Feeding strategy and trophic ontogeny in *Epinephelus marginatus* (Serranidae) from Southern Brazil

by

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ABSTRACT. - The stomach contents of 257 specimens of *Epinephelus marginatus* (197-920 mm TL) obtained between February 1999 and December 2003 in Santa Catarina State (South Brazil) were investigated in order to analyse their diet composition and understand the feeding strategy and interspecific diet overlap. *E. marginatus* from south Brazil fed mainly on brachyuran crustaceans, followed respectively by teleost fish and cephalopods. In ontogenetic terms the importance of these groups remains practically the same and the feeding strategy also did not show significant shifts. A generalist strategy with heterogeneous feeding is present in all four size classes and the increase of nutritional requirements during the life cycle is satisfied by predating on larger prey instead of a greater number of preys. Changes in the relative importance of the main prey species and brachyuran prey size-range appear to be an important mechanism to prevent dietary niche overlap in *E. marginatus* from south Brazil.

RÉSUMÉ. - Stratégie alimentaire et variations ontogéniques chez *Epinephelus marginatus* (Serranidae) dans le sud du Brésil.

Les estomacs de 257 *Epinephelus marginatus* (197-920 mm LT) obtenus entre février 1999 et décembre 2003 dans l'État de Santa Catarina (sud du Brésil) ont été étudiés pour en analyser le contenu, pour comprendre la stratégie alimentaire de l'espèce, et pour comparer son alimentation avec celles d'autres espèces. *E. marginatus*, au sud du Brésil, s'alimente surtout de crustacés brachyoures puis, respectivement, de téléostéens et de céphalopodes. Pendant la croissance, l'importance de ces groupes de proies se maintient de façon similaire dans les quatre classes de taille, sans différence significative. La stratégie généraliste, caractérisée par une alimentation hétérogène, se vérifie pour les quatre classes de taille. L'augmentation des besoins alimentaires avec la taille se traduit par une prédation de proies plus grosses et non par une augmentation du nombre de proies. Des changements dans l'importance relative des proies les plus importantes et dans la taille des brachyoures constituent un mécanisme important de prévention de recouvrement de la niche trophique entre classes de taille au sein de la population d'*E. marginatus* du sud du Brésil.

Key words. - Serranidae - *Epinephelus marginatus* - Dusky grouper - ASW - Brazil - Diet - Feeding strategy - Trophic ontogeny.

The dusky grouper, *Epinephelus marginatus* (Lowe, 1834) is a widely distributed species that occurs in the Mediterranean, the Eastern Atlantic from British Isles to South Africa and southwest Indian Ocean in Southern Mozambique (Heemstra and Randall, 1993; Fennessy, 2006; Barreiros, pers. obs.). In Western Atlantic the species is reported from south Bahia State (Brazil) to northern Patagonia (Riguelet and Aramburu, 1960; Heemstra and Randall, 1993; Irigoyen *et al*., 2005; Hostim-Silva *et al*., 2006).

E. marginatus is a coastal, demersal, marine fish, commonly found over irregular rocky bottoms from shallow water to 50 m deep (Figueiredo and Menezes, 1980; Heemstra and Randall, 1993). Some authors suggest that its bathymetric distribution is positively correlated with size (Harmelin and Harmelin-Vivien, 1999; Kara and Derbal, 1999; Machado *et al*., 2003).

The species has an essential role in maintaining the ecological balance of marine rocky shore ecosystems, acting as an important predator in epibenthic and demersal food webs (Goeden, 1982; Parrish, 1987; Renõnes *et al*., 2002). Although the species' ecology has been reasonably documented in the Mediterranean basin, western Atlantic populations are barely beginning to be studied, especially in Brazil. Recent pioneering works include those on their reproductive biology (Bertoncini *et al*., 2003) and habitat use by juveniles (Machado *et al*., 2003) while this study is the first approach ever made to study the feeding ecology of a western Atlantic (in this case Brazilian) population of *E. marginatus*.

The description of the diet composition of *E. marginatus* and the analyses of feeding strategies and ontogenic trophic relations focussed on this study are of central importance to a better understanding on the niches occupied by this preda-

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tor. This information will contribute to the understanding of the ecological role of this species in Brazilian demersal marine communities.

MATERIAL AND METHODS

Sampling

Stomach were obtained from 257 specimens (197 to 920 mm TL) collected in the north-central part of Santa Catarina State coastline, between São Francisco do Sul and Florianópolis, South Brazil (Fig. 1). From February 1999 to November 2001, 85 specimens were collected by spear fishing, at depths between 1 and 15 m. The other 172 specimens were obtained in local fish markets from October 2002 to December 2003 through a collaborative research program (Gerhardinger *et al.*, 2006a). These specimens came from traditional fisheries, that mainly use hand lines, but also deep long-lines and gill nets down to depths of 30 m. Specimens from both sources were kept in ice immediately after capture until evisceration. All stomachs were isolated in the laboratory, cutting the oesophagus near the mouth cavity and the intestine in the area anterior to the pyloric caeca. Stomachs were preserved in 70º alcohol for later examination. Only stomachs with food were studied in order to create the sampling curves, the diet characterization analyses and the trophic ontogeny.

