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Diet and feeding of the cutlassfish *Trichiurus lepturus* in the Subtropical Convergence Ecosystem of southern Brazil

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The diet and feeding of the cutlassfish *Trichiurus lepturus* were studied based on analyses of the stomach contents of larvae, juveniles, and adults collected along the continental shelf and shelf break off southern Brazil, from the Cape of Santa Marta Grande (28°36′S) to Chuí (34°45′S). The larvae and pre-juveniles with a total length of <5 cm were found to have fed almost exclusively on calanoid copepods, whereas juveniles (5 to 30 cm) fed on small zooplanktonic crustaceans such as *Lucifer faxoni* and *Promysys atlantica*. On the other hand, sub-adults (30 to 70 cm), fed on euphausiids, mainly *Euphausia similis*, and small fish, mostly anchovy *Engraulis anchoita*. Adults (70 to 160 cm) fed on a wide range of larger prey, such as anchovy, sciaenid fish, cephalopods and coastal shrimps, as well as euphausiids. The juveniles and sub-adults fed more intensively than adults during the warm-water season whereas adults fed more intensively during the cold-water season. Feeding activity was more intense at night, while cannibalism was more frequent during the warm season, when biological productivity was lower. Finally, diet diversity was higher in coastal waters, during the warm season. The abundance of cutlassfish off southern Brazil may be explained by the fact that it is adapted to feed on a wide size-range of both pelagic and demersal prey.

INTRODUCTION

The cutlassfish or largehead hairtail, *Trichiurus lepturus* (Linnaeus, 1758) is a cosmopolitan coastal pelagic fish inhabiting warm and warm-temperate shelf waters in various parts of the world (Nakamura & Parin, 1993). It occurs in the western Atlantic from Cape Cod, Massachusetts (40°N) to the Rio de la Plata (37°S) (Fischer, 1978). In the last decade the cutlassfish has been reported in the UN Food and Agriculture Organization statistics as one of the ten marine species with the highest landings worldwide. In recent studies, it was found to be one of the most frequent and abundant bony fish captured in southern Brazil in mid-water and bottom trawl surveys on the continental shelf (Mello et al., 1992; Haimovici et al., 1994, 1996). Because of its importance in the region, its biology and population dynamics have received increasing attention in recent years: Martins & Haimovici (1997) analysed its distribution and abundance in relation to ecological variables and Martins & Haimovici (2000) described its reproductive cycle and estimated its batch fecundity.

The main oceanographic feature in the coastal waters of southern Brazil is the winter northward penetration of cold low salinity waters resulting from the mixing of the inner branch of the Malvinas current with the run-off of the La Plata River. This process leads to the enrichment processes that enhance biological production (Ciotti et al., 1995). The outer shelf and upper slope are strongly influenced by the western boundary of the Subtropical Convergence between the Malvinas and Brazil Currents (Castro & Miranda, 1998). Cyclonic shelf-break vortices result in upwelling and increased production during the whole year but mainly in winter and spring (Zavialov et al., 1998).

The shelf of southern Brazil houses the reproductive, feeding and nursery grounds of commercially important species of both subtropical and temperate origin (Haimovici et al., 1997). In transitional environments such as the Subtropical Convergence Ecosystem (Castello et al., 1997), non-specialized, widely distributed species may be dominant (Parrish et al., 1983). The cutlassfish probably belongs to this group as it attains high abundance at the southernmost limit of its distribution along shelf and shelf-break fronts off the southern coast of Brazil (Martins & Haimovici, 1997).

Due to its cosmopolitan nature, the survival and abundance of the cutlassfish depends on its adaptability to diverse environments. Studies of the diet and feeding strategy of this species may help to understand its ubiquity. Over the years, several surveys on the shelf and upper slope of southern Brazil have provided a large number of stomach contents of *T. lepturus* from different seasons and a wide range of sizes and depth-ranges. In this paper the diet and its ontogenetic and seasonal changes are presented. Furthermore, the daily feeding activity, cannibalism and feeding habits in relation to different oceanographic conditions were also analysed.

