FOOD RESOURCE UTILIZATION OF THE SKATES *Rioraja agassizii* (MÜLLER & HENLE, 1841) AND *Psammobatis extenta* (GARMAN, 1913) ON THE CONTINENTAL SHELF OFF UBATUBA, SOUTH-EASTERN BRAZIL

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ABSTRACT

The feeding habits of *Rioraja agassizii* (syn. *Raja agassizii*) and *Psammobatis extenta* (syn. *Psammobatis glansdissimilis*) of the South-eastern Brazilian coast were studied by means of stomach content analysis. The samples were obtained on eight seasonal oceanographic cruises, carried out between October 1985 and July 1987. The importance of each food item was evaluated on the basis of the Index of Relative Importance and the feeding similarity by Percentage of Similarity. The results indicated that both species are benthic feeders, preying mainly on Crustacea, especially Amphipoda, Caridea and Brachyura. Teleostei were also important for *R. agassizii*. Seasonal variation of the diet seems to be associated with the availability of the prey, whose distribution and abundance are related to the dynamics of the water masses of the region. Juveniles and adults of *P. extenta* exploited the same resources while juveniles and adults of *R. agassizii* presented low diet similarity during most of the year. Caridea were an important food for all length classes of *R. agassizii*, while Amphipoda were for smaller specimens, and Teleostei for larger ones. The feeding overlap between the two species was higher during autumn 1986, winter 1986 and winter 1987.

Key words: Rajidae, stomach content, feeding habits, South Atlantic, Brazil.

RESUMO

Utilização dos recursos alimentares pelas raias *Rioraja agassizii* (Müller & Henle, 1841) e *Psammobatis extenta* (Garman, 1913) na plataforma continental de Ubatuba, sudeste do Brasil

Os hábitos alimentares de *Rioraja agassizii* e *Psammobatis extenta* da região costeira de Ubatuba, SP, foram investigados por meio da análise de conteúdos estomacais. As amostras foram obtidas em oito campanhas oceanográficas sazonais realizadas no período de outubro de 1985 a julho de 1987. A importância do item alimentar foi avaliada pelo Índice de Importância Relativa e a sobreposição alimentar pela Porcentagem de Similaridade. As duas espécies se alimentaram de organismos bentônicos, principalmente crustáceos. Os Amphipoda, os camarões Caridea e os Brachyura foram as presas mais importantes. Além dessas presas, Teleostei foi importante na dieta de *R. agassizii*. A variação sazonal da alimentação das raias esteve associada à disponibilidade de suas presas, cuja distribuição e abundância estão relacionadas às variações sazonais das condições oceanográficas da região. A alimentação de jovens e adultos de *P. extenta* foi muito semelhante, enquanto jovens e adultos de *R. agassizii* apresentaram baixa similaridade alimentar na maioria das estações do ano. Caridea foi importante para todos os tamanhos de *R. agassizii*, Amphipoda para exemplares menores e Teleostei para indivíduos maiores. A sobreposição alimentar entre as duas espécies foi alta no outono de 1986 e nos invernos de 1986 e 1987.

Palavras-chave: Rajidae, conteúdo estomacal, hábitos alimentares, Atlântico Sul, Brasil.

INTRODUCTION

Studies of feeding habits are essential to the understanding of the functional role of fish within the ecosystem. Nikolsky (1963) has already pointed out the importance of understanding how fish exploit food resources and their interaction with other predators, in order to develop a rational method of commercial stock exploitation. In the last ten years, the importance in using food data in multispecific system models has been emphasized by many authors (Livingston *et al.*, 1986; Greenstreet, 1995). Although some species have no fishery interest, information about their feeding is helpful in assessing fishery stocks, since they may be potential competitors or predators of commercially important species, thus interfering in their mortality rate.

The demersal community of the continental platform of Ubatuba, their relationship with the environment and some aspects of the life cycle of the most abundant fish species have been investigated within the multidisciplinary research project "Rational Utilization of Coastal Ecosystems of the Brazilian Tropical Region", carried out by the Instituto Oceanográfico (Universidade de São Paulo). In the region between the coast and the 50 m isobath, 111 species of demersal fish have been identified (Rocha & Rossi-Wongtschowski, 1998). The skates *Rioraja agassizii* and *Psammobatis extenta* are very important in this system, in terms of abundance and biomass. Both species are endemic to the Argentinean Marine Zoogeographical Province, which comprises the region between "Cabo Frio" (Brazil) and "Península Valdés" (Argentina) (Figueiredo, 1981). Recent phylogenetic analysis of skates have raised *Rioraja* to generic status (McEachran & Dunn, 1998), *Rioraja agassizii* (Müller & Henle, 1841) being synonymous with *Raja agassizii*. *Psammobatis extenta* (Garman, 1913) is a senior synonym of *Psammobatis glansdissimilis* McEachran, 1983 (Carvalho & Figueiredo, 1994).

Studies on the diet of Brazilian skates are very few (Bacescu & Queiroz, 1985; Pires, 1987; Gouvêia & Queiroz, 1988; Soares *et al.*, 1992) and some of them focus on specific taxonomic groups of prey.

The aim of this study is the analysis of the food resource utilization of *R. agassizii* and *P. extenta* and detect dietary changes, taking into account abiotic (seasonal) and biotic (sex, life cycle and length of the skates) variables.

Study area

The area under study is located on the continental platform of Ubatuba (23°20'S-24°00'S, 44°30'W-45°30'W), South-eastern Brazil. The shelf can be divided in two different areas, in accordance with its oceanographic features. The inner domain, where the dynamics is controlled by the wind, is limited by the coast and the 40-50 m isobath. The outer domain extends from this isobath to the shelf break, and is influenced not only by the wind but also suffers the direct influence of the Brazil Current (Castro Filho *et al.*, 1987).

Three water masses occur in the region: the South Atlantic Coastal Water (SACW) with low temperatures (13°C) and salinity (35.4), Tropical Water (TW) with high temperatures (24°C) and salinity (37.0) and Coastal Water (CW) related to high temperatures (24°C) and low salinity (34.9). The seasonal pattern of the dynamics of these water masses provides distinct thermohaline conditions in the summer and winter.

During the summer, the inner domain presents stratification of the water column, with the development of a thermocline. In this season, the upper layer (less than 20 m in depth) of the region is basically occupied by the CW, which mixes with TW offshore, while the SACW predominates on the bottom, mixing with CW just near the coast. During winter, when the SACW moves offshore, the inner shelf is occupied by the CW and the thermocline disappears.

MATERIAL AND METHODS

Sampling and laboratory procedure

The samples were collected at nine sites located from the coast line to the 50 m isobath (Fig. 1). A total of eight seasonal cruises were made on R/B Veliger II, between October, 1985 and July, 1987. Sampling was carried out by means of a 16.5 m otter trawl bottom net of 40 mm stretch mesh in the body and sleeve and 25 mm in the cod mesh. One-hour hauls at a speed of 2 knots were carried out at the nine sites, during daylight. On board, the fish were sorted and stored in ice. Bottom water temperature and samples for salinity and oxygen estimation were obtained at each site (Fig. 1).

At the laboratory, data on total mass (nearest 0.1 g), total length (mm) and sex were recorded for each specimen. The skates were measured from the tip of the snout to the end of the tail. Specimens were classified as juveniles and adults according to the length at first maturity, which is 330 mm for *R. agassizii* and 220 mm for *P. extenta* (Ponz Louro, pers. comm.). The stomachs were collected and preserved in 10% buffered formalin solution. The degree of stomach fullness was recorded on a five level scale, ranging from empty stomach to full stomach (> 75%) with three intermediate levels: almost empty (> 0% to 25%), half full (> 25% to 50%) and almost full (> 50% to 75%). Stomach contents were sorted and the food items were identified to the lowest possible taxonomic level. For each prey group, occurrence, number and wet mass (nearest 0.001 g) were recorded.

Data analysis

The length distribution frequency of the skates was calculated, taking into account length classes of 50 mm and 20 mm for *R. agassizii* and *P. extenta*, respectively.