Diet analyses

Stomach contents were extracted and analysed macroscopically. The food items were identified to the lowest possible taxonomic level, considering type and digestion state of each prey item. To evaluate the adequacy of the sample size we used the pooled quadrat method (Pielou, 1966; Hurtubia, 1973; Pierce and Boyle, 1991) where the cumulative numbers of randomly pooled stomachs were plotted against the cumulative trophic diversity. The Shannon Index (Magurran, 1988) was employed to measure the diversity as:

$$H' = -\sum_{i=1}^{n} Pi(\log_e Pi)$$

where Pi is the proportion of individuals of the i^{th} species. Because the cumulative diversity curves are based on random orders of quadrats, 1000 random orders of stomachs for each sample were calculated. The mean curve for each sample was then estimated and plotted. Each diversity curve was considered asymptotic if at least two previous values to the total sample trophic diversity (H') were in the range $H' \pm 0.05H'$ (Alonso *et al.*, 2002).

Traditional indices were employed to analyse the general diet composition (Hyslop, 1980): frequency of occurrence (%F), numerical proportion (%N) and weight proportion (%W) was calculated for each prey item i; $\%F_i$ = (number of stomachs where prey i occurs / number of stomachs with food) x 100; $\%N_i$ = (total number of prey item i / total number of prey items of all taxa) x 100; $\%W_i$ = (total weight of prey item i / total weight of prey items of all taxa) x 100.

The general feeding strategy was analysed following Costello method (1990) with the modifications suggested by Amundsen *et al.* (1996). The diagram generated by this method is based on a two-dimensional representation, in which each prey point is obtained by plotting the frequency of occurrence ($\%F_i$) against prey-specific abundance (P_i), calculated according to the following formula:

$$P_i = \left(\sum S_i / \sum S_{t_i}\right) * 100$$

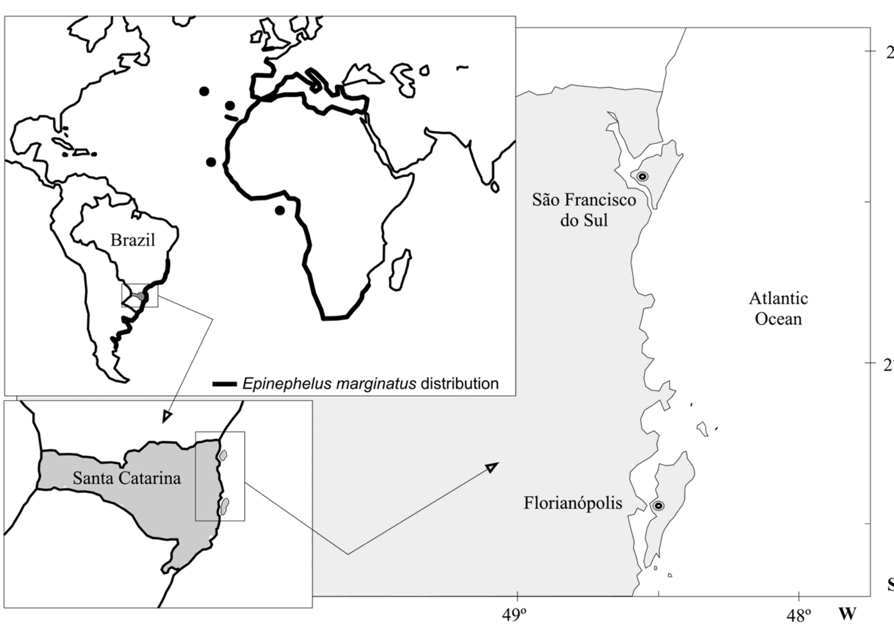

Figure 1. - Geographic distribution of *Epinephelus marginatus* (•) and location of Santa Catarina State's Coast in S Brazil. *[Distribution géographique d'*E. marginatus (•) *et carte du littoral de l'État de Santa Catarina, Sud du Brésil.]*

where Si is the stomach content (weight) of prey item i and S_{t_i} is the total stomach content (weight) of only those predators with prey item i in their stomach. Feeding strategy and prey importance can be determined by examining the distribution of points along the axes and the diagonal of the diagram: (1) feeding strategy is represented in the vertical axis from bottom (generalization) to top (specialization); (2) relationship between feeding strategy and between- or within-phenotype contribution to the niche width is represented in the diagonal from the lower right (high within-phenotype) to upper left (high between-phenotype); (3) prey importance is represented in the diagonal from lower left (rare prey) to upper right (dominant prey).

Trophic ontogeny

Specimens were classified into four size classes (TL in mm): < 400, 401 - 500, 501 - 600 and > 600. The pooled quadrat method mentioned above was applied to these classes in order to generate cumulative trophic diversity curves for evaluation of adequacy of sampling for each size class. The same three traditional indices used above in the general approach (Hyslop, 1980) were also applied in the ontogenetic diet analysis.