MATERIALS AND METHODS

Adult and juvenile cutlassfish were sampled in 13 bottom trawl surveys of the RV 'Atlântico Sul', from 1980 to 1987. The first nine surveys covered the area between the latitudes of Solidão (30°43′S) and Chuí (33°45′S), at depths ranging from 10 to 160 m. The last four covered the outer shelf and upper slope between Chuí and Cape Santa Marta Grande (28°40′S), at depths from 124 to 587 m (Figure 1). Most hauls were carried out between dusk and dawn and lasted 60 min at 3 knots. Bottom and surface temperatures were recorded at the end of each haul. Further details on the sampling design in the bottom trawl surveys can be found in Haimovici et al. (1996) and Haimovici et al. (1994). Additional samples were collected with a beach seine net, a shrimp trawling and a pelagic trawl. Larvae were collected with a bongo net (Table 1).

After most hauls, a random sample of up to 50 cutlassfish was measured (total length [TL]) and examined for the presence of food in their stomachs, and up to 30 stomachs containing food were fixed in 10% formalin and subsequently preserved in 70% ethanol.

Food items were identified to the lowest possible taxon, counted, weighed to the nearest tenth of a gram (except those from larvae), and measured in millimetres (TL for fish, shrimp and zooplankton, mantle length for cephalopods, and carapace width for crabs). Where the entire body of the prey was not available, sizes were inferred from otoliths or head length for fish, rostrum length of beaks for cephalopods, and carapace length for shrimps. Specimens were grouped by size into five categories: (1) 'larvae' (hatched individuals to the complete metamorphosis, 0.5 to 5 cm TL); (2) 'juveniles' (no gonadal development, 5 to 30 cm TL); (3) 'sub-adults' (initial gonadal development, 30 to 70 cm TL); (4) 'small adults' (mature, 70 to 100 cm TL); and (5) 'large adults' (>100 cm TL).

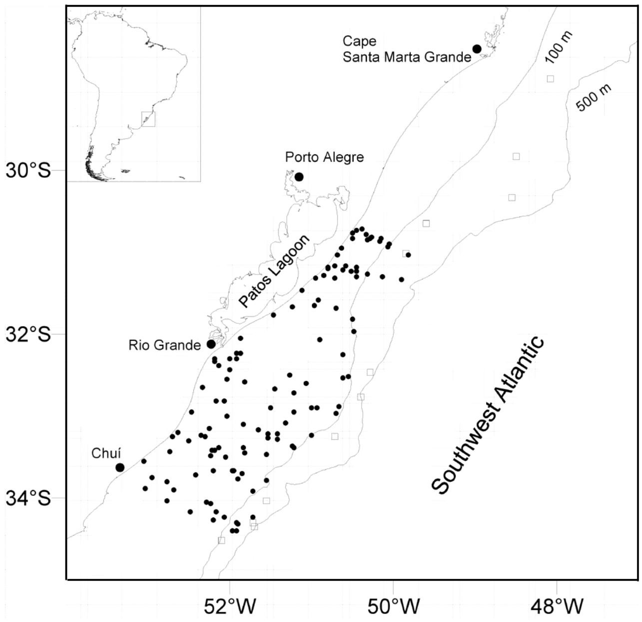

Figure 1. Study area, full circles (1980–1983) and empty squares (1986–1987) represent the bottom trawl hauls in which *Trichiurus lepturus* were collected for feeding studies on the continental shelf and shelf break along the southern Brazilian coast.

The relative importance of different prey items in the diet of cutlassfish were recorded in percentage frequency of occurrence (% FO) and percentage weight (% W).

The association between prey items and ontogeny was investigated with a non-metric multidimensional scaling (nMDS) analysis performed using the PcOrd computer program. The relative Sørensen distance was used to calculate the quadratic matrix distances, because it retains sensitivity in heterogeneous data sets and gives less weight to outliers (McCune & Mefford, 1999).

The percentages of specimens having stomach contents in a given group of hauls corresponding to seasons or diel intervals was defined as an index of feeding intensity.