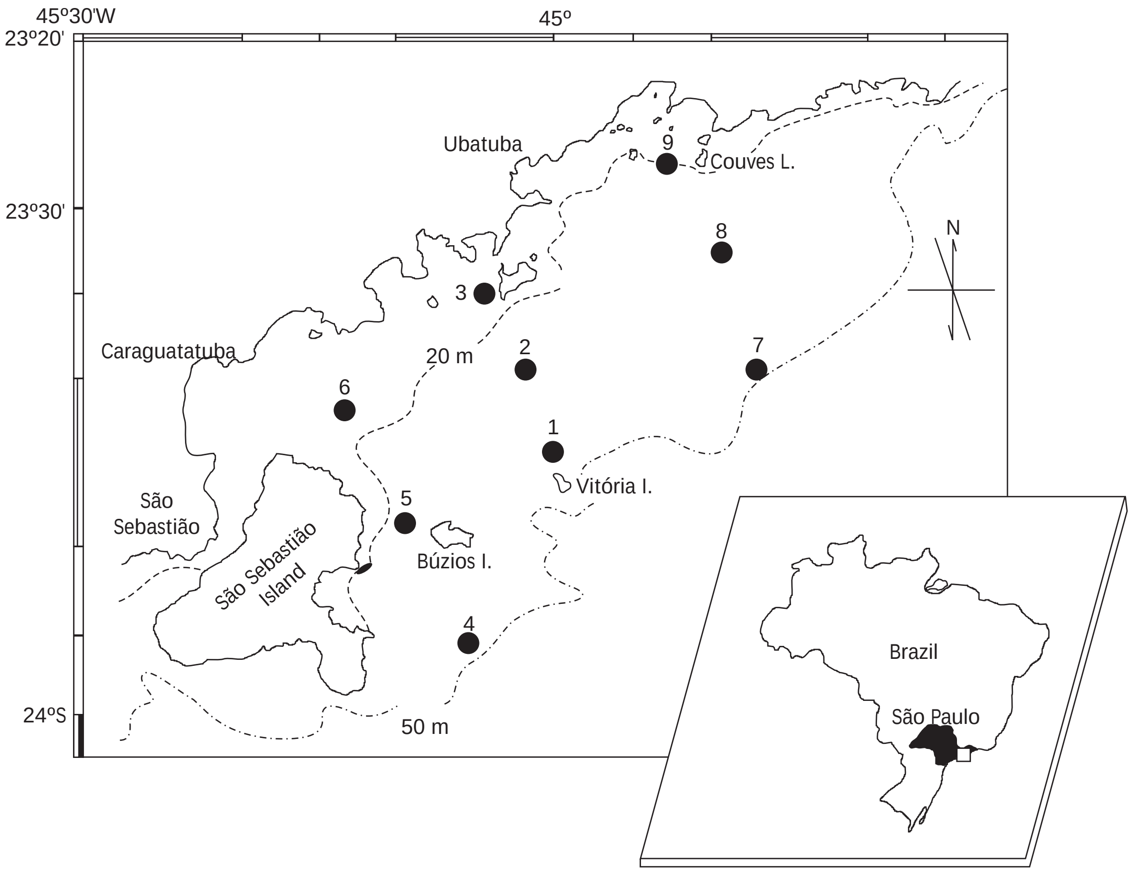

Fig. 1 — Map of the area showing the sampling sites.

Diet composition was analyzed by the relative frequency of occurrence, number and mass (Berg, 1979; Hyslop, 1980). The Index of Relative Importance (IRI) was calculated for the major prey categories (Pinkas *et al.*, 1971) as: IRI = (% N + % M) % F, where N is number, M is mass and F is the occurrence of prey in the stomach contents. In order to compare the samples, IRI values were transformed into percentages. Although nematods occurred frequently in the stomachs, this group was not considered as a prey item, since they are regarded as parasites. Data on prey mass by season are presented in Appendixes 1 and 2, due to their importance for trophic modelling.

Aiming at detecting inter and intraspecific dietary overlap, the Shoener's index (Linton *et al*., 1981) was used: $\mathbf{PS = 100 - 0.5\ \Sigma\ |\ P_{xi} - P_{yi}\ |}$ where PS is Percentage of Similarity, P_{xi} and P_{yi} are the proportion of a particular prey group i in the diet of predators **x** and **y**. The index ranges from **zero** (completely different diets) to **100** (identical diets). The P_{xi} and P_{yi} values used to estimate the PS were the recalculated IRI (%), in which unidentified crustaceans, decapods, crabs and shrimps were not considered, since these groups included Brachyura, Anomura, Caridea, Penaeidea, Peracarida and others. PS values over 60% were considered as high diet overlaps. In order to compare multiple samples, cluster analysis (Q-mode) was performed using the Percentage of Similarity Index and the UPGMA (unweighted pair-group arithmetic average clustering) method of hierarchical agglomeration (Sneath & Sokal, 1973). Interspecific comparisons were made considering the diet of juveniles and adults on a seasonal basis.

RESULTS

Distribution of the species over the sampled area

Neither species occurred in the shallowest area (site 6) near São Sebastião Island (Figs. 1 and 2). The skate *R. agassizii* showed broad distribution and was present at almost all locations (from 17 m to 50 m depth. A more restricted distribution was observed for *P. extenta* which was invariably sampled at site 7 and frequently caught around the 50 m isobath. High spatial overlaping (67%) of both species occurred in summer 1986 and both winters. No overlap was observed during summer 1987 (Fig. 2).

Length Distribution

A total of 429 specimens of *R. agassizii* and 334 of *P. extenta* were captured in the area. The total length of *R. agassizii* collected over the period ranged from 80 to 580 mm, though 69% of the individuals measured between 280-479 mm in length. The lengths of *P. extenta* ranged from 81 to 286 mm, most of them (82%) distributed in the 220-239 and 240-259 mm length classes (Table 1, Fig. 3).

Overall diet

The diet of *Rioraja agassizii* was composed of crustaceans (mainly caridean), fish and polychaetes (Table 2). Caridean shrimps occurred in 70% of the total stomachs and constituted 49% of the total prey number.

Fish were the most important item in terms of mass, despite their low numerical frequency. Other food categories presented low IRI values (< 5.5%). *Psammobatis extenta* is a crustacean feeder, preying mainly on amphipods, caridean shrimps and brachyurans, which occurred in at least 60% of the stomachs (Table 3). Amphipods accounted for 43% of the total number of prey items, and carideans for 48% of the total mass. Other items contributed less than 8% to the IRI (Tables 2 and 3).

Seasonal comparisons

Rioraja agassizii – A few empty stomachs of *R. agassizii* were collected (0.9%) and the proportion of stomachs with at least half their volume of food was 52% (Fig. 4).

During both winters full and almost full stomachs predominated in the samples. Seasonal differences in prey ingested as well as in prey importance were evident throughout the year (Fig. 5A). From the classification analysis two major groups may be observed, one composed of both summers and the other of both springs and winters (Fig. 5B). In autumn 1986 the diet was similar to that of the summers and that of autumn 1987 to those of the springs and winters.

Seasonal changes in the diet followed the same pattern during both years. Caridean shrimps, fish (mainly teleostean) and amphipods were the most important prey groups in both springs, in addition to brachyuran crabs in spring 1986 (Fig. 5A, Table 4).

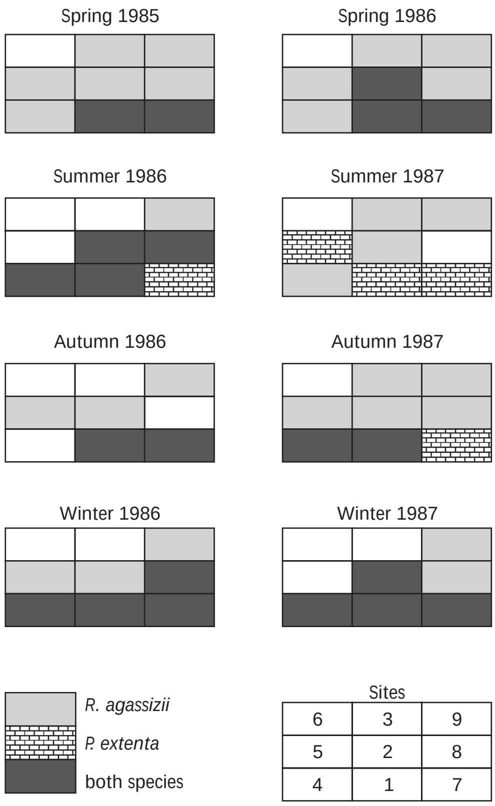

Fig. 2 — Spatial distribution of *R. agassizii* and *P. extenta* in the sampled area.

Fish and brachyuran crabs (portunids, leucosiids, majids and cancrids) were the major prey items during both summers, but amphipods (mainly the gammarids *Ampelisca*) were also important in summer 1986 and penaeidean shrimps (*Trachypenaeus constrictus* and *Sicyonia* sp.) in summer 1987. During autumn 1986, demersal fish were the main prey, while in autumn 1987 caridean shrimps (mainly *Leptochela serratorbita*) and brachyurans (portunids, leucosiids and cancrids) were the most important food. Shrimps made a major contribution to the diet during winter, especially the caridean *L. serratorbita*. Penaeidean shrimps were also important during winter 1987, mostly *T. constrictus* (Table 4, Figs. 4, 5A and 5B).

Psammobatis extenta – This species did not present any empty stomachs (Fig. 6). In summer 1986, spring 1986 and both winters, full stomachs were the most frequent in the sample. Almost empty and half full stomachs predominated in autumn 1986. Although prey composition had been similar over the year, the relative importance of the prey items changed (Fig. 7A). The dendogram illustrates two major groups, showing that the winter diets differed from those of other seasons (Fig. 7B). Amphipods and brachyurans were the major food during the springs, summers and autumns of the two years (Fig. 7A).

