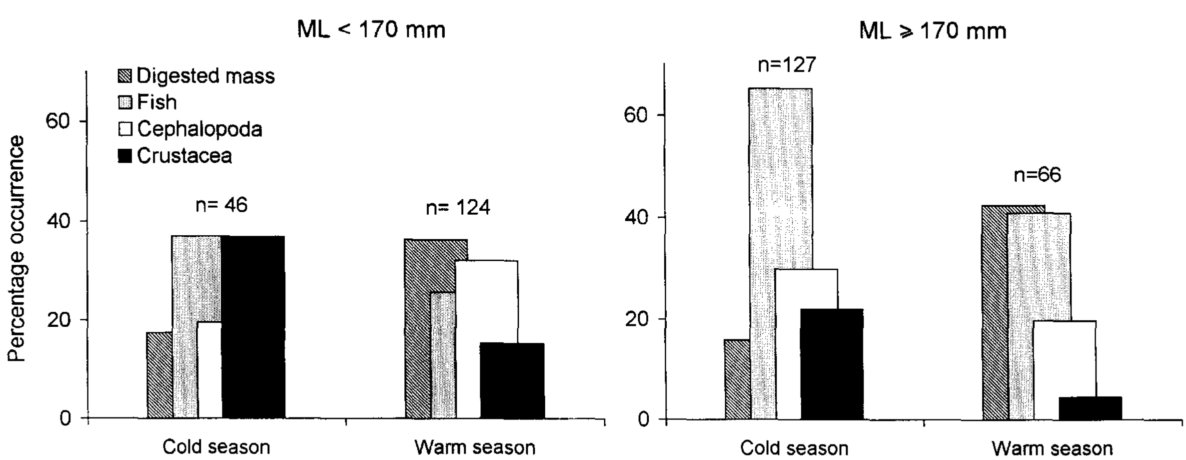

Fig. 5. Percentage occurrence of prey items in the stomach contents of *I. argentinus* smaller and larger than 170 mm ML in the cold and in the warm seasons off southern Brazil (26°S–34°S). (n = number of stomachs with food examined).

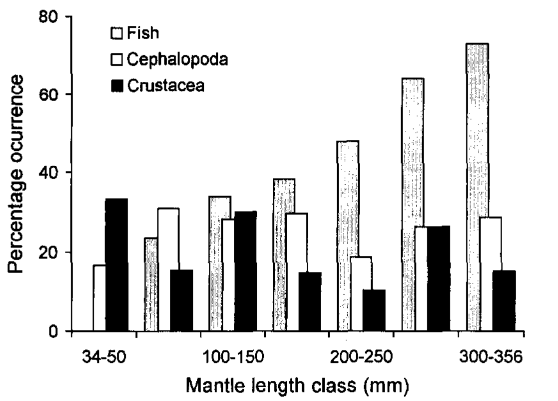

Fig. 7. The relative frequency of occurrence of fish, cephalopods and crustaceans in different mantle length classes of *I. argentinus* ($n = 363$) off southern Brazil (26°S–34°S).

Frequencies of occurrence of fish, cephalopods and crustaceans in the stomach contents for *I. argentinus* smaller and larger than 170 mm ML were calculated for different seasons (Fig. 5). Among squids smaller than 170 mm ML, crustaceans were more frequent in the cold season ($\chi^2_{v=1} = 9.42$; $P < 0.05$) while the percentages of cephalopods and fish did not differ significantly between seasons ($\chi^2_{v=1} = 2.63$; $P = 0.104$ and $\chi^2_{v=1} = 2.03$; $P = 0.154$, respectively). Among squids larger than 170 mm ML, crustaceans and fish were more frequent in the cold season ($\chi^2_{v=1} = 9.9$ and $\chi^2_{v=1} = 10.6$; $P < 0.01$, respectively) while cephalopods did not differ between seasons ($\chi^2_{v=1} = 2.33$; $P = 0.126$). However, the results are not conclusive due to the great differences observed in occurrence of the unidentified digested food between seasons in the two squid size groups.

Both sexes appeared to feed during and after spawning, as the proportion of stomachs with contents increased consistently with maturity stage (Fig. 6).

The proportions of fish, cephalopods and crustaceans in the diet by predator size are shown in Fig. 7. The occurrence of fish increased regularly with size ($\chi^2_{v=6} = 52.8$; $P < 0.001$). No significant differences among size classes were found for either cephalopods ($\chi^2_{v=6} = 2.99$; $P = 0.810$) or crustaceans ($\chi^2_{v=6} = 11.2$; $P = 0.082$).