To investigate the influence of the seasonal variation of the oceanographic conditions, samples were grouped in three categories: (1) warm-water season (autumn) cruises (WWC) in April 1981 and April 1983 with a bottom temperature in most hauls over 20°C; (2) cold-water season (winter) cruises (CWC) in August 1981 and September 1983 with most bottom temperatures below 15°C; and (3) inter-seasonal (late spring and early summer) cruises (ISC) in January 1982 and November 1983 with bottom temperatures between 15°C and 20°C.

Diel variations in feeding intensity were analysed from data pooled in six periods: (1) early dusk (hauls set between 1 and 2 h before dusk); (2) dusk (hauls set from 1 h before to 2 h after dusk); (3) night (hauls set between 2 h after dusk and 2 h before dawn); (4) early dawn (hauls set 1 to 2 h before dawn); (5) dawn (hauls set from 1 h before to 2 h after dawn); and (6) day (hauls set between 2 h after dawn and 2 h before dusk). This classification was considered more suitable than fixed time categories because winter–summer differences in daylight time in southern Brazil can reach over three hours.

Table 1. *Gears, depth-ranges, periods and size-ranges of* Trichiurus lepturus *sampled in southern Brazil for feeding intensity and diet composition.*

			Stomachs examined		Total length-ranges (cm)				
Gear	Depth-range	Period	Repletion	Content	0.9–5	5–30	30–70	70–100	>100
Bongo net	10–120 m	1980	48	28	28				
Pelagic trawl	10–120 m	1982	22	9				7	2
Beach seine net	<10 m	1982	45	14				14	
Shrimp trawling	10–20 m	1990	30	30	1	29			
Bottom trawling	10–160 m	1980–1984	2983	830		151	133	297	249
Bottom trawling	124–587 m	1986–1987	154	50			2	27	21
Total			3232	961	29	180	135	345	272

Table 2. *Percentages of occurrence and weight of food items at different sizes of* Trichiurus lepturus *in southern Brazil and size-ranges of all identified prey.*