TABLE 1

Sampling periods, water temperature (T) and salinity (S), number (N) of specimens and size range (TL = total length) of *R. agassizii* and *P. extenta* collected on Ubatuba shelf.

Sampling	Mean		*R. agassizii*		*P. extenta*	
	T ºC	S	N	TL (mm)	N	TL (mm)
Spring 1985	16.60	35.563	33	277-535	50	81-262
Summer 1986	16.94	35.505	27	192-504	64	129-271
Autumn 1986	22.41	35.669	93	96-538	5	243-263
Winter 1986	21.21	35.807	51	174-550	48	130-286
Subtotal			204	96-550	167	81-286
Spring 1986	18.70	35.606	79	89-580	43	221-260
Summer 1987	16.77	34.438	35	110-533	36	133-265
Autumn 1987	21.13	35.402	66	133-545	44	206-276
Winter 1987	20.85	34.738	45	184-532	44	223-278
Subtotal			225	89-580	167	133-278
TOTAL			429	89-580	334	81-286

TABLE 2

Prey items of *R. agassizii* stomach contents for the total sample (O = occurrence, N = number, M = mass (g) and IRI = Index of Relative Importance).

Prey items	Total			
	% O	% N	% M	% IRI
POLYCHAETA	21.88	2.14	0.26	0.51
CRUSTACEA (TOTAL)	**98.12**	**95.03**	**52.70**	**81.26**
unidentified crustaceans	20.71	2.81	0.02	0.57
crustaceans larvae	0.24	0.04	< 0.01	< 0.01
unidentified decapods	20.00	2.57	0.03	0.50
unidentified shrimps	73.41	24.13	3.08	19.34
post larvae	1.41	0.12	< 0.01	< 0.01
Caridea	70.12	48.96	21.77	48.01
Penaeidea	24.94	3.55	16.31	4.79
unidentified crabs	15.76	1.27	1.78	0.46
megalopa	0.24	0.01	< 0.01	< 0.01
Brachyura	41.88	4.47	8.95	5.44
Anomura	2.82	0.22	0.05	0.01
Amphipoda	33.18	6.08	0.48	2.10
Cumacea	2.12	0.13	< 0.01	< 0.01
Isopoda	0.47	0.03	< 0.01	< 0.01
Mysidacea	0.47	0.04	< 0.01	< 0.01
Stomatopoda	5.41	0.36	0.21	0.03
Tanaidacea	1.41	0.09	0.01	< 0.01
FISH	37.65	2.98	47.04	18.23
TOTAL		7,583	291.54 g	10,331
Stomachs analyzed	425			

Ampelisca brevisimulata and *Portunus spinicarpus*, were, respectively the most frequent amphipod and brachyuran species in the stomach contents (Table 5).

In autumn 1987, caridean shrimps were also important, *Leptochela serratorbita* being of particular note. During the winters, caridean shrimps (mainly *L. serratorbita*) predominated in the diet, contributing 82% and 78% to the IRI in 1986 and 1987, respectively. Despite the low IRI values of polychaetes, this item was consumed mainly during autumn, occurring in 50% (1986) and 68% (1987) of the stomachs analyzed (Table 5). During spring 1986 it occurred in 51% of the stomachs, rarely being ingested during both winters (Table 5, Figs. 6, 7A and 7B).

Changes with fish length

Preliminary examination showed that the diets of males and females of both skates species were very similar, thus data on stomach contents was pooled and comparisons were made between juveniles and adults.

***Rioraja agassizii* –** Diet comparison within 50 mm length classes showed dietary changes with fish length (Fig. 8A, B). The diet of the specimens smaller than 180 mm differed from that of the larger ones due to the consumption of amphipods.

For larger skates, caridean shrimps predominated in the diet. Fish was important only for specimens over 480 mm, which were all females. (Figs. 8A, B).

Seasonal comparison between juvenile and adult diets showed that PS was higher during both winters, spring 1986 and autumn 1987. Shrimps (mostly caridean) were the main food items consumed by these groups in these periods (Fig. 9).

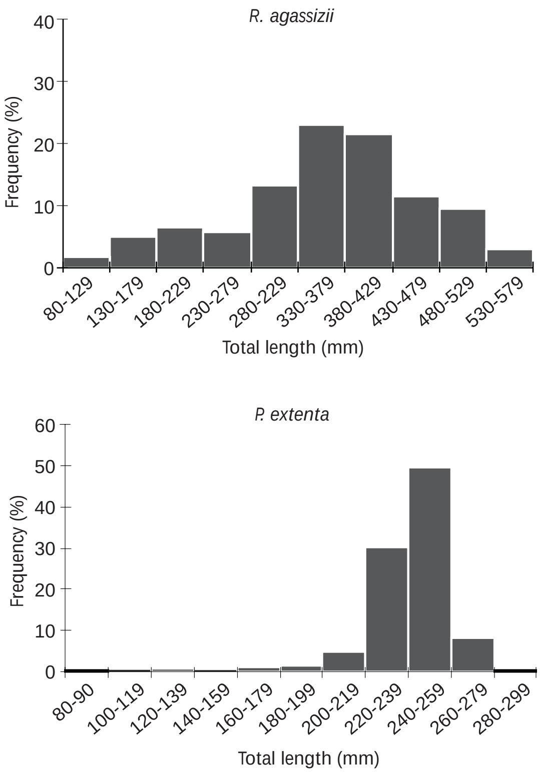

Fig. 3 — Length frequency distribution of *R. agassizii* and *P. extenta* from the overall sampling period.

Brachyurans were also important for adult diets in spring 1986 and autumn 1987.

In the other seasons juveniles and adults preyed on caridean and penaeidean shrimps, brachyuran crabs, amphipods and fish at different levels. Some differences were observed during spring, summer and autumn of the first year when amphipods were very important for juveniles but not for adults, while the inverse occurred for the item fish. During spring 1985, brachyurans were also important for juveniles and caridean shrimps for adults. In summer 1986, juveniles fed mainly on amphipods, brachyurans and fish, while adults consumed brachyurans and fish. In autumn 1986, amphipods and shrimps predominated in the juvenile diets, fish and shrimps being the most important food for adults. In summer 1987, juveniles fed mainly on brachyurans, followed by shrimps and amphipods. The major food items for adults were fish, penaeidean shrimps and brachyurans (Fig. 9).

***Psammobatis extenta* –** Specimens of 180 to 259 mm presented very similar diets, though differing from that of the larger skates (Figs. 10A, B).

Amphipods were the most important prey for smaller skates, decreasing in importance for the larger ones. As the skates grew the consumption of caridean shrimps increased (Figs. 10A, B).

The diets of juveniles and adults were very similar in spring 1985 and both summers, in which the amphipods were the main prey, followed by brachyurans (Fig. 11). Juveniles were not captured in the area during autumn and winter (Fig. 11).

Interspecific comparisons

Classification analysis showed that in the first year (1985/86), high interspecific feeding overlap occurred between juveniles of *R. agassizii* and juveniles/adults of *P. extenta* during summer, due to the consumption of amphipods (Figs. 9, 11 and 12A). The same was observed during autumn between juveniles of *R. agassizzi* and adults of *P. extenta* (Figs. 7A and 9).

Juveniles and adults of both species displayed a very similar diet during winter as well, feeding mainly on the caridean shrimp *L. serratorbita*.

Results of the classification were a little different in the second year (1996/97), showing two major groups (Fig. 12B). High feeding overlap occurred between the two species only during winter, when juveniles/adults of *R. agassizii* and adults of *P. extenta* consumed a large quantity of the caridean shrimp *L. serratorbita* (Figs. 7A and 9). The diet of *R. agassizii* during summer differed from that of the other groups, but juveniles of this species presented more feeding similarity with *P. extenta* (Figs. 12A, B).

DISCUSSION

The nature of the ingested food depends, first, on the morphology and feeding behavior of the fish, and secondly, on the composition and amount of food available (Pillay, 1952). The flat body and ventral mouth of the skates suggest a benthic feeding habit. Furthermore, rajids skates display mechanisms of oral suction which enables them to feed on benthic invertebrates (Moyle & Cech-Jr., 1988).

TABLE 3

Prey items of P. extenta stomach contents for the total sample (O = occurrence, N = number, M = mass (g) and IRI = Index of Relative Importance).