The Tokeshi graphical method (Tokeshi, 1991) was used to determine the feeding strategy of different size classes. The feeding strategy is interpreted by the position of data points on the graph, where the mean individual prey diversity (D_I) is plotted against the population prey diversity (D_P). The values of D_I and D_P, based on the Shannon-Wiener diversity index (H), were calculated according to the following formulas:

$$D_I = \left(-\sum P_{ij} \ln P_{ij}\right) / \text{N}$$

$$D_P = -\sum P_i \ln P_i$$

where N = total number of stomachs per size class, P_{ij} = the proportion of prey-type i in the jth stomach, P_i = the proportion of the prey-type i in all size classes. These diversity indexes were calculated using the weight proportions. According to this method, in the graphical interpretation it is considered that: a) size classes with a low value for both population and mean individual prey diversity can be described as specialists; b) size classes with a generalist strategy present high population prey diversity, and either high mean individual prey diversity (where homogeneous and/or similar feeding is apparent) or low mean individual prey diversity (where heterogeneous and/or variable feeding is apparent).

Diet overlap between size classes was evaluated by the Schoener index, R_o (Schoener, 1970):

$$\text{i n} R_o = 1 - 0.5 \times \sum_{i=1}^{i=n} \left| P_{xi} - P_{yi} \right|$$

which, P_{xi} and P_{yi} are the numerical proportion (%N) of item i in the size classes x and y. Following Langton (1982) and Reñones *et al.* (2002), diet overlap was considered low (0-0.29), moderate (0.3-0.59) or high (≥ 0.6).

The homoscedasticity of variances of mean number of prey, mean individual prey weight and mean carapace width in crustaceans (Decapoda: Reptantia) was tested by Kolmogorov-Smirnov test (Zar, 1998). The one-way ANOVA was applied in cases of homoscedastic variances and the Kruskal-Wallis test was used when this was not verified (Zar, 1998).

RESULTS

General diet composition

The stomach analyses produced a vacuity index of 37.7%. Stomach contents of 160 specimens between 197 and 920 mm TL (mean 492 mm; SD = 128) were analysed, revealing 261 prey species belonging to 42 different taxa. The number of stomachs examined appears sufficient to study the general diet of *E. marginatus*, with trophic diversity curve reaching an asymptote at 18 stomachs (Fig. 2).

Brachyuran crustaceans, which were present in 83.75% of stomachs, were the most important prey items of this population of *E. marginatus*. This group represented 61.7% of the total number of ingested prey items and 48.9% of total prey weight (Tab. I). Of the brachyuran crustaceans, the most important species identified was *Cronius ruber*, which was present in 19.38% of stomachs and represented 21.9% of total prey weight. The second most important prey group was composed of teleost fishes (35.0% F, 21.84% N, 38.3% W). The species of this group was few representatives in terms of frequency of occurrence and numerical composition. Despite this some fish species contributed substantially

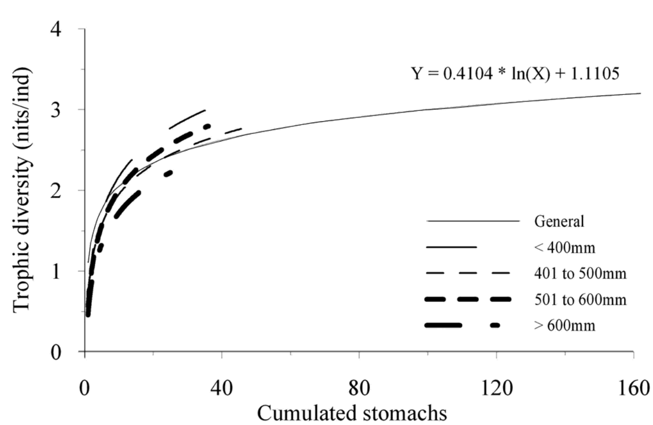

Figure 2. - Cumulative trophic diversity curves of *Epinephelus marginatus* specimens sampled from Santa Catarina. *[Courbes de diversité trophique cumulée pour les individus d'*E. marginatus *échantillonnés à Santa Catarina.]*

Table I. - Diet composition of *Epinephelus marginatus* (n = 160 stomachs with contents), from Santa Catarina. Values of frequency of occurrence (%F), numerical proportion (%N) and weight proportion (%W) for each food item are presented. ni = not identified. *[Composition de l'alimentation d'*E. marginatus *(n = 160 estomacs avec des proies) de Santa Catarina. Les valeurs de fréquence d'occurrence (%F), proportion numérique (%N) et proportion en poids (%W) sont présentées pour chaque proie présente. ni = non identifié.]*