	Total length-classes (cm)											
	0.9–5	5–30	30–70	70–100	>100	5–30	30–70	70–100	>100			
	Number of analysed stomachs											
	29	180	135	345	272	180	135	345	272		Prey size-range (mm)	
	Percentage of occurrence					Percentage in weight				Label	Minimum	Maximum
Copepods	100.0	19.4	0.7			<0.1	<0.1				0.3	2.5
Calanus sp.		0.6				<0.1						
Centropages velificatus	3.4										2.0	2.0
Eucalanus monachus		2.8				<0.1					2.2	2.3
Eucalanus pilleatus	6.9										2.0	2.5
Eucalanus sewelli	6.9										1.3	2.5
Oithona sp.	6.9										0.3	0.5
Oncaea sp.	3.4										0.6	0.6
Paracalanus sp.	6.9										0.5	0.8
Undet. Calanoida	55.2	8.9				<0.1					0.3	2.5
Undet. Cyclopoida	3.4										0.5	0.5
Undet. Copepoda	44.8	7.2	0.7			<0.1	<0.1				0.3	2.5
Mysidaceans	6.9	60.6	3.7	3.2	6.6	1.1	0.3	0.6	0.5		3.0	25.0
Mysidopsis coelhoi		5.0				<0.1						
Promysis atlantica		22.2				0.9				1	3.0	5.0
Siriella sp.		3.3				<0.1					3.0	4.0
Undet. Mysidacea	6.9	31.7	2.2		0.7	0.2	<0.1		<0.1	2	3.0	8.0
Undet. Mysidacea A			1.5	3.2	6.3		0.3	0.6	0.5	3	10.0	25.0
Hiperids		1.1	0.7	2.3	1.8	<0.1	0.1	0.2	0.1		3.0	20.0
Brachyscelum crusculum				0.3	0.4			<0.1	<0.1		8.0	8.0
Phronimopsis sp.		1.1	0.7	0.9	0.4	<0.1	0.1	<0.1	<0.1	4	3.0	10.0
Phrosina semilunata				1.4	1.1			0.2	0.1	5	15.0	20.0
Vibilia armata					0.4				<0.1		17.0	17.0
Euphasids		3.3	76.3	33.9	11.0	<0.1	60.0	19.5	0.6		7.0	25.0
Euphausia similis			37.0	20.9	9.6		33.5	14.7	0.6	6	7.0	25.0
Thysanopoda monacantha				0.3				<0.1				
Undet. Euphausiacea		3.3	39.3	12.8	1.5	<0.1	26.5	4.8	<0.1	7	7.0	20.0
Decapod crustaceans		55.6	0.7	16.2	9.2	48.2	<0.1	8.0	1.2		2.0	115.0
Acetes americanus		1.1				<0.1					8.0	35.0
Artemesia longinaris				7.2	2.9			4.5	0.3	8	40.0	157.0
Callinectes danae				0.3				0.5		9		
Leptochela serratorbita		11.7				<0.1					4.0	4.0
Lucifer faxoni		22.8	0.7			<0.1	<0.1				2.0	12.0
Metanephrops rubellus				0.6				<0.1			13.0	35.0
Peisos petrunkevitch		14.4				4.0				10	18.0	21.0
Pleoticus muelleri				2.6	4.0			1.3	0.7	11	27.5	115.0
Plesionika sp.					0.4				<0.1		30.0	30.0
Portunus spinicarpus				0.6				0.9		12	14.0	30.0
Undet. Sergestidae		8.9				<0.1					7.0	8.0
Undet. Dendrobranquiata				5.2	1.8			0.7	0.1	13	60.0	75.0
Undet. Decapoda		1.7		0.3	0.7	44.2		0.1	<0.1	14	2.0	4.0
Stomatopods		0.6	0.7	4.1	2.2	44.2	0.1	0.7	0.3		4.0	120.0
Undet. Stomatopoda					1.1				0.3	15	120.0	120.0
Undet. Stomatopoda larvae		0.6	0.7	4.1	1.1	44.2	0.1	0.7	<0.1	16	4.0	25.0
Undet. crustacean		1.1	2.2	2.9	1.8	<0.1	0.5	0.5	<0.1	17		
Heteropoda			<0.1	<0.1			<0.1	<0.1				
Undet. Heteropoda			0.7	0.3			<0.1	<0.1				
Cephalopods		0.6	1.5	9.0	11.0	<0.1	2.2	5.3	1.9		3.0	200.0
Argonauta sp.				1.4	0.7			0.2	<0.1	18	15.0	35.5
Illex argentinus			0.7	2.3	2.2		0.2	2.2	0.3	19	21.9	200.0
Licoteuthis diadema					1.5				<0.1		81.5	84.0
Loligo sampaulensis			0.7	3.8	4.0		2.1	2.4	1.4	20	20.7	102.0
Ommastrephes bartrami					0.4				0.1	21	90.0	90.0
Semirrossia tenera				0.3	0.7			<0.1	<0.1			
Undet. Oegopsida				0.3	0.4			<0.1	<0.1		14.0	14.0
Undet. Teuthoidea		0.6		1.4	2.2	<0.1		0.5	0.1	22	3.0	55.0

continued

Table 2. *(Continued)*.