Prey items	Total			
	% O	% N	% M	% IRI
POLYCHAETA	33.63	2.77	3.09	1.57
ECHINODERMATA	0.30	0.01	< 0.01	< 0.01
MOLLUSCA	0.30	0.01	< 0.01	< 0.01
CRUSTACEA (TOTAL)	**100.00**	**96.89**	**95.16**	**98.31**
unidentified crustaceans	17.72	1.95	0.87	0.40
unidentified decapods	27.03	4.04	0.20	0.91
unidentified shrimps	65.17	9.34	4.20	7.02
post larvae	0.30	0.02	< 0.01	< 0.01
Caridea	60.66	19.71	48.37	32.86
Penaeidea	25.83	1.68	7.77	1.94
unidentified crabs	14.11	1.15	0.50	0.19
megalopa	11.11	1.46	0.40	0.16
Brachyura	63.66	12.95	12.72	13.00
Anomura	1.20	0.04	0.02	< 0.01
Palinura	0.60	0.02	0.17	< 0.01
Amphipoda	84.38	42.75	19.21	41.60
Cumacea	15.32	1.06	0.21	0.16
Isopoda	2.70	0.11	0.01	< 0.01
Mysidacea	4.50	0.25	0.07	0.01
Stomatopoda	8.11	0.35	0.44	0.05
SIPUNCULA	0.30	0.01	< 0.01	< 0.01
FISH	7.51	0.29	1.74	0.12
TOTAL		9,119	77.879 g	12,567
Stomachs analyzed	333			

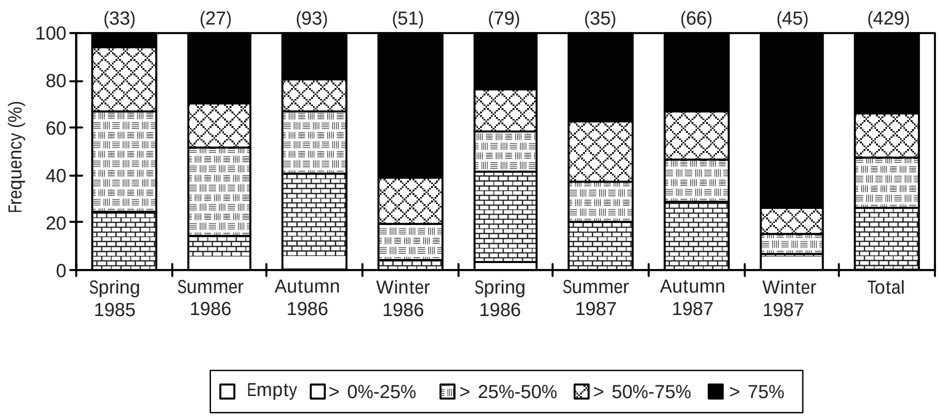

Fig. 4 — Seasonal variation of the degree of stomach fullness in *R. agassizii*.

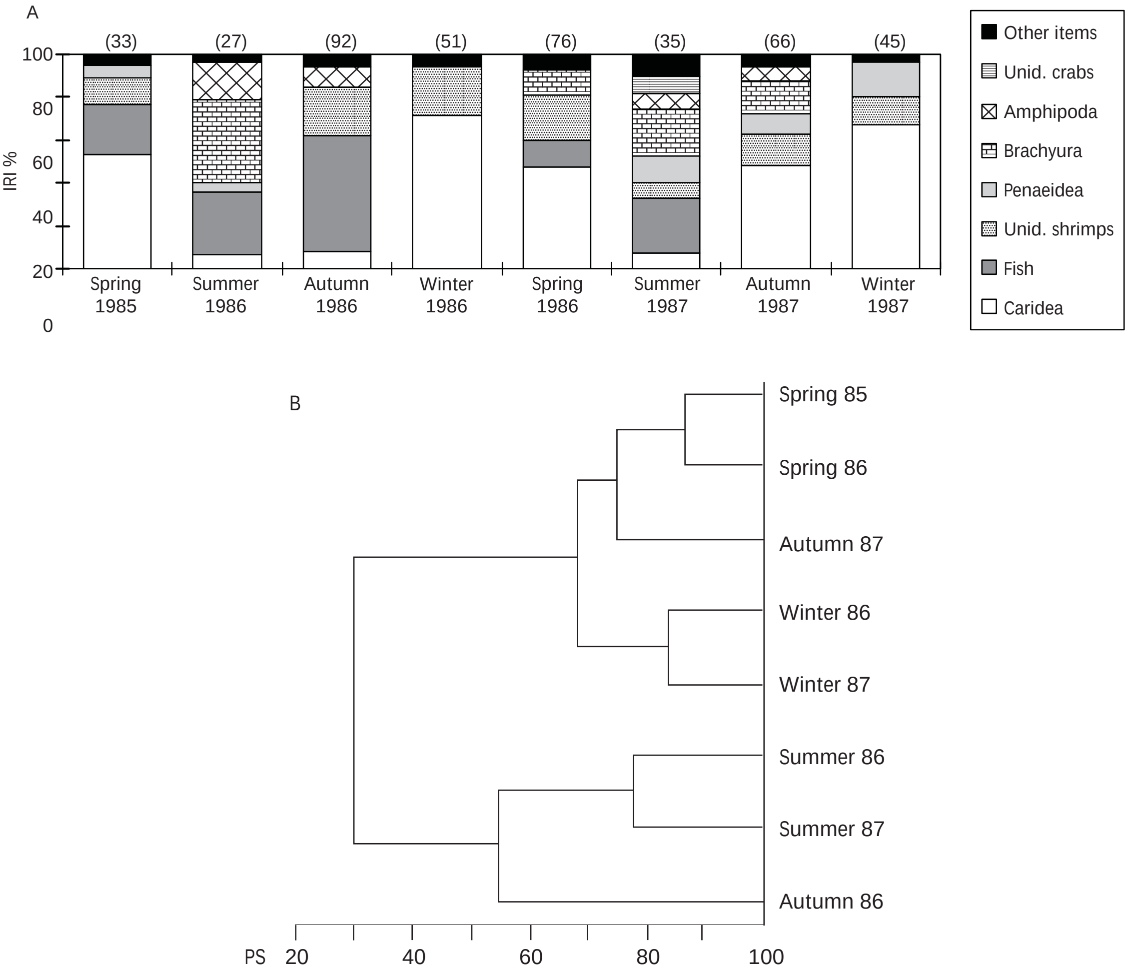

Fig. 5 — A) Seasonal variation of the stomach contents of *R. agassizii* (IRI = Index of Relative Importance; PS = Percentage of Similarity, number in brackets is of stomachs analyzed). **B)** Dendogram showing temporal feeding similarity.

The results demonstrated that *Rioraja agassizii* and *Psammobatis extenta* feed on benthic prey items, mainly crustaceans. The dominance of this group in the diet of many rajids has been observed by many authors (McEachran *et al.*, 1976; Ajayi, 1982; Abd El-Aziz, 1986; Pedersen, 1995).

Other groups such as polychaetes, molluscs and fish also display important roles in the feeding of some skates.

Many studies on the natural feeding of fish draw attention to the large variety of prey in the stomach content and a generalist character has been attributed to the group (Tyler, 1972). However, studies concerning food resource partition in the demersal fish community reveal fish specialization when analysis of the main prey items is made. In spite of the broad food spectrum, a few prey categories predominated in the diet of both skates. The most important prey items for both species were amphipods, carideans and brachyurans, in addition to fish for *R. agassizii*. Polychaete and penaeidean shrimps were also important in some seasons.

Data on prey habitat is a helpful indicator of the predator's feeding habits. The most abundant amphipod consumed by the skates was *A. brevisimulata*, a tubicolous species of the infauna that feeds on organic detritus (Mills, 1967). Most of the shrimps, crabs and fish eaten by the skates are bottom dwellers as well. Despite the pelagic habit of the shrimp *L. serratorbita*, this species displays vertical migration (Jones, 1982) and could have been eaten by the skates near the bottom.

TABLE 4
List of prey items consumed by *R. agassizii*. Frequency of occurrence (%O).

Prey taxon	**%O**	**Spring 85**	**Summer 86**	**Autumn 86**	**Winter 86**	**Spring 86**	**Summer 87**	**Autumn 87**	**Winter 87**
POLYCHAETA	Total	3	4	37	10	20	23	36	
	Aphroditacea				2			9	
	Sigalionidae		4	9		13	9	9	
	Polynoidae					1			
	Onuphidae	3		10					
CRUSTACEA									
Caridea	Total	70	41	50	100	75	37	79	100
	Pasiphaeidae								
	Leptochela sp.	30	7	4	22	12		42	84
	L. serratorbita	58	19	4	98	62	23	73	98
	L. papulata	3	11	1	20	1		12	2
	Processidae			4		1			
	Processa sp.	9	4	24	6	24	14	6	
	P. hemphilli	9		18	12	12		2	
	P. profunda			1	2				
	Ogyrididae								
	Ogyrides sp.	3				7	6		
	O. alphaerostris	3	4			12	11	3	2
	Hipollytidae								2
	Latreutes parvulus	3							
	Alpheidae		4						
	Alpheus sp.			4					
	Automate sp.			1					
	Palaemonidae				2	1			
Penaeidea	Total	36	19	3	37	14	23	23	73
	Solenoceridae	6					3	8	7
	Solenocera sp.								4
	Pleoticus sp.	3							
	Pleoticus muelleri	6						2	
	Mesopenaeus sp.	3							
	Mesopenaeus tropicalis	3	4				3		
	Penaeidae	3	4		20	5			13
	Penaeus sp.			1					
	Parapenaeus americanus				10				
	Trachypenaeus constrictus	9		1	4	7	9	6	40
	Sicyoniidae	3	4	1				2	