The relationships between the ML of cephalopods and TL of fish prey and the ML of *I. argentinus* are shown in Fig. 8. As the points represent only the prey that could be sized measuring beaks or otoliths, this figure does not represent an unbiased picture of the relationship between prey and predator sizes. Juvenile and subadult *I. argentinus* (< 206 mm ML) appear to be cannibalistic on specimens from 19% to 70% of its ML and despite larger *I. argentinus* also are cannibalistic, no information on the sizes was

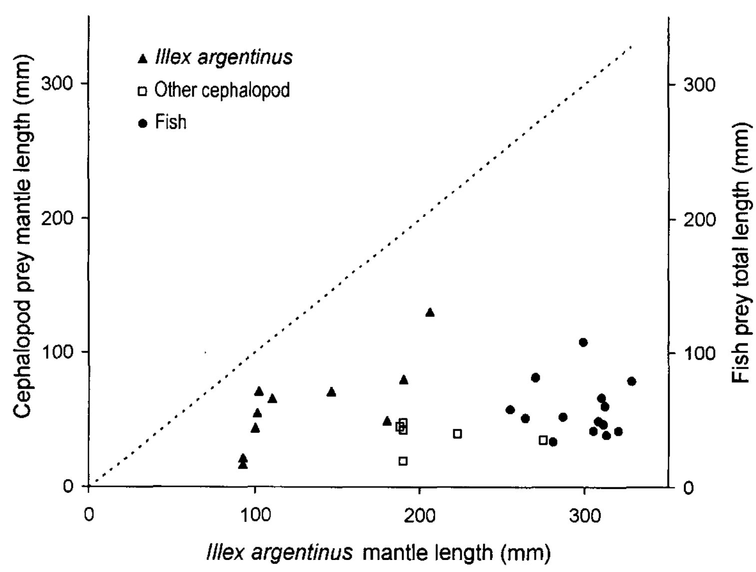

Fig. 8. Relationships between the size of *I. argentinus* (ML) and the size of fish (TL) and cephalopod (ML) prey found in the stomachs.

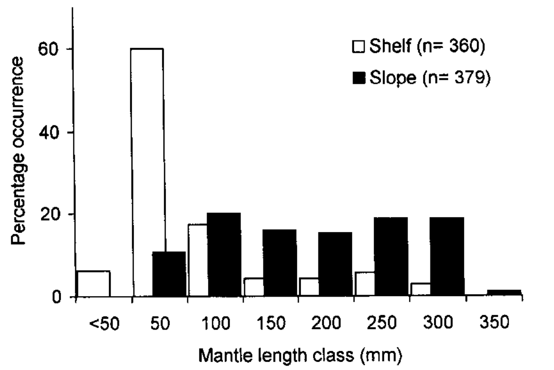

Fig. 9. Mantle length distribution of *I. argentinus* sampled on shelf (50–200 m) and upper slope (200–800 m) off southern Brazil. (n = total number of stomachs examined).

obtained as beaks of *I. argentinus* larger than 131 mm ML were not found in the stomachs. Estimated total length of ingested fishes ranged from 35 to 108 mm and from 12% to 36% of the ML of *I. argentinus* larger than 250 mm ML and, although smaller short-finned squid also prey on fish, no information on the sizes was obtained as no otoliths were found in their stomachs. Squids are known to discard the heads and hard parts of larger fish prey, thus the ingestion of fishes larger than those shown in the figure cannot be ruled out.

3.3. *Effect of depth*

Smaller squids were collected mainly from the shelf (50–200 m) while the larger ones were collected along the upper slope (200–800 m, Fig. 9). Feeding was significantly more intense in the upper slope, where 61.2% of the stomachs examined had food against 42.9% of those from the shelf ($\chi^2_{v=1}$ = 24.79; $P < 0.001$). With respect to the type of prey found, fish was more frequent on the upper slope ($\chi^2_{v=1}$ = 15.7; $P < 0.01$) while crustaceans and cephalopods were more frequent on the shelf ($\chi^2_{v=1}$ = 7.2; $P < 0.01$ and $\chi^2_{v=1}$ = 11.3; $P < 0.01$, respectively) (Fig. 10).