	Total length-classes (cm)											
	0.9–5	5–30	30–70	70–100	>100	5–30	30–70	70–100	>100			
	Number of analysed stomachs											
	29	180	135	345	272	180	135	345	272		Prey size-range (mm)	
	Percentage of occurrence					Percentage in weight				Label	Minimum	Maximum
Fish		28.3	35.6	60.6	79.4	6.4	37.3	65.8	95.3		5.0	1006
Anchoa marini			0.7	0.3			0.8	0.4		23	65.0	65.0
Conger orbygnianus					0.4				3.2	24		
Ctenosciena gracilicirrhus					0.4				0.4	25	107.0	107.0
Cynoscion guatucupa			0.7	2.0	6.3		4.4	2.0	5.5	26	53.0	279.0
Diaphus dumerilli					0.7				<0.1		40.0	55.0
Engraulis anchoita		8.9	18.5	16.5	25.4	0.4	22.1	30.3	31.6	27	20.0	150.0
Macrodon ancylodon				0.3	0.4			2.6	0.2	28	204.0	204.0
Maurolicus muelleri				5.2	2.2			2.8	0.8	29	30.0	50.0
Merluccius hubbsi				0.9	1.8			0.3	0.5	30	45.0	106.0
Mugil sp.				0.3				0.1		31	55.0	55.0
Mustelus schimiti					0.4				0.4	32	230.0	230.0
Paralonchurus brasiliensis				0.6	0.4			<0.1	0.1	33	26.0	75.0
Porichtys porosissimus					1.5				1.2	34	50.0	180.0
Raneya fluminensis					0.7				0.2	35	128.0	128.0
Saurida caribaea				0.3	1.5			0.1	0.1	36	45.0	70.0
Synagrops spinosus				0.3				0.2		37	52.0	52.0
Syngnathus folleti			0.7				0.1			38	69.0	69.0
Trachurus lathami		0.6		0.6	2.9	2.7		2.7	3.0	39	30.0	180.0
Trichiurus lepturus		2.2	0.7	0.6	7.4	2.0	0.1	1.2	29.5	40	35.0	1006
Umbrina canosai				0.3	1.1			0.1	1.2	41	37.2	200.0
Urophycis brasiliensis					1.1				1.1	42	80.0	118.0
Urophycis mistacea					0.4				<0.1			
Undet. *Congridae*					0.7				0.6	43	117.0	200.0
Undet. sciaenidae				0.9	0.7			0.9	0.2	44	100.0	100.0
Undet. teleostei		12.2	13.3	32.5	28.7	1.3	9.5	22.1	15.7	45	25.0	250.0
Undet. teleostei larvae		4.4	2.2	0.3		<0.1	0.4	<0.1		46	5.0	10.0

Undet., undetermined.

RESULTS

A total of 3232 stomachs from specimens ranging from recently hatched larvae of 5 mm to large adults of 160 cm TL was examined. From these, 64% were empty and 6.2% were lost during transport. In the remaining 961 stomachs, we found 23 species of pelagic or demersal–pelagic bony fish, one elasmobranch, 21 pelagic crustaceans, seven benthic crustaceans, six pelagic and demersal cephalopods. The frequency of the most common prey items in the stomach contents of males and females did not differ significantly (χ^2-tests, $P<0.05$). Therefore, data from both sexes were pooled for further analysis.

Table 2 includes the relative frequencies of occurrence, percentage in weight and the size-ranges of prey for different ontogenetic stages of cutlassfish. The larvae under 9 mm TL had empty stomachs. From 9 to 50 mm TL, their diet included only copepods measuring 0.3 to 2.5 mm, mainly the filter-feeder, pelagic calanoids *Eucalanus pilleatus* and *E. sewelli*. The diet of the juveniles (TL 5–30 cm) was mostly of coastal, warm water small decapod crustaceans (sergestids, *Lucifer faxoni*, *Peisos petrunkevitch* and larvae of *Leptochela serratorbita*) (48% W) and unidentified stomatopods (42% W). Mysidaceans (*Promysys atlantica* and *Mysidopsis coelhoi*) were very frequent (60% FO) but insignificant in weight (1% W).

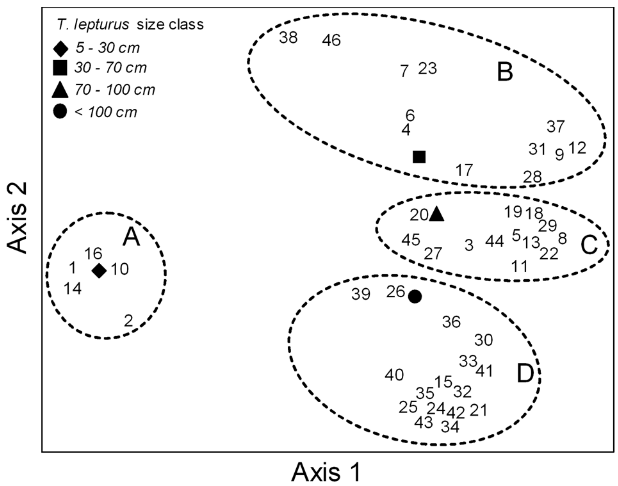

Figure 2. Labels corresponding to the prey items in Table 2 scattered in a two main axis space of a multidimensional scaling analysis. Dotted line clusters relate prey items to size-class of *Trichiurus lepturus*.