TABLE 4 (*Continued*)

Prey taxon	**%O**	**Spring 85**	**Summer 86**	**Autumn 86**	**Winter 86**	**Spring 86**	**Summer 87**	**Autumn 87**	**Winter 87**
	Sicyonia sp.				8	4	11		4
	Sergestidae								
	Acetes sp.	3							
Brachyura	Total	48	63	35	22	47	63	52	22
	Portuninae			4					
	Portunidae	9	30	15	2	17	49	17	2
	Portunus sp.	6		2		3	3	3	
	P. spinicarpus		4		2	20		11	
	Callinectes sp.					1			
	Majidae	12	11			7	11		
	Libinia sp.						3		
	Pisinae sp.						3		
	Leucosiidae	3	4	1	2	1		5	
	Persephona sp.				1	5	3		9
	P. mediterranea				4				
	Cancridae								
	Cancer sp.	3		11		7	6	3	11
	Iliinae					3			
	Parthenopidae								2
	Cryptopodia sp.					1			2
Anomura	Total		4			1	29		
	Porcellanidae						26		
	Paguridae		4			1			
Amphipoda	Total	18	52	47	16	33	46	39	7
	Gammaridea		7	9	4	4	3	3	
	Ampelisca sp.	9	33	21	8	11	26	27	7
	A. brevisimulata	6	19	27	4	17	29	26	
	A. pugetica		7	2		3	3	3	
	Hiperiidae			2					
	Caprellidae			1					
Cumacea	Total			3					
	Diastylidae			1					
Mysidacea	Mysidae				2				
Stomatopoda	Total						29		
	Squila sp.						3		
FISH	Total	27	59	57	14	47	40	24	
	Bothidae			1		1			
	Symphurus sp.	3							
	Ophidiidae	3							

TABLE 4 ***(Continued)***

Prey taxon	%O	Spring 85	Summer 86	Autumn 86	Winter 86	Spring 86	Summer 87	Autumn 87	Winter 87
FISH	Scorpaenidae		4			1			
	Serranidae			1					
	Bathrachoididae								
	Porichthys porosissimus			1					
	Ophichthidae								
	Ophichthus sp.					1			
	Ophidiidae						6		
	Ophidion sp.						3		
	Bregmacerotidae								
	Bregmacerus sp.							2	
	Bregmacerus atlanticus			1					
	Rajidae	3							
Total stomachs analyzed		33	27	92	51	76	35	66	45

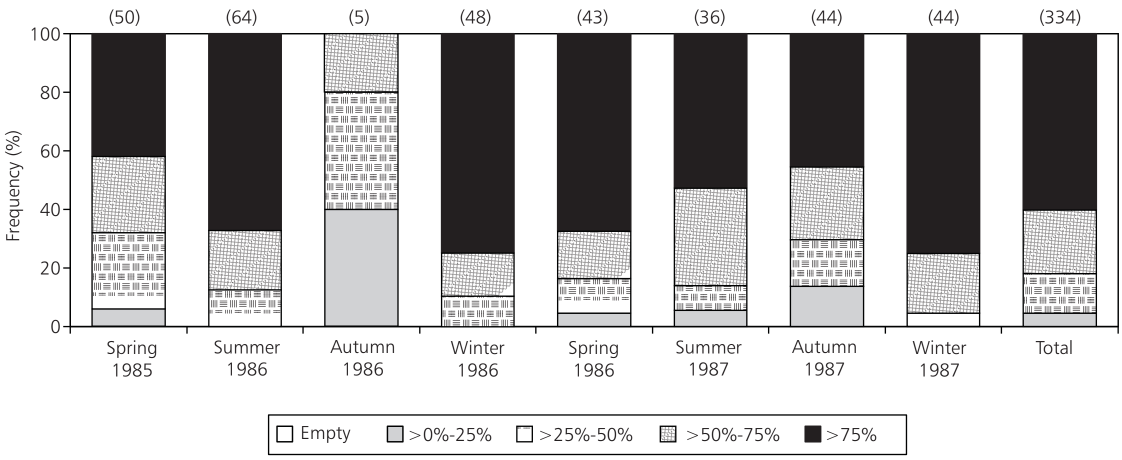

Fig. 6 — Seasonal variation of the degree of stomach fullness in *P. extenta*.

The degree of digestion of the polychaetes in the stomach contents made it difficult to identify this group to specific level, therefore data on this item has certainly been underestimated. Polychaetes are the most important group in the macrofauna on the Ubatuba shelf (Pires-Vanin, 1993) and represent an important resource in the area studied. This prey were more frequently eaten by *P. extenta* than by *R. agassizii*. According to the trophic guilds of polychaetes defined by Fauchald & Jumars (1979), *R. agassizii* consumed mainly carnivore polychaetes (aphroditacea, sigalionids, onuphids and polynoids) whereas *P. extenta* consumed not only carnivores (aphroditacea, sigalionids and onuphids) but surface deposit feeders (terebellids) and subsurface deposit feeders as well (capitelids and maldanids), suggesting that this species digs into the sediment in search for food.

TABLE 5
List of prey items consumed by *P. extenta*. Frequency of occurrence (%O).

Prey taxon	% O	Spring 85	Summer 86	Autumn 86	Winter 86	Spring 86	Summer 87	Autumn 87	Winter 87
POLYCHAETA	Total	32	39	50	13	51	28	68	
	Aphroditacea		27	50	6	16	6	5	
	Capitelidae		2			7	3		
	Maldanidae	2	13		2	7		14	
	Sigalionidae	4				23		7	
	Onuphidae					2			
	Terebellidae					2			
ECHINODERMATA	Total	2							
	Spantagoidea (larvae)	2							
MOLLUSCA	Total	2							
	Pelecypoda	2							
CRUSTACEA									
Caridea	Total	38	47		98	70	11	66	98
	Pasiphaeidae								
	Leptochela sp.	2			46	23		36	91
	L. serratorbita	26	2		98	47	6	61	95
	L. papulata		41		21	2		2	
	Processidae					2			
	Processa sp.	2			8	9		7	2
	P. hemphilli	2			4	19			
	Ogyrididae								
	Ogyrides alphaerostris								2
	Hippolytidae	2					3		
	Latreutes sp.	4							
	Latreutes parvulus	10					3		2
	Alpheidae		5			5			2
	Alpheus amblyonyx	2							
	Hipolitidae								
	Latreutes parvulus								
	Cangronidae		2						
Penaeidea	Total	32	25		29	16	14	9	55
	Solenoceridae	2	3						2
	Pleoticus sp.	4							
	Pleoticus muelleri	16	13			2	11	7	7
	Mesopenaeus sp.								
	Mesopenaeus tropicalis								
	Penaeidae		2		15				7
	Trachypenaeus constrictus					2			2
	Sicyoniidae								9
	Sicyonia sp.				2	5			2
	Sicyonia typica				2				
Brachyura	Total	92	83	100	4	91	89	77	5
	Portunidae	80	41	25		58	81	64	
	Portunus sp.		3			12	3	2	
	P. spinicarpus	18	42	50		40	61	36	
	Callinectes sp.	2				2			
	Majidae	8	13			28	6		
	Leucosiidae		2			2			
	Persephona sp.	2				5			
	P. mediterranea	4				7	3		2
	Micropsis sp.					2			
	Cancridae						3		
	Cancer sp.	2	2			2			
	Parthenopidae		2						
	Pinotheridae								
	Parapinnixa sp.					2			

TABLE 5 (*Continued*)

Prey taxon	O%	Spring 85	Summer 86	Autumn 86	Winter 86	Spring 86	Summer 87	Autumn 87	Winter 87
Anomura	Total	4	2						
	Galatheidae	2							
	Hippidae								
	Emerita sp.		2						
Palinura	Total					2			
	Scylaridae								
	Scylarus sp.					2			
Amphipoda	Total	100	100	100	48	100	94	82	61
	Gammaridea	44	20		4	21	6	5	
	Ampeliscidae								
	Ampelisca sp.	80	75	50	33	84	67	70	32
	A. brevisimulata	82	98	50	31	95	92	68	43
	A. pugetica	30	45		2	40	11	20	
	Hiperiidae	2				2			
	Liljeborgiidae						3		
	Liljeborgia quinquidentata					2	3		
	Phoxocephalidae								
	Heterophoxus videns					2	6		
	Dulichiidae								
	Podocerus sp.	4							
	P. brasiliensis	12							
	Stenothoidae								
	Stenothoe valida	2							
	Hyale media	2							
	Amphilocus sp.	2							
	Caprellidae		2						
Cumacea	Total			25					
Isopoda	*Asellota* sp.		2						
Mysidacea	Total				17				
Stomatopoda	Total	8	27				8		
	Squila sp.	2	2						
FISH	Total	6	5		4	23	8	9	
	Bregmacerotidae					5			
Total Stomachs Analyzed		50	64	4	48	43	36	44	44

The amount and quality of the food ingested by fish are associated with the diel cycle, seasonal variations of the food, fish size, territorial behavior and differential digestion rate (Bowen, 1983).