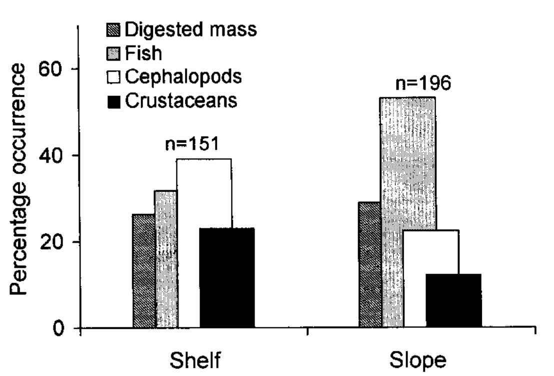

Fig. 10. Percentage occurrence of prey items of *I. argentinus* in relation to the total number of stomachs with food examined (n) for shelf (50–200 m) and upper slope (200–800 m) of southern Brazil (26°S–34°S).

4. Discussion

Ommastrephids feed almost exclusively on crustaceans, fish and cephalopods (Amaratunga, 1983), and *I. argentinus* is not an exception. The proportions of each of these categories of prey and the overall percentage of stomachs with food differ throughout the distribution range of the species. A comparison of the relative importance of the major food items in different regions of the distribution range of *I. argentinus* was possible, despite some differences in the presentation of the results. In southern Brazil (this study) the occurrence of fishes increased with predator size from under 20% to over 60%, while the occurrence of crustaceans (10% and 30%) and cephalopods (15%–35%), with a high rate of cannibalism, remained equally important for all sizes. In the Rio de La Plata Front and on the Patagonian shelf, Ivanovic and Brunetti (1994) found that *I. argentinus* of all sizes fed primarily on crustaceans such as mysids, euphausiids, hyperiids (pooled FO frequently over 80%, for specimens smaller than 200 mm ML and frequently over 60% for the larger ones as shown by the authors in Fig. 5), while only the larger specimens fed also on fish and squid. Koronkiewicz (1986) found that along the outer Patagonian shelf and slope, decapods, mainly *Munida gregaria*, were the main prey for small *I. argentinus* and that larger squid fed more intensely on micronektonic fishes and cephalopods, the latter including members of the same species.

Off Uruguay and Argentina, pelagic crustaceans occur in dense swarms and are easier to catch than fast swimming prey such as fish, thus it seems that in the southern range of distribution of the species, crustaceans were more available. In fact, the zooplankton availability along the Argentinean shelf, where juveniles and subadult *I. argentinus* feed, is comparable to other regions of the world of high plankton production (Carreto et al., 1981) and higher than in southern Brazil (Hubold, 1980a,b).

The percentages of cephalopods, found in this work, were comparable to those found by Ivanovic and Brunetti (1994) off northern Argentina and Uruguay, in the winter and spring samples, but higher than those observed in summer and autumn. In contrast, on the Patagonian shelf and slope, cephalopods were absent from the diet of *I. argentinus* under 180 mm ML and did not exceed 20% for the larger specimens, which suggested that there were low rates of cannibalism among subadults on the feeding grounds, before the reproductive migration (Koronkiewicz, 1986; Ivanovic and Brunetti, 1994).

The increase in cannibalism with size seems to be a common behaviour of migratory ommastrephids and it may be attributed to a strategy that favours energy transfer from smaller to larger specimens (Amaratunga, 1983; O'Dor and Wells, 1987). Cannibalism by large specimens was also observed in southern Brazil. In this region, juveniles and subadults short-finned squids were preyed upon by larger juveniles and subadults as their spatial distributions overlap along the narrow shelf break of southern Brazil (Haimovici and Perez, 1990). This cannibalistic behaviour of juveniles and subadults suggests a limited food supply. A similar pattern was observed by Dawe (1988) in Newfoundland where subadult *I. illecebrosus* appears to resort to cannibalism when fish prey becomes unavailable.

The occurrence of stomachs with food in spawning short-finned squid observed in southern Brazil was also observed by Ivanovic and Brunetti (1994) in summer, along the Argentinean shelf. Laptikhovsky and Nigmatullin (1993) concluded that individual females of *I. argentinus* spawn in batches and Santos and Haimovici (1997) observed partly spawned specimens in southern Brazil. Feeding during spawning may contribute to increase fecundity and opportunities for at least some hatchlings to encounter favourable conditions in a less productive environment compared with the Uruguayan and Argentinean shelves (Hubold, 1980a,b). In fact, partly spawned females of *I. argentinus* were observed in the western boundary of the Brazil Current, along the slope of southern Brazil from July to November (Haimovici and Perez, 1990; Santos and Haimovici, 1997).