The sub-adults (TL 30–70 cm) were found to be feeding primarily on euphausiids (mainly *Euphausia similis*) (60% W) and small fish, mainly juvenile of *Engraulis anchoita* (37% W), on the shelf.

The small adults (TL 70–100 mm) that had a spatial and seasonal distribution similar to that of sub-adults fed mainly upon the same prey as the sub-adults, but in different proportions: 66% W of small fish, mostly *E. anchoita*, and 12 other fish, 19% W of euphausiids, 8% W of crustaceans as shrimps (*Artemesia longinaris*, *Pleoticus muelleri*) and hyperiids and amphipods, and 5% W of cephalopods, mostly *Illex argentinus* and *Loligo sanpaulensis*.

The large adults over 100 cm TL fed on a wide spectrum of pelagic and demersal fish (95% W) including *E. anchoita*, *T. lepturus*, *Cynoscion guatucupa*, and 15 other fish, very few cephalopods (2% W) and decapod crustaceans (1% W).

Ontogenetic changes along growth were further investigated with MDS based in a matrix of main prey items as rows (99% W of the stomach contents) and, as columns, the percentage weight in each of the four size-ranges, as shown in Table 2. The prey items scattered in two axis space and grouped in four interpretable clusters are shown in Figure 2: the first 'A' represents the demersal planktonic coastal diet of juveniles (5–30 cm). In the cluster 'B' the most important prey are pelagic macrozooplanktonic, mainly euphausiids and small coastal fish, associated with the sub-adults (30–70 cm). Cluster 'C' comprises adults (70–100 cm) that feed predominantly on small pelagic fish such as *Engraulis anchoita*, but also on a wide range of coastal and continental shelf prey in plankton and benthos. Finally, the cluster 'D' includes mostly fish associated with large adults (>100 cm). These confirm the visual analysis shown in Table 2.

Cannibalism was important in the cutlassfish's diet, mainly for large adults, representing 7.4% FO and 29.5%

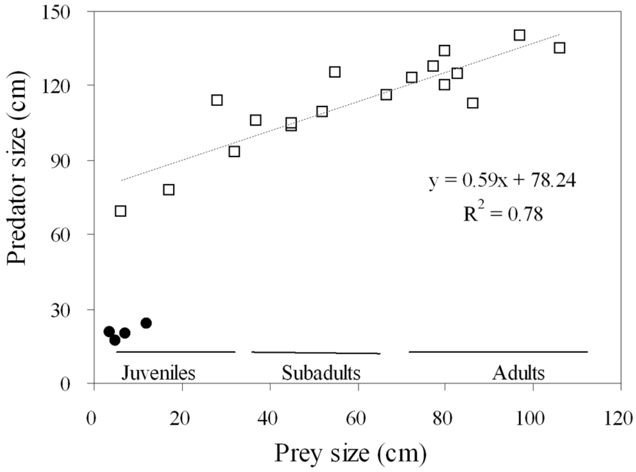

Figure 3. Relationship between prey and predator sizes for cannibalistic *Trichiurus lepturus*. The regression line describing the relationship between predator size (total length [TL]) and prey size (TL) for adult predator (>70 cm) is drawn over the data.