Prey Items	%F	%N	%W
Algae	1.25	0.77	0.02
Crustacea total	92.50	67.05	49.48
Cirripedia ni	2.50	1.53	0.21
Amphipoda ni	0.63	0.38	0.00
Anomura ni	0.63	0.38	0.08
Brachyura total	83.75	61.69	48.96
Calappa angusta	0.63	0.38	0.51
Callinectes danae	0.63	0.38	0.63
Callinectes larvatus	0.63	0.77	1.69
Callinectes sp.	0.63	1.15	0.19
Cronius ruber	19.38	13.79	21.89
Cryptodromiopsis antillensis	0.63	0.38	0.04
Eurypanopeus abbreviatus	1.88	1.15	0.07
Libinia spinosa	0.63	0.77	0.08
Lithadia brasiliensis	1.25	0.77	0.15
Mithraculus forceps	0.63	0.38	0.08
Mithrax sp.	0.63	1.15	0.13
Mithrax hispidus	2.50	1.53	1.05
Menippe nodifrons	1.25	0.77	0.37
Ovalipes trimaculatus	1.88	1.15	0.79
Panopeus austrobesus	9.38	6.13	7.58
Panopeus sp.	1.88	1.15	1.29
Pilumnus sp.	0.63	1.15	0.01
Petrolisthes galathinus	6.88	4.60	0.77
Tetraxanthus rathbunae	0.63	0.38	0.04
Portunidae ni	5.63	4.98	5.61
Xanthidae ni	1.88	1.15	1.30
Brachyura ni	23.75	17.62	4.68
Macrura Natantia	5.00	3.07	0.23
Mollusca total	15.00	9.58	12.14
Bivalvia	5.63	3.45	0.19
Gastropoda	3.75	2.68	0.52
Cephalopoda - *Octopus vulgaris*	5.63	3.45	11.43
Echinodermata Ophiuroidea	1.25	0.77	0.03
Teleostei total	35.00	21.84	38.33
Lycengraulis grossidens	1.88	1.15	0.85
Genidens genidens	0.63	0.38	6.49
Porichthys porosissimus	1.88	1.15	10.22
Hemiramphus brasiliensis	0.63	0.38	0.62
Mugil sp.	0.63	0.38	0.89
Stegastes fuscus	0.63	0.38	3.58
Clupeidae ni	0.63	0.38	0.14
Labrisomidae ni	0.63	0.38	1.15
Blenniidae ni	0.63	0.38	0.04
Gobiidae ni	0.63	0.38	0.59
Teleostei ni	26.25	16.48	13.77

to the diet in terms of weight proportion, such as *Porichthys porosissimus* (10.2% W) and *Genidens genidens* (6.5% W). Similarly, the cephalopod (*Octopus vulgaris*) was important in terms of proportion by weight (11.4% W), despite a low frequency of occurrence and numerical proportion (5.6% F, 3.5% N).

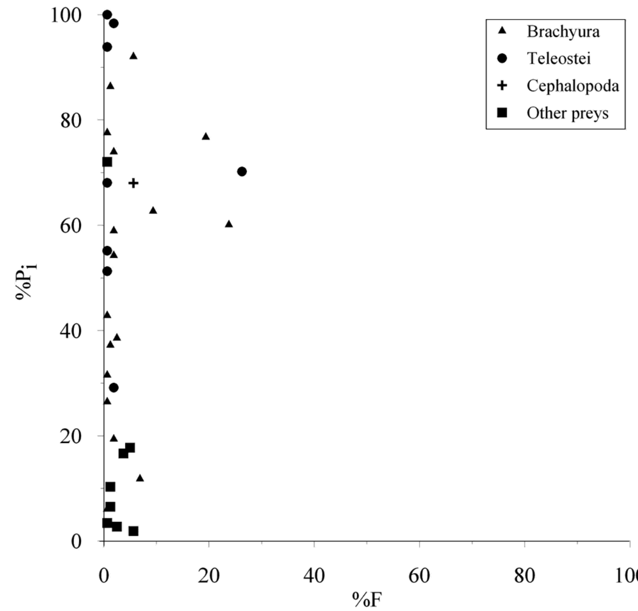

Figure 3. - General feeding strategy plot based on Amundsen *et al*. (1996) for *Epinephelus marginatus* from Santa Catarina (%F_i = frequency of occurrence of prey *i*; %P_i = prey specific abundance). *[Stratégie générale d'alimentation établie d'après Amundsen* et al. *(1996) pour l'échantillonnage d'*E. marginatus *de Santa Catarina.]*

The graphical analyses of feeding strategy demonstrate a high between-phenotype contribution to the niche width, with most of prey points positioned toward the upper left corner of the graph (Fig. 3). This observation indicates that there is specialization on different prey items by individual *E. marginatus*, with each food category consumed by only a limited fraction of the specimens examined. The prey points located in the lower left corner represent rare and less important prey such as cirripeds, amphipods, bivalves, gastropods, ophiuroids and vegetable matter.

Trophic ontogeny

Samples distributed in the four size classes showed asymptotic tendencies between the 23rd (400-500 and > 600 mm) and the 28th (< 400 mm) stomach with food (Fig. 2). This result allowed us to consider the number of stomachs analysed sufficient to undertake an ontogeny analysis. Frequency of occurrence and numerical proportion of prey items were dominated by brachyurans in all four size classes of *E. marginatus* (Tab. II). In terms of weight proportions, fish prey was also important, especially in the first three size classes.

Ontogenetic changes in brachyuran prey importance were not obviously apparent. However, we noted a decrease in the diet importance of fishes and a concomitant increase

Table II. - Diet composition of four *Epinephelus marginatus* size classes, from Santa Catarina. Values of frequency of occurrence (%F), numerical proportion (%N) and weight proportion (%W) for each food item are presented. ni = not identified. *[Composition de l'alimentation pour les quatre classes de taille (LT) d'*E. marginatus *échantillonnés à Santa Catarina. Les valeurs de fréquence d'occurrence (%F), de proportion numérique (%N) et de proportion en poids (%W) sont présentées pour chaque proie. ni = non identifié.]*