A gradient of increasing body size of *I. argentinus* with depth was observed, in all seasons, by Haimovici and Perez (1990). Juveniles, which occur mostly on the outer shelf, feed less intensely than subadults and adults that occur mostly along the upper slope. The distribution of juvenile or adult squids in southern Brazil does not overlap with the most abundant neritic forage fish in the region, the anchovy *Engraulis anchoita*, which is abundant in winter on the inner shelf (Lima and Castello, 1995). Main fish prey species of *I. argentinus* in this study were juvenile *Merluccius hubbsi* and small mesopelagic fishes that occur on the upper slope of the region (Haimovici et al., 1994).

The direct observation of diel vertical migrations of *I. argentinus* (Moiseev, 1991), the observation of relatively undigested food in stomachs throughout the day and the presence of both demersal and pelagic prey in the diet, suggest that this squid forages throughout the water column following its prey to the upper layers at dusk and early night.

The overall low proportion of stomachs with food, the high rate of cannibalism and the low frequency of occurrence of crustaceans for the juveniles and subadults in all seasons, but particularly in the summer and autumn, reflect a limited availability of food in the region. This unfavourable feeding environment and the demonstrated low abundance of juvenile *I. argentinus* in the warm months in southern Brazil supports the hypothesis that egg masses and paralarvae spawned off southern Brazil in winter–spring are probably carried southward by the Brazil Current (Haimovici et al., 1995) and main nursery grounds for these squids are likely to be off the Rio de La Plata Front or in the offshore confluence between the Brazil and Malvinas Currents, where primary and secondary production is higher than off southern Brazil (Hubold, 1980a,b) and thereby food for post-hatchlings is more available.

A similar scenario probably exists in the northwestern Atlantic Ocean, where *I. illecebrosus*, as *I. argentinus*, is associated with a western boundary current system. Peak spawning occurs south of Cape Hatteras in winter–spring and the egg masses are transported north to more productive waters by the

Gulf Stream (O'Dor and Balch, 1985; Black et al., 1987).

References

Amaratunga, T., 1983. The role of cephalopods in the marine ecosystem. In: advances in assessment of world cephalopod resources. FAO Fish. Tech. Pap. 231, 379–415.

Black, G.A.P., Rowell, T.W., Dawe, E.G., 1987. Atlas of the biology and distribution of the squids *Illex illecebrosus* and *Loligo pealei* in the Northwest Atlantic. Can. Spec. Publ. Fish. Aquat. Sci. 100, 1–62.

Breiby, A., Jobling, M., 1985. Predatory role of the flying squid (*Todarodes sagittatus*) in North Norwegian Waters. NAFO Sci. Coun. Studies 9, 125–132.

Brunetti, N.E., 1990. Escala para la identificación de estadios de madurez sexual del calamar *Illex argentinus*. Frente Maritimo 7, 45–51.

Carreto, J.I., Ramirez, F., Dato, C., 1981. Zooplancton y producción secundaria: Parte II. Distribución y varación estacional de la biomasa zooplanctónica. INIDEP Contr. 383, 213–232.

Collins, M.A., de Grave, S., Lordan, C., Burnell, G.M., Rodhouse, P.G., 1994. Diet of the squid *Loligo forbesi* Steentrup (Cephalopoda: Loliginidae) in Irish waters. ICES J. Mar. Sci. 51, 337–344.

Dawe, E.G., 1988. Length–weight relationships for short-finned squid in Newfoundland and the effect of diet on condition and growth. Trans. Am. Fish. Soc. 117, 591–599.

Dawe, E.G., Brodziak, J., in press. Trophic relationships and possible effects of ecosystem variability on recruitment of pelagic squid, with particular reference to the genus *Illex*. In: Dawe, E.G., Rodhouse, P.G., O'Dor, R.K. (Eds.), Squid Recruitment Dynamics: Influences on Variability Within the Genus *Illex*. FAO Fish. Tech. Pap.

FAO, 1995. Fisheries statistics 1993. Catches and landings. FAO Fish. Series, Vol. 76, no. 44, 685 p.

Haimovici, M., Perez, J.A.A., 1990. Distribución y maduración sexual del calamar argentino *Illex argentinus* (Castellanos, 1960) (Cephalopoda: Ommastrephidae), en el sur de Brasil. Scient. Mar. 54 (2), 179–185.

Haimovici, M., Martins, A.S., Figueiredo, J.L., Vieira, P.C., 1994. Demersal bony fish of the outer shelf and upper slope of the southern Brazil subtropical convergence ecosystem. Mar. Ecol. Prog. Ser. 108, 59–77.