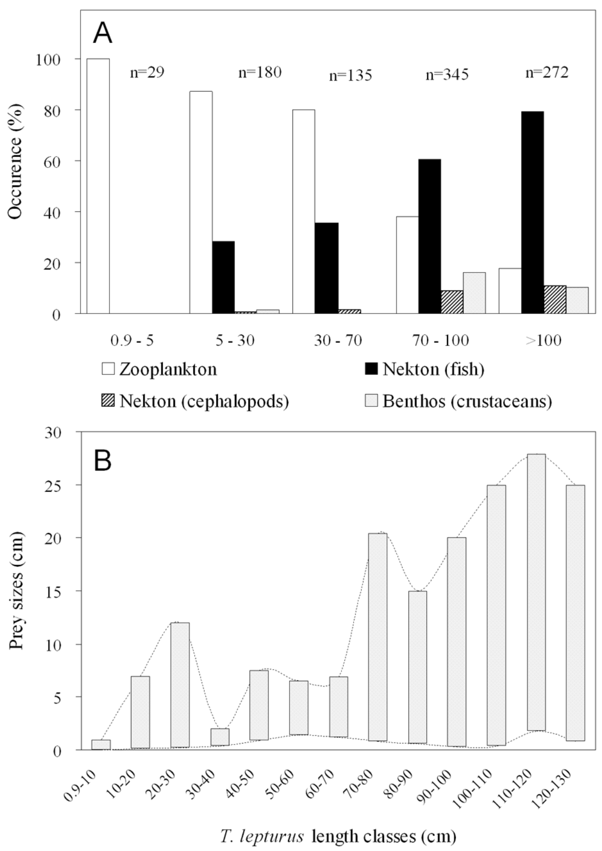

Figure 4. (A) Percentage of occurrence of prey categories ingested by the cutlassfish *Trichiurus lepturus* in southern Brazil at different length-classes and (B) size-ranges of prey ingested by the cutlassfish, *Trichiurus lepturus* in southern Brazil during its ontogeny.

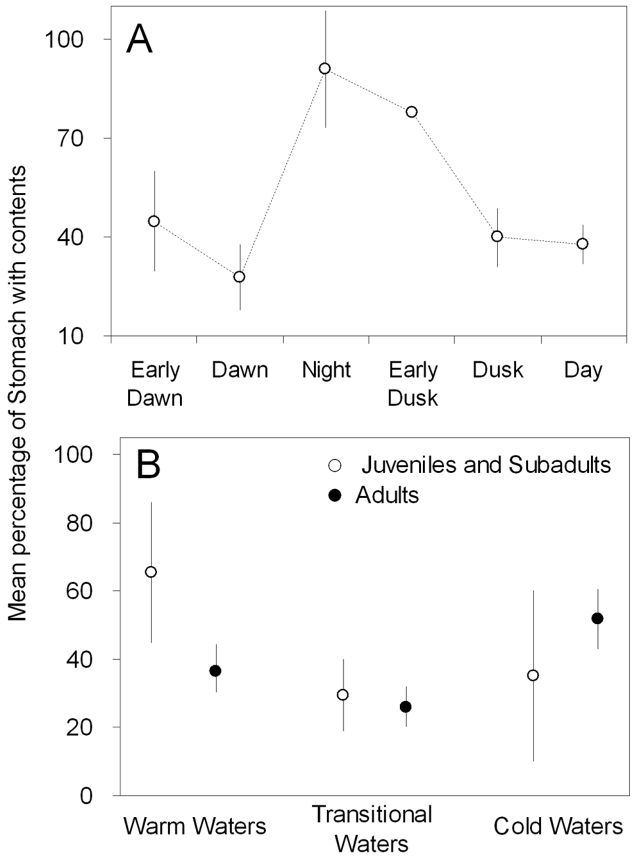

Figure 5. (A) Diel variation of the mean index of feeding intensity (IFI) for *Trichiurus lepturus* from juveniles to sub-adults and adults. The 95% confidence intervals are given (vertical lines) and (B) mean IFI and 95% confidence intervals (vertical lines) for sub-adults and adults of *T. lepturus* on warm, inter-seasonal and cold water cruises.

W (Table 2) and mostly restricted to this length-class, with them preying upon sub-adults and small adults. However, some juveniles (mean TL of about 20 cm) also preyed on smaller juveniles (mean TL 7 cm) (Figure 3). This was more frequently observed during warm-water cruises (68%).

Despite the great variety of prey consumed by *T. lepturus*, the number of different items per individual stomach was low: 67% had only one item; 27% had two and only 6% two items or more, indicating a preference for feeding upon large patches of prey.