In relation to feeding activity, *R. agassizii* (Soares *et al*., 1999) and *R. erinacea* (McEachran *et al.*, 1976) feed continuously during a 24-hour cycle. In skates, the detection and capture of a prey involve mainly smell, touch and electroreception associated with feeding behavior (Raschi & Adams, 1988; Berestovskiy, 1989).

As sight seems to be less important for prey detection, the food intake by skates is less dependent on the light/dark cycle. The low frequency of empty stomachs verified in *R. agassizii* and *P. extenta*, as well as in some rajids (Ezzat *et al.*, 1987; Abd El-Aziz, 1986), may be the result of continuous feeding activity.

This behavior may be associated with the high abundance and low energetic value of their main prey items (amphipods, carideans and crabs) which would impel this species to a continuous feeding intake in order to meet their energetic requirements.

The seasonal shift in the diet of teleosts (Blaber & Bulman, 1987) and some rajids (Ajayi, 1982; Abd El-Aziz, 1986) has been attributed to the fluctuation in the abundance of prey items. The structure and dynamics of the benthic macrofauna (Pires-Vanin, 1993) and megafauna (Pires, 1992) on the Ubatuba shelf are associated with the seasonal dynamics of the water masses. Seasonality in the *R. agassizii* and *P. extenta* diets seems to be related to food availability since the distribution of their major prey items is related to seasonal environmental changes. The main brachyurans eaten by the skates were portunids, majids, callapids and leucosiids. The most abundant of them, *Portunus spinicarpus*, occurs on the frontal edge of the cold South Atlantic Coastal Water (SACW), and its distribution is associated with the dynamics of this water mass (Sartor, 1989). According to Matsuura (1986), the intrusion of SACW onto the inner shelf occurs through the bottom layer during late spring and early summer, when a thermocline can be observed. During autumn and winter, this water mass moves back to the edge of the continental shelf and the water column temperature becomes homogeneous. Therefore, *P. spinicarpus* is more abundant on the inner shelf during spring and summer, although juveniles can occur throughout the year.

This would explain the high frequency of portunids in the stomach contents of *R. agassizii* during summer, since this species is distributed throughout the area, occurring both in the shallow and deep parts of the inner shelf. The consumption of brachyuran crabs (mainly portunids) by *P. extenta* over the year, except during winter, may be related to the differential occurrence of this species around the 50 m isobath, where portunid crabs are available throughout the year.

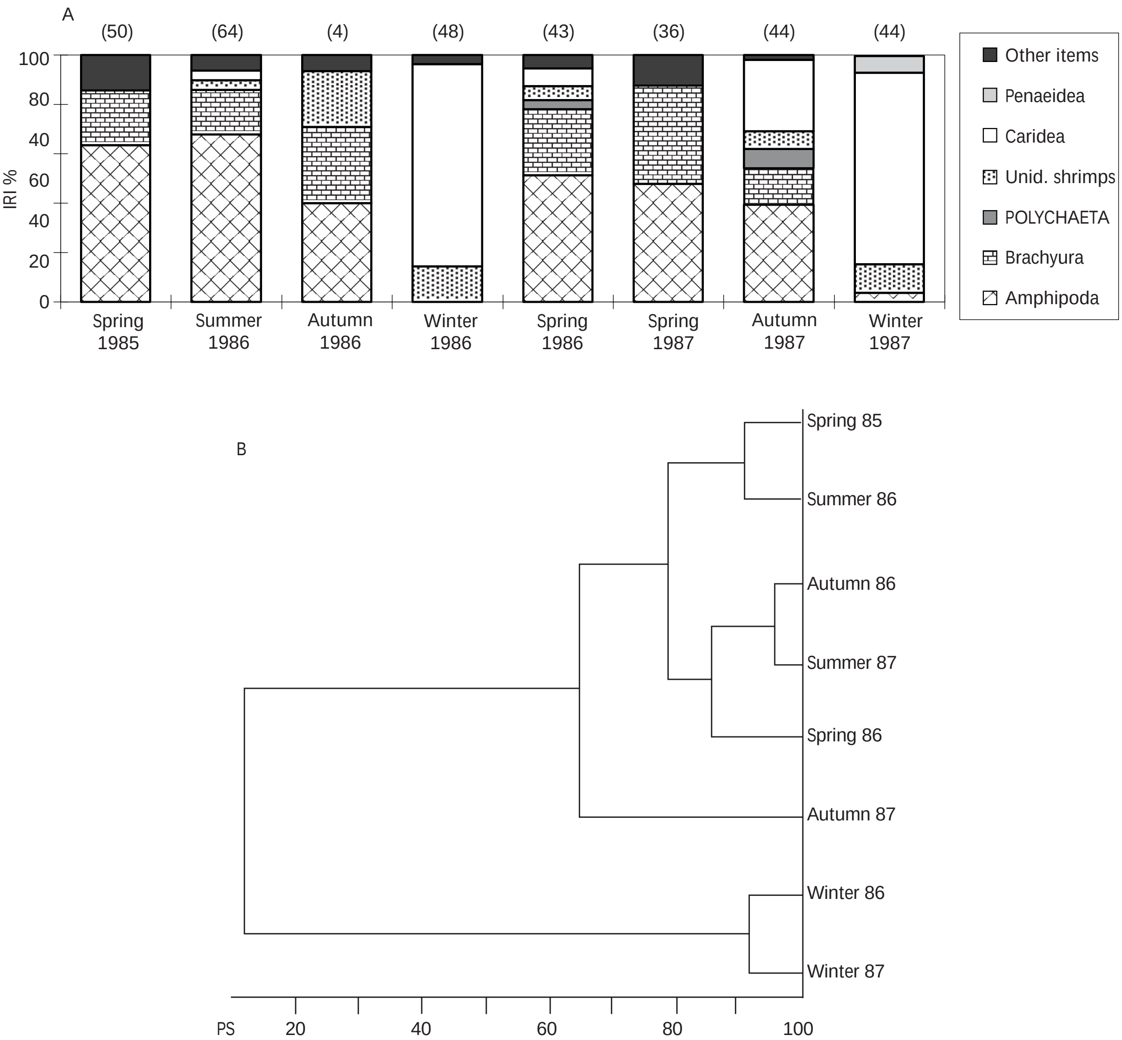

Fig. 7 — A) Seasonal variation of the stomach contents of *P. extenta* (IRI = Index of Relative Importance; PS = Percentage of Similarity, number in brackets is of stomachs analyzed. **B)** Dendogram showing temporal feeding similarity.

The shrimp *L. serratorbita* was the main food for both skates during winter, when the cold South Atlantic Coastal Water (SACW) was further offshore and the inner shelf was occupied by the warm Coastal Water (CW) (Castro Filho *et al.*, 1987). Rios (1994) verified that this shrimp was the major prey for the croaker *Ctenosciaena gracilicirrhus* during winter time, in the same region. The greater abundance of *L. serratorbita* seems to be associated with high water temperatures.

This shrimp was also an important food for *R. agassizii* in both the springs and in autumn 1987, whereas *P. extenta* was feeding on amphipods during these periods.