Haimovici, M., Vidal, E.A.G., Perez, J.A.A., 1995. Larvae of *Illex argentinus* (Castellanos, 1960) from five surveys on the continental shelf of southern Brazil. ICES Mar. Sci. Symp. 199, 414–424.

Haimovici, M., Brunetti, N.E., Rodhouse, P.G., Csirke, J., Leta, R.H., in press. Chapter 3. *Illex argentinus*. In: Dawe, E.G., Rodhouse, P.G., O'Dor, R.K. (Eds.), Squid Recruitment Dynamics: Influences on Variability Within the Genus *Illex*. FAO Fish. Tech. Pap.

Hatanaka, H.S., Kawahara, S., Uozumi, Y., Kasahara, S., 1985. Comparison of life cycles of five ommastrephid squids fished by Japan: *Todarodes pacificus*, *Illex illecebrosus*, *Illex argentinus*, *Nototodarus sloani sloani* and *N. sloani gouldi*. NAFO Sci. Com. Studies 9, 59–68.

Hubold, G., 1980a. Hydrography and plankton off Southern Brazil and Rio de La Plata, August–November, 1977. Atlântica 4 (1), 1–22.

Hubold, G., 1980b. Second report on hydrography and plankton off Southern Brazil and Rio de La Plata, Autumn cruise: April–June, 1978. Atlântica 4 (1), 23–42.

Hyshop, E.J., 1980. Stomach contents analysis—a review of methods and their application. J. Fish Biol. 17, 411–429.

Ivanovic, M., Brunetti, N.E., 1994. Food and feeding of *Illex argentinus*. Antartic Sci. 6 (2), 185–193.

Koronkiewicz, A., 1986. Growth and life cycle of squid *Illex argentinus* from Patagonian and Falkland Shelf and Polish Fishery of squid for this region, 1978–1985. ICES C.M. 1986/K:27 Shellfish Committee. (mimmeo) 11 p + tab. e fig.

Laptikhovsky, V.V., Nigmatullin, Ch.M., 1993. Egg size, fecundity, and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). ICES J. Mar. Sci. 50, 393–403.

Lima, I.D., Castello, J.P., 1995. Distribution and abundance of southwest atlantic anchovy spawners (*Engraulis anchoita*) in relation to oceanographic process in the Southern Brazilian shelf. Fish. Oceanogr. 4 (1), 1–16.

Moiseev, S.I., 1991. Observation of the vertical distribution and behaviour of nektonic squids using manned submersibles. Bull. Mar. Sci. 49 (1-2), 446–456.

O'Dor, R.K., Balch, N., 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. NAFO Sci. Coun. Studies 9, 69–76.

O'Dor, R.K., Wells, M.J., 1987. Energy and nutrient flow. In: Cephalopods Life Cycles, Vol. II, pp. 109–134.

Rocha, F., Castro, B.G., Gil, M.S., Guerra, A., 1994. The diets of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Northwestern Spanish Atlantic waters. Sarsia 79, 119–126.

Roper, C.F.E., Sweeney, M.J., Nauen, C.E., 1984. FAO Species Catalogue: Vol. 3. Cephalopods of the world. FAO Fish. Synop. 125 (3), 227.

Santos, R.A., 1992. Relações tróficas do calamar argentino *Illex argentinus* (Castellanos, 1960) (Teuthoidea: Ommastrephidae) no sul do Brasil. Magister Thesis Fundação Universidade do Rio Grande, Rio Grande-RS, Brazil, p. 85.

Santos, R.A., Haimovici, M., 1997. Reproductive biology of winter–spring spawners of *Illex argentinus* (Cephalopoda: Ommastrephidae) off southern Brazil. Scient. Mar. 61 (1), 53–64.

Vidal, E.A.G., Haimovici, M., in press. Feeding and the possible role of the proboscis and mucus cover in the ingestion of microorganisms by rhynchoteuthion paralarvae (Cephalopoda: Ommastrephidae). Bull. Mar. Sci.

Yesaki, M.E., Rahn, E., Silva, G., 1976. Sumário das explorações de peixe de arrasto de fundo ao longo da costa sul do Brasil. Sér. Doc. Téc. SUDEPE-PDP 19, 1–37.

Zavala-Camin, L.A., 1981. Hábitos alimentares e distribuição de atuns e afins (Osteichthyes-Teleostei) e suas relações ecológicas com outras espécies pelágicas das regiões Sudeste e Sul do Brasil. Doctoral Thesis Instituto de Biociências da Universidade de São Paulo. São Paulo, 237 p.