Prey items/size groups (TL, mm)	%F				%N				%W			
	< 400	401-500	501-600	> 600	< 400	401-500	501-600	> 600	< 400	401-500	501-600	> 600
Algae	0.00	2.13	2.78	0.00	0.00	1.37	1.79	0.00	0.00	0.04	0.04	0.00
Crustacea total	108.57	108.51	80.56	84.38	69.74	75.34	58.93	68.89	50.49	50.84	43.97	54.77
Cirripedia ni	5.71	2.13	2.78	0.00	2.63	1.37	1.79	0.00	1.02	0.44	0.04	0.00
Amphipoda ni	2.86	0.00	0.00	0.00	1.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Anomura ni	2.86	0.00	0.00	0.00	1.32	0.00	0.00	0.00	1.06	0.00	0.00	0.00
Brachyura total	94.29	100.00	72.22	81.25	63.16	69.86	53.57	66.67	48.33	50.11	43.58	54.67
Calappa angusta	0.00	0.00	0.00	3.13	0.00	0.00	0.00	2.22	0.00	0.00	0.00	1.49
Callinectes danae	0.00	0.00	2.78	0.00	0.00	0.00	1.79	0.00	0.00	0.00	2.20	0.00
Callinectes larvatus	0.00	0.00	2.78	0.00	0.00	0.00	3.57	0.00	0.00	0.00	5.88	0.00
Callinectes sp.	2.86	0.00	0.00	0.00	3.95	0.00	0.00	0.00	2.62	0.00	0.00	0.00
Cronius ruber	14.29	21.28	22.22	25.00	6.58	15.07	19.64	20.00	18.81	20.80	20.58	25.57
Cryptodromiopsis antillensis	2.86	0.00	0.00	0.00	1.32	0.00	0.00	0.00	0.54	0.00	0.00	0.00
Eurypanopeus abbreviatus	8.57	0.00	0.00	0.00	3.95	0.00	0.00	0.00	0.95	0.00	0.00	0.00
Libinia spinosa	0.00	2.13	0.00	0.00	0.00	2.74	0.00	0.00	0.00	0.29	0.00	0.00
Lithadia brasiliensis	5.71	0.00	0.00	0.00	2.63	0.00	0.00	0.00	2.06	0.00	0.00	0.00
Mithraculus forceps	2.86	0.00	0.00	0.00	1.32	0.00	0.00	0.00	1.07	0.00	0.00	0.00
Mithrax sp.	2.86	0.00	0.00	0.00	3.95	0.00	0.00	0.00	1.86	0.00	0.00	0.00
Mithrax hispidus	2.86	6.38	0.00	0.00	1.32	4.11	0.00	0.00	2.48	3.10	0.00	0.00
Menippe nodifrons	2.86	0.00	0.00	0.00	1.32	0.00	0.00	0.00	3.77	0.00	0.00	0.00
Ovalipes trimaculatus	5.71	0.00	0.00	3.13	2.63	0.00	0.00	2.22	2.33	0.00	0.00	1.83
Panopeus austrobesus	0.00	19.15	8.33	9.38	0.00	13.70	5.36	6.67	0.00	7.15	4.75	12.25
Panopeus sp.	0.00	0.00	5.56	3.13	0.00	0.00	3.57	2.22	0.00	0.00	1.24	2.73
Pilumnus sp.	2.86	0.00	0.00	0.00	3.95	0.00	0.00	0.00	0.17	0.00	0.00	0.00
Petrolisthes galathinus	11.43	10.64	2.78	3.13	6.58	6.85	1.79	2.22	5.57	0.84	0.41	0.07
Tetraxanthus rathbunae	0.00	2.13	0.00	0.00	0.00	1.37	0.00	0.00	0.00	0.14	0.00	0.00
Portunidae ni	2.86	6.38	8.33	6.25	1.32	5.48	5.36	11.11	2.44	6.46	3.03	8.00
Xanthidae ni	0.00	4.26	2.78	0.00	0.00	2.74	1.79	0.00	0.00	3.05	1.53	0.00
Brachyura ni	25.71	27.66	16.67	28.13	22.37	17.81	10.71	20.00	3.66	8.27	3.96	2.73
Macrura Natantia	2.86	6.38	5.56	3.13	1.32	4.11	3.57	2.22	0.08	0.28	0.35	0.10
Mollusca total	11.43	14.89	22.22	9.38	5.26	9.59	16.07	6.67	0.73	1.78	9.36	24.23
Bivalvia	5.71	6.38	11.11	0.00	2.63	4.11	7.14	0.00	0.28	0.13	0.46	0.00
Gastropoda	2.86	2.13	5.56	3.13	1.32	1.37	5.36	2.22	0.03	0.34	0.92	0.42
Cephalopoda - *Octopus vulgaris*	2.86	6.38	5.56	6.25	1.32	4.11	3.57	4.44	0.42	1.31	7.97	23.82
Echinodermata - Ophiuroidea	2.86	0.00	2.78	0.00	1.32	0.00	1.79	0.00	0.25	0.00	0.04	0.00
Teleostei total	48.57	21.28	33.33	34.38	23.68	13.70	21.43	24.44	48.53	47.34	46.59	20.99
Lycengraulis grossidens	8.57	0.00	0.00	0.00	3.95	0.00	0.00	0.00	11.92	0.00	0.00	0.00
Genidens genidens	0.00	0.00	2.78	0.00	0.00	0.00	1.79	0.00	0.00	0.00	22.58	0.00
Porichthys porosissimus	0.00	2.13	2.78	3.13	0.00	1.37	1.79	2.22	0.00	22.19	3.61	8.51
Hemiramphus brasiliensis	2.86	0.00	0.00	0.00	1.32	0.00	0.00	0.00	8.78	0.00	0.00	0.00
Mugil sp.	0.00	0.00	2.78	0.00	0.00	0.00	1.79	0.00	0.00	0.00	3.09	0.00
Stegastes fuscus	0.00	2.13	0.00	0.00	0.00	1.37	0.00	0.00	0.00	12.67	0.00	0.00
Clupeidae ni	0.00	0.00	0.00	3.13	0.00	0.00	0.00	2.22	0.00	0.00	0.00	0.40
Labrisomidae ni	0.00	0.00	0.00	3.13	0.00	0.00	0.00	2.22	0.00	0.00	0.00	3.35
Blenniidae ni	2.86	0.00	0.00	0.00	1.32	0.00	0.00	0.00	0.51	0.00	0.00	0.00
Gobiidae ni	0.00	2.13	0.00	0.00	0.00	1.37	0.00	0.00	0.00	2.09	0.00	0.00
Teleostei ni	34.29	14.89	25.00	25.00	17.11	9.59	16.07	17.78	27.31	10.38	17.31	8.73