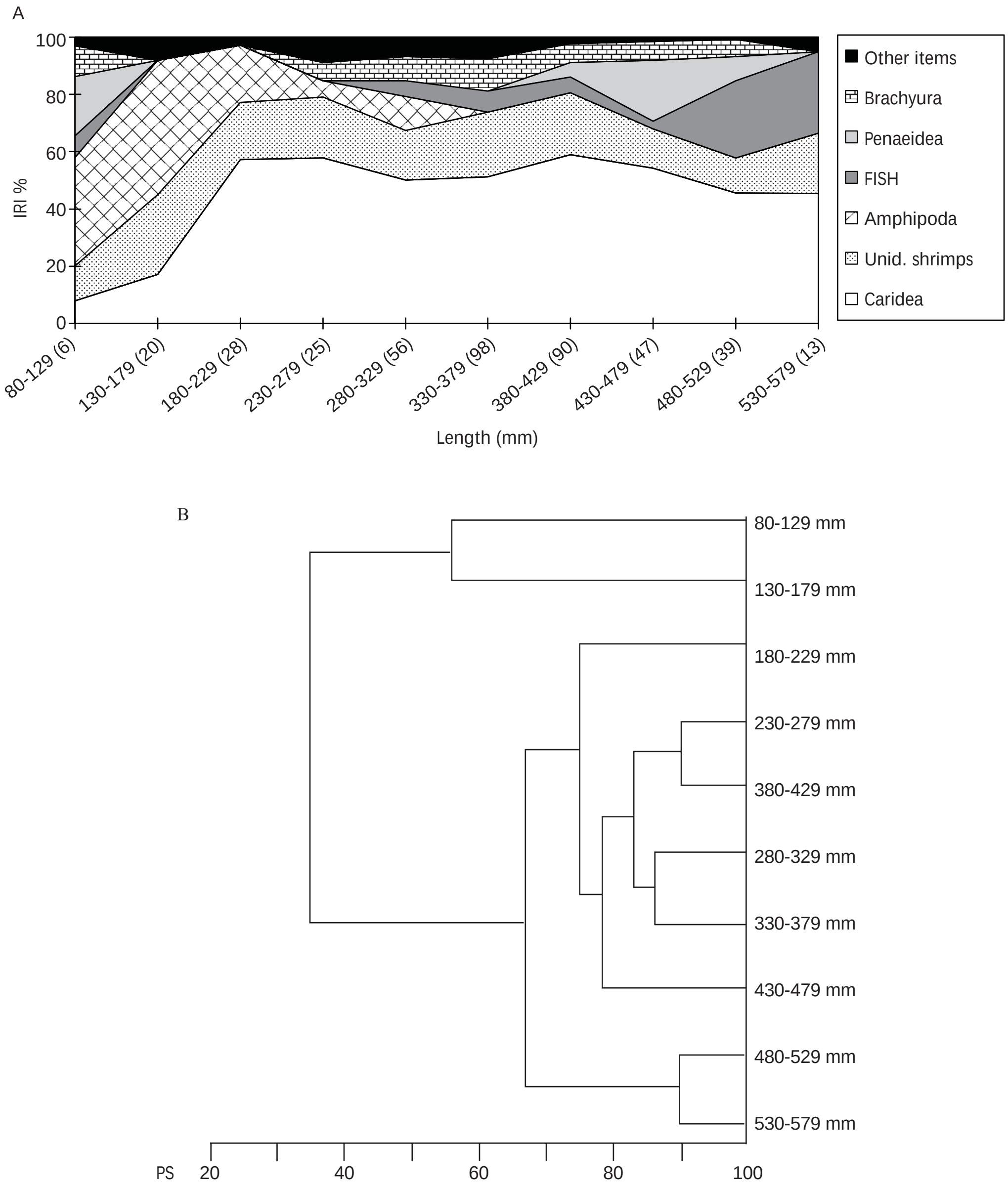

Fig. 8 — A) Ontogenetic variation of the Index of Relative Importance (IRI%) of prey items consumed by *R. agassizii* (PS = Percentage of Similarity, number in brackets is of stomachs analyzed). **B)** Dendogram showing feeding similarity among length classes.

The most representative family of amphipods in the Ubatuba region (Valério-Berardo, 1992) was the ampeliscid, which was the most important prey for *P. extenta* during spring, summer and autumn. During winter, it fed on caridean shrimps and the diet shift must be associated with the decrease of the *Ampelisca brevisimulata* population, which did not occur on the inner shelf during winter due to bottom turbulence caused by winds (Valério-Berardo, 1992), associated with the availability of *L. serratorbita*.

The structure and dynamics of the benthic macrofauna (Pires-Vanin, 1993) and megafauna (Pires, 1992) of the Ubatuba shelf are greatly influenced by the dynamics of the water masses and the seasonal diet shift presented by some brachyuran crabs in the region is related to prey availability (Petti, 1990).

Selectivity in prey size (Werner & Hall, 1974), prey abundance (Griffiths, 1975), availability and mobility (Moyle & Cech-Jr., 1988) are important features for prey selection by predators.

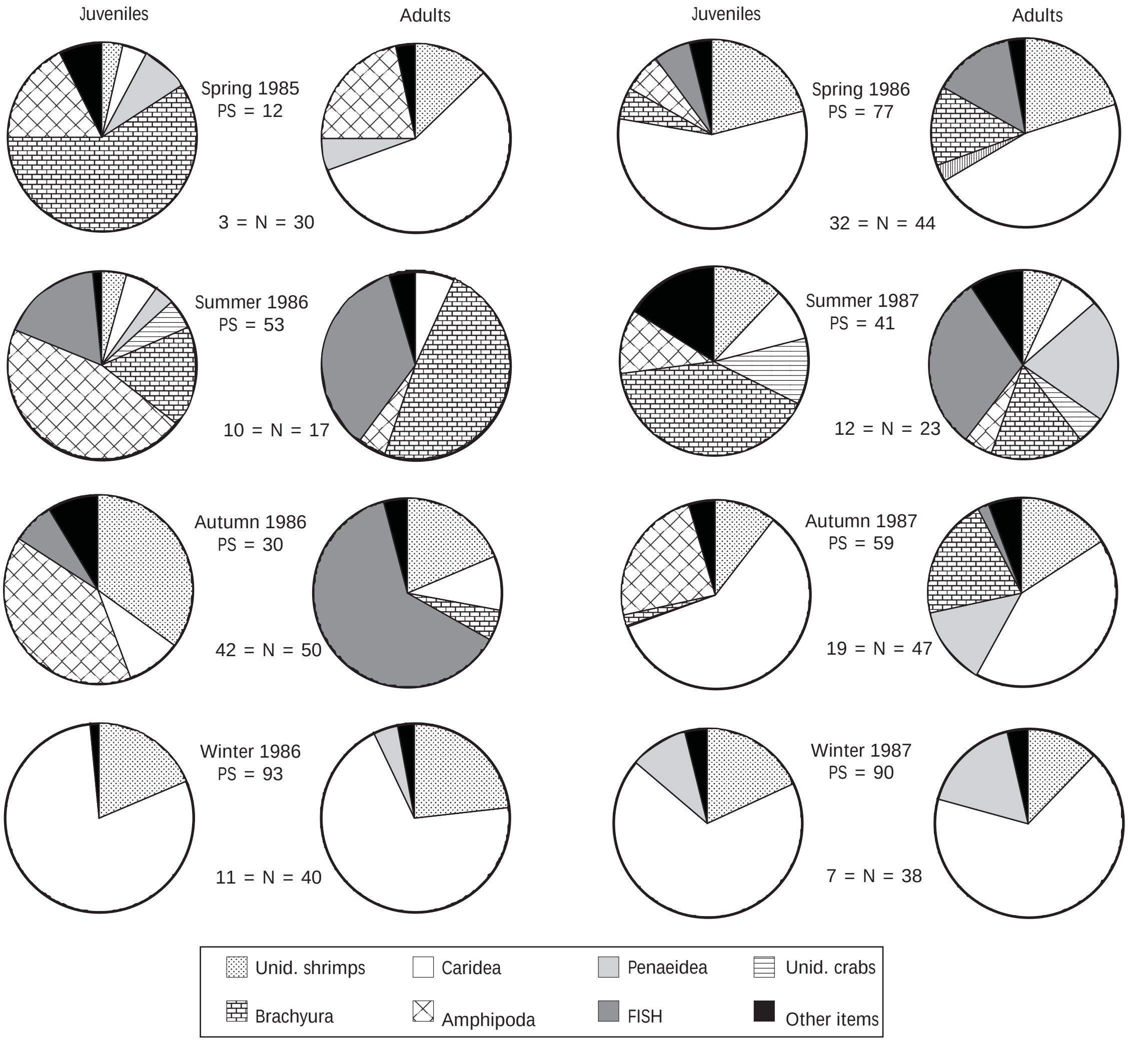

Fig. 9 — Index of Relative Importance (IRI%) of prey items consumed by juveniles and adults of *R. agassizii*, by season (PS = Percentage of Similarity, N = number of stomachs analyzed).