The relative frequencies of prey grouped by different size-ranges of cutlassfish are shown in Figure 4B. Three trends in the diet can be identified during the growth of the fish. First, the importance of nektonic and demersal–benthic prey increased with predator size. Second, filter feeders and pelagic–mesopelagic preys were dominant in the diet of sub-adult and small adult cutlassfish. Third, a relatively low diversification of prey types and sizes was observed for sub-adults, compared with small and large adults (Figure 4A,B).

Indices of feeding intensity of sub-adults and adults at different times of the day and night showed a significant peak of nocturnal feeding activity but no difference in feeding activity between early dusk, dusk, day, early dawn or dawn (Figure 5A). Mean seasonal feeding intensity was calculated for juveniles/sub-adults and adults separately (Figure 5B). The juveniles and sub-adults appeared to feed more intensely than the adults in both the warm and cold seasons.

DISCUSSION

Feeding habits of cutlassfish involving the same types of organisms as in southern Brazil have been reported in other seas: juveniles feeding on calanoid copepods and adults on *Engraulis japonicus* in the Sea of Japan (Munekiyo & Kuwahara, 1984), juveniles on euphausiids and clupeids in the Indian Ocean (Portsev, 1980) and juveniles on fish larvae off the Indian coast (Narasimham, 1972).

The wide range of prey sizes of *Trichiurus lepturus* may be explained by its adaptations: it has relatively large eyes and a laterally compressed body with no caudal fin, and a long semi-vertical lateral line that can detect subtle alterations in the pressure field produced by small potential prey as far as 32 m away (Bone & Marshall, 1982). The detection and capture of small crustaceans undergo little ontogenetic change in southern Brazil. Euphausiids were frequently found in the stomach contents of all sizes of cutlassfish. Moreover, the large mouth with its powerful teeth allows for the ambush feeding of fish and squid, including cannibalism (Nakamura & Parin, 1993).

The higher nocturnal feeding intensity observed was consistent with lower catches during night trawls observed by Martins & Haimovici (1997), indicating that the cutlassfish was feeding higher in the water column and could not be caught by the bottom trawl gear. Nocturnal pelagic feeding behaviour was observed by the senior author (A.S.M.) in Porto Belo Bay (26° S), where cutlassfish were seen feeding on a school of juvenile *E. anchoita* of about 5 cm TL in surface waters, ascending rapidly with anguilliform movements, in a semi-vertical position, sometimes propelling themselves out of the water. Cannibalism between individuals of a similar size was also observed during the same event. The predator used its jaws to cut off the head of the prey before biting other parts of the body. This behaviour corresponds with our observations of stomach content data. The relatively high incidence of cannibalism can be explained by the high abundance of this species in southern Brazil and its aggregated feeding behaviour. It could also be associated with low food availability, which occurred during warm-water periods in late summer and autumn, when biological productivity and standing fish biomass in the region are known to be lower (Castello et al., 1997).

The low prey diversity in individual stomachs can be explained by the aggregated distribution of its most frequent prey species (i.e. anchovies, euphausiids) and the limited mobility of the cutlassfish, which appears to feed on dense patches of prey and follow their vertical migrations (Munekiyo, 1990).

The cutlassfish proved to be well adapted to feed on many of the most abundant planktonic and nektonic organisms from both coastal and continental shelf waters. These included the euphausiid *Euphausia similis*, frequently found in stomach contents of pelagic and demersal–pelagic fish (Schwingel & Castello, 1994), the anchovy *Engraulis anchoita*, which has an estimated winter biomass of more than two million tons (Lima & Castello, 1995) and the weakfish, *Cynoscion guatucupa* which is the most abundant bony fish in demersal trawl surveys (Haimovici et al., 1996).

The abundance of cutlassfish off the coast of southern Brazil, where the environment presents large variations in physical characteristics and biological production, may be explained by its adaptations for feeding simultaneously on several trophic levels and on a variety of small dense patches of prey as well as larger prey that are mobile throughout the water column. Most of its energy budget comes from relatively short pelagic food chains, but these are flexible enough to include demersal and even benthic prey when necessary.

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