of cephalopod importance as *E. marginatus* grows. This is most apparent between the two largest size classes and is mainly evidenced by an increase in weight proportion of this prey category (Tab. II). In the size class > 600 mm, cephalopods replaced the fishes and became the second most representative prey item (Fig. 4). The prey items grouped in "other prey" were relatively commonly recorded and numerous, but with a low contribution in terms of weight.

At the species level, the most important prey identified was the brachyuran *C. ruber*, which became increasingly frequent in larger specimens, occurring in 25% of stomachs from the size class > 600 mm. Other important brachyuran,

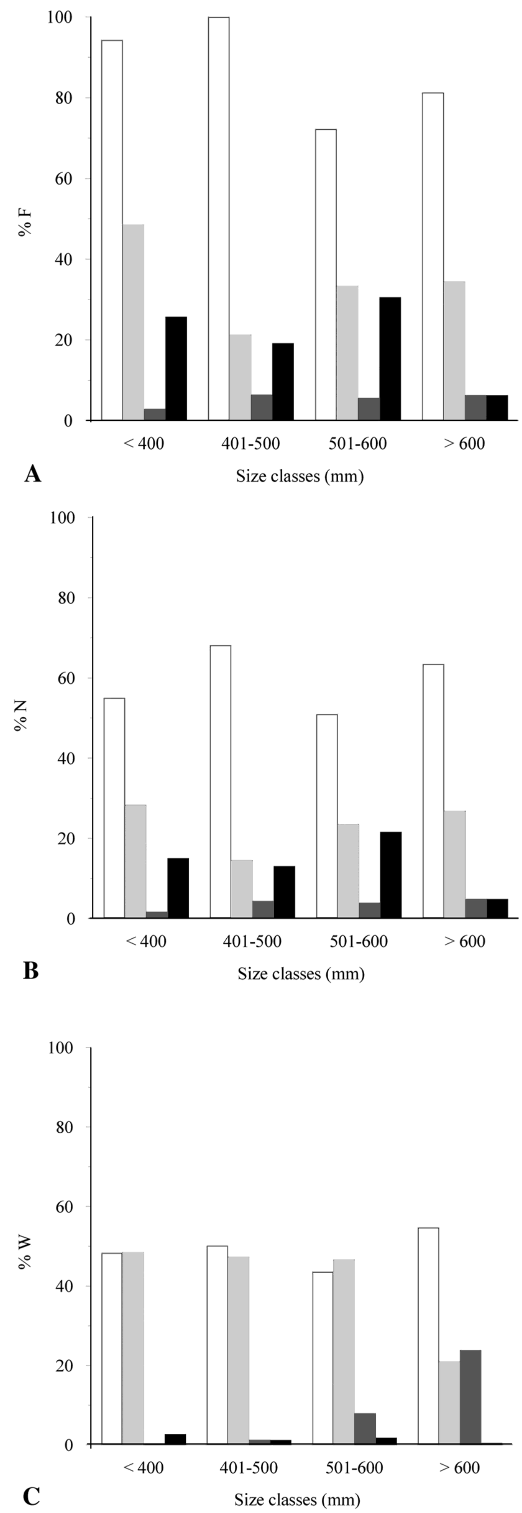

Figure 4. - **A**: Frequency of occurrence (%F); **B**: Numerical proportion (%N); **C**: Weight proportion (%W) of main prey groups in four *Epinephelus marginatus* size classes (TL) from Santa Catarina. *[**A** : Fréquence d'occurrence (%F) ; **B** : Proportion numérique (%N) ; **C** : Proportion en poids (%W) des principales proies pour les quatre classes de taille (LT) d'*E. marginatus *échantillonnés à Santa Catarina.]*