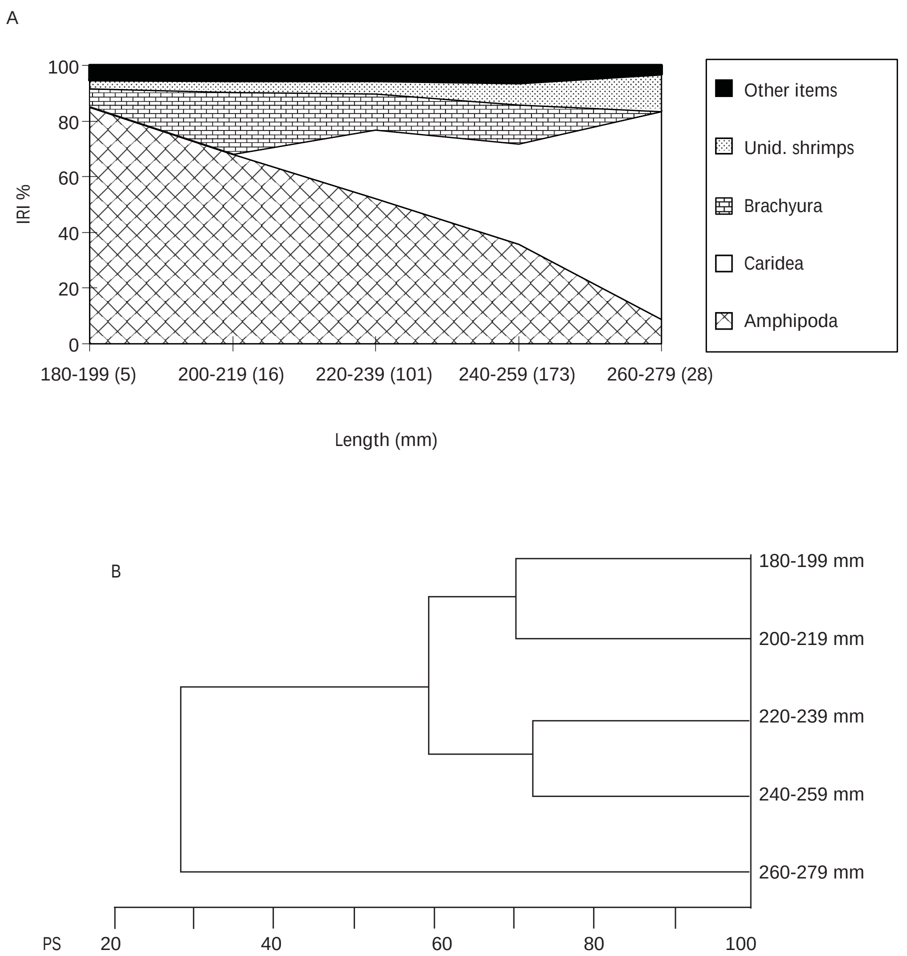

Fig. 10 — A) Ontogenetic variation in the Index of Relative Importance (IRI%) of prey items consumed by *P. extenta* (PS = Percentage of Similarity, number in brackets is of stomachs analyzed). **B)** Dendogram showing feeding similarity among length classes.

Usually, larger fish show greater ability in capturing larger prey items, in order to be able to meet their energetic requirements, feeding on small amounts of larger prey (Keast, 1977).

This strategy provides a better energy budget than does feeding on smaller and more abundant prey (Kerr, 1971).

Smaller specimens of both skates fed mainly on a large quantity of *A. brevisimulata* and *L. serratorbita*, small organisms that grow to 9 mm (Dickinson, 1982) and 4.1 mm, respectively, in length (Williams, 1984). The larger specimens of *R. agassizii*, which are larger than *P. extenta*, fed also on larger prey (fish, crabs and penaeidean shrimps). The diet shift according to the size of the skate and the importance of amphipods for juveniles have been observed by many researchers (McEachran *et al.*, 1976; Du Buit, 1972; Queiroz, 1986).

From results of the cluster analysis associated with the first maturity length, it seems that the diet shift is associated with the size of the skate rather than with its sexual maturity. This pattern was more evident for *R. agassizii*.

At first, *P. glansdisiimilis* seems to display an ontogenetic shift in its diet, changing from amphipods to carideans, as the skate grows. However, as data is on the total sample, regardless of the season, this result relates to the consumption of carideans by adults during winter, when no juveniles were captured.

A diet shift pattern during the life cycle is observed in many teleosts (Keast, 1977; Blaber & Bulman, 1987) as much as in the elasmobranchs (Ajayi, 1982; Sedberry, 1983; Cunha *et al.*, 1986) and constitutes a strategy for intraspecific resource partitioning in fish assemblages. On the whole, amphipods were more important for juveniles and fish for adults of *R. agassizii*, which is similar to the result observed for *Raja clavata*, *R. montagui*, *R. microocellata* (Steven, apud Ajayi, 1982) and *R. miraletus* (Ezzat *et al.*, 1987). Juveniles of these species feed on small crustaceans and adults on fish.

However, seasonality can influence the degree of diet overlap between juveniles and adults, as verified for *R. agassizii* when caridean shrimps seems to be more abundant.

This is closely in line with the statement that higher diet overlaping between age classes occurs during prey abundance peaks (Keast, 1977).

Juveniles and adults of *P. extenta* presented a very similar diet during spring 1985-86 and summer 1987 due to the consumption of amphipods, brachyurans and carideans. In the other seasons, juveniles of this species were absent.

Inter and intraspecific comparisons showed that juveniles of *R. agassizii* presented higher feeding similarity with juveniles of *P. extenta* than with adults of their own species, while diets of juveniles and adults of *P. extenta* were very similar.

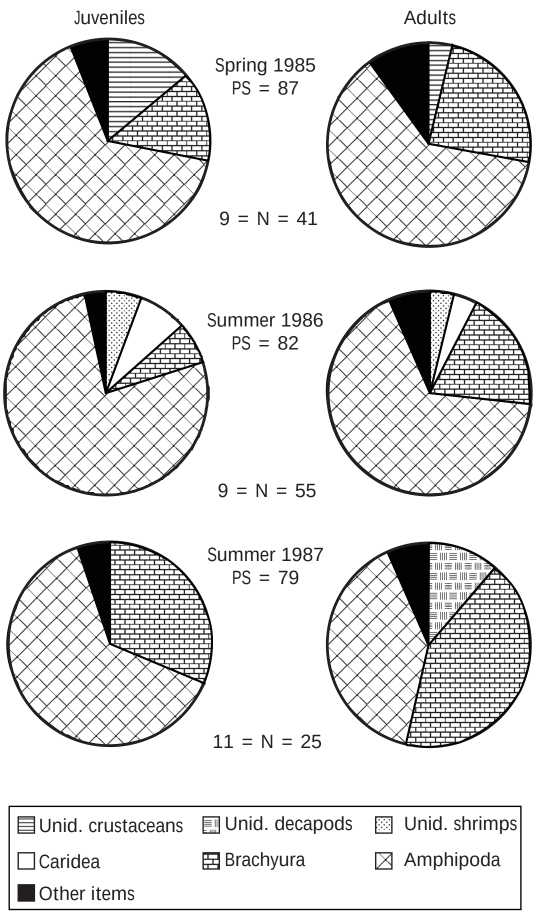

Fig. 11 — Index of Relative Importance (IRI%) of prey items consumed by juveniles and adults of *P. extenta*, by season (PS = Percentage of Similarity, N = number of stomachs analyzed).

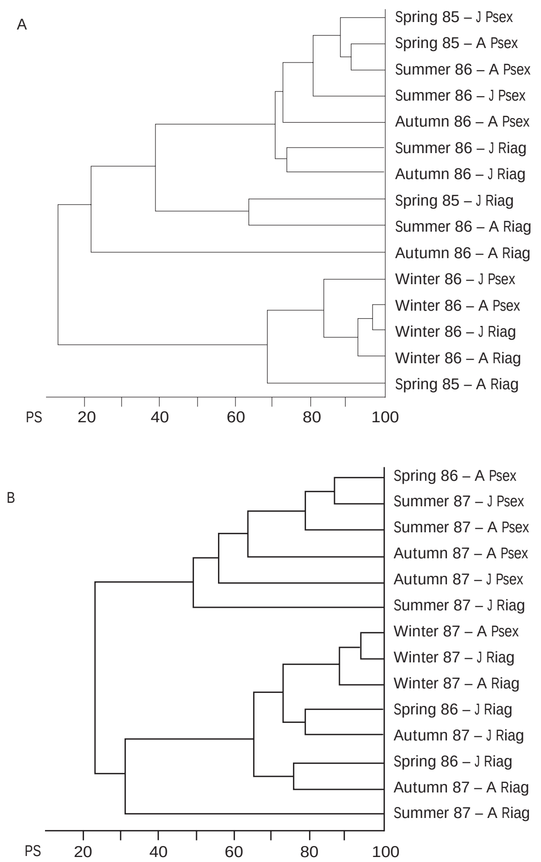

Fig. 12 — Dendogram showing the seasonal feeding similarity among juveniles and adults of *R. agassizii* and *P. extenta* in the first (A) and second (B) year of sampling.

The low intraspecific feeding overlap verified in *R. agassizii* must be related to the greater ability of adults in the consumption of a broader range of prey, due to their size. Larger predators may exploit a broader range of prey size, and food diversity in terms of types of prey or species, may be higher in larger animals (Schoener, 1971).

The absence of juveniles of *P. extenta* during autumn and winter might be associated with the high inter and intraspecific feeding overlap, which may be leading this group to spatial segregation.

The low diet overlap between the two skates during most of the year, is partially to be explained by their differential distribution, since *P. extenta* occurred around the 50 m isobath, while *R. agassizii* occurred in the shallower area.

Higher diet overlap, as well as spatial overlap, occurred during both winters, when the skates fed mainly on *L. serratorbita*.

The exploitation of the same resource in these periods seems to be related to the availability and abundance peaks of this shrimp, that allows food sharing, associated with the decrease in the abundance of amphipods, the main prey of *P. extenta* in the other seasons.

Food sharing in conditions of high abundance of prey has been corroborated by many workers (McEachran *et al.*, 1976; Ross, 1978; Tyler, 1972).

This strategy of resource utilization showed the species's interactions, as well as their abiotic interactions over the year.

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