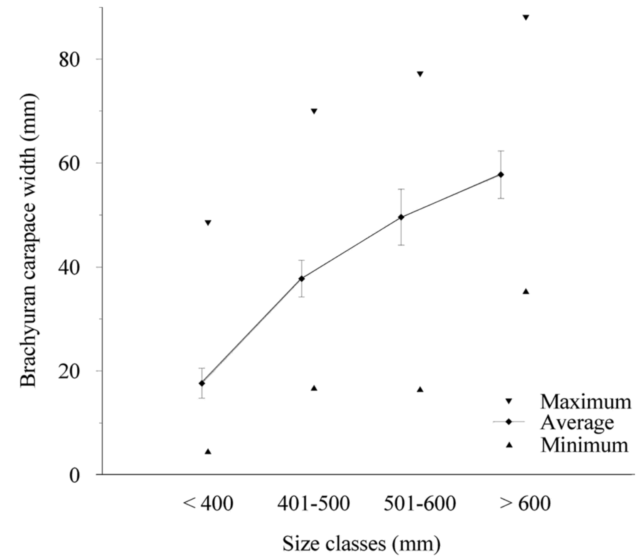

Figure 5. - Average carapace width of brachyurans preyed upon by four *Epinephelus marginatus* size classes (TL) from Santa Catarina (± standard error). *[Largeur moyenne des carapaces des crustacés brachyoures trouvées dans les estomacs des quatre classes de taille (LT) d'*E. marginatus *échantillonnés à Santa Catarina.]*

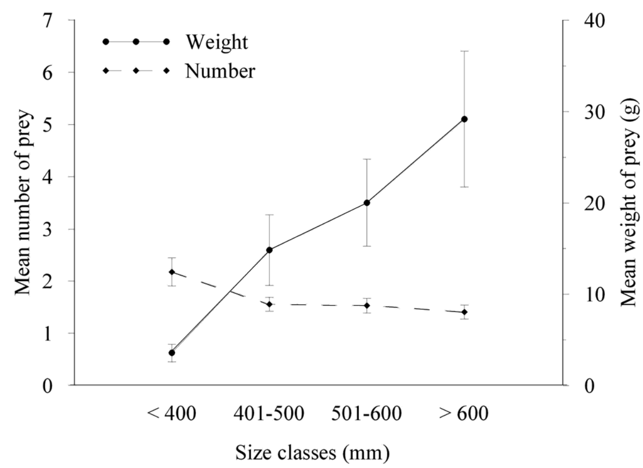

Figure 6. - Prey item average number and average weight in four *Epinephelus marginatus* size classes (TL) from Santa Catarina (± standard error). *[Nombre et poids moyen des proies pour les quatre classes de taille (LT) d'*E. marginatus *échantillonnées à Santa Catarina.]*

Panopeus austrobesus are more frequent in the second size class (401-500 mm), but also with relatively high representation in the last two size classes. However the brachyuran *Petrolisthes galathinus* was more frequently found in stomachs of smaller specimens.

An ontogenetic shift in preyed brachyuran size-range during predator life cycle was evidenced by the significant increase ($F = 29.43$; df (3:75); $p < 0.001$) in the mean carapace width found in the stomachs. Minimum and maximum carapace widths (Fig. 5) show that as *E. marginatus* grows, it predates on larger brachyurans, apparently rejecting small-

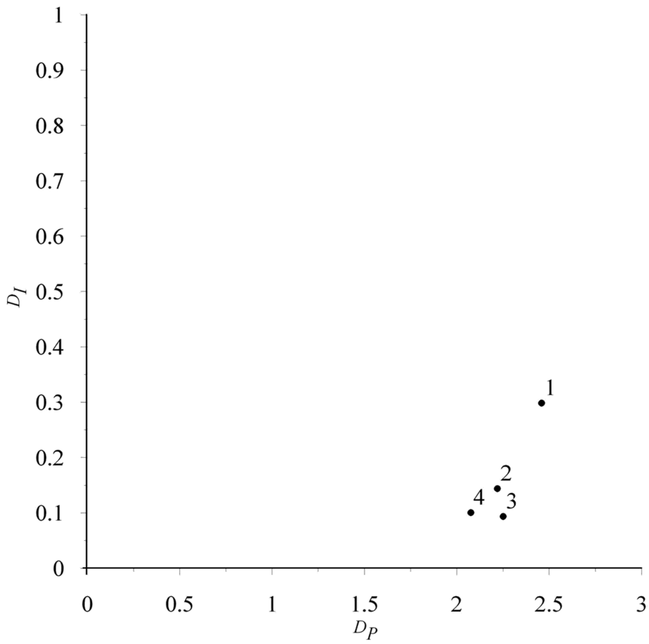

Figure 7. - Tokeshi plot of the feeding strategy of each size class of *Epinephelus marginatus* from Santa Catarina (DI = mean individual prey diversity; DP = population prey diversity. *[Analyse de Tokeshi pour la stratégie alimentaire de chaque classe de taille d'*E. marginatus *de Santa Catarina.]*

Table III. - Schoener's index of diet overlap between the four size classes of *Epinephelus marginatus* from Santa Catarina. *[Index de Schoener de recouvrement de la niche alimentaire pour les quatre classes de taille d'*E. marginatus *échantillonnés à Santa Catarina.]*

Size groups (mm)	< 400	401-500	501-600
401-500	0.51		
501-600	0.46	0.66	
> 600	0.53	0.66	0.71

er individuals. On the other hand, smaller *E. marginatus* are limited to preying on smaller brachyurans.

The Kruskal-Wallis test revealed non-significant relationships ($H_{(3, 150)} = 7.01$; $p = 0.07$) between *E. marginatus* size and number of prey captured. However, there was a significant increase in mean prey weight ($H_{(3, 250)} = 41.65$; $p < 0.01$) with size. Between the smallest (< 400 mm) and the largest (> 600 mm) size class, mean prey weight increased from 3.56 to 28.17 g per stomach (Fig. 6).

The Tokeshi graphical method revealed that there are no ontogenetic differences in the feeding strategy. All four size classes demonstrate a generalist strategy with heterogeneous feeding (Fig. 7). Despite this method suggesting that the same strategy is employed by different size class specimens, Schoener index of diet overlap demonstrated a distinct niche being occupied by the smaller size class (< 400 mm TL), and also showed the largest diet overlap between other size classes ($R_o \geq 0.66$) (Tab. III).

Closer examination of prey items per size class showed that smaller specimens (TL < 400 mm) had the wider niche, consuming 61.9% of all identified taxa, while the three other size classes only consumed 45.2%, 47.6% and 35.7% respectively. In addition, of the 26 taxa preyed upon by smaller specimens (TL < 400 mm), 13 were absent from the stomachs of the other size classes.

DISCUSSION

The diet composition of *Epinephelus marginatus* from Southern Brazil described in this work confirms the important ecological role of this predator to coastal demersal ecosystems of this region. The species showed a wide niche spectrum, within which individuals specialize in capturing different prey types. In fact the specialization of same individuals to prey upon benthic organisms has been shown in recent papers that report *E. marginatus* as followers of snake eels and octopus (Gerhardinger *et al.*, 2006b; Machado and Barreiros, in press).

E. marginatus from Southern Brazil have a diet based on brachyuran crustaceans, teleost fish and cephalopods. Studies from the Mediterranean (Neill, 1967; Bruslé, 1985; Derbal and Kara, 1996; Harmelin and Harmelin-Vivien, 1999; Reñones *et al.*, 2002; Linde *et al.*, 2004), the Azores (Azevedo *et al.*, 1995; Barreiros and Santos, 1998) and South Africa (Smale, 1986) also found these taxa to be important in diets. In Southern Brazil, rare items, such as cirripeds, amphipods, bivalves, gastropods, ophiuroids and vegetable matter were also found in stomachs. These were probably ingested accidentally, possibly being entangled between brachyuran legs, as suggested by Linde *et al.* (2004), or were adhered to octopus suckers, or even by being sucked up during the capture of epibenthic prey.

As shown in studies undertaken in the Mediterranean with samples of size-ranges similar to our study (Derbal and Kara 1996; Linde *et al.*, 2004), brachyuran decapods were more frequently preyed upon followed, respectively, by teleost fish and cephalopods. However, in our South Brazil population brachyurans were more representative reducing the importance of teleosts and cephalopods. The high level of brachyuran representativity (%F; %N; %W) observed in Brazil when compared with other populations (Derbal and Kara, 1996; Barreiros and Santos 1998; Harmelin and Harmelin-Vivien, 1999; Reñones *et al.*, 2002; Linde *et al.*, 2004) may reflect differences in the prey's abundance. Thus, the generalist character of *E. marginatus* diet could be a key factor to this adaptability throughout its wide geographic range.

In spite of known habitat changes carried out by *E. marginatus* in South Brazil (Machado *et al.*, 2003), there were only few ontogenetic changes in their feeding ecology. We observed for example that, as dusky groupers grow, they satisfy their nutritional requirements, by capturing larger preys and not through the ingestion of a greater number of preys. This result agrees with the observations of Linde *et al.* (2004) in a study of a Mediterranean population.

Contrary to other studies with different populations (Derbal and Kara, 1996; Barreiros and Santos 1998; Harmelin and Harmelin-Vivien, 1999; Reñones *et al.*, 2002; Linde *et al.*, 2004) there were not relevant changes in the proportions (%F; %N; %W) of dominant prey groups, with brachyurans being the most representative, followed respectively by teleost and cephalopods, during eventually their entire life cycle.

The ontogenetic change in the feeding strategy observed by Linde *et al.* (2004) was not verified in our results and the generalist strategy was present all the time. The registered increase of cephalopods weight proportion in largest specimens could be characterized as a specialization in the capture of octopuses, but it is not verified by the Tokeshi method and the values cited in previous studies were never reached (Derbal and Kara, 1996; Barreiros and Santos 1998; Harmelin and Harmelin-Vivien, 1999; Reñones *et al.*, 2002; Linde *et al.*, 2004).

In terms of niche, an important difference was observed between size classes. Due the consumption of different prey species, the smaller specimens (TL < 400 mm) appear in a distinguished niche, while the others share similar resources. This niche differentiation can be correlated with the habitat change cited by Machado *et al.* (2003), where juveniles and pre-adults *E. marginatus* from South Brazil remain in shallow rocky coastal areas until approximately the first maturation (47 cm; see Bertoncini *et al.*, 2003), when they disperse to occupy the typical adults habitat. Thus, the influence of this relevant habitat change appears as one of the most important mechanisms to prevent intra-specific niche overlap in the studied predator population.

In conclusion, this study has shown that *E. marginatus* is an important rocky shore predator whose diet in South Brazil comes mainly from benthic food sources and less neuston, without ontogenetic changes in the feeding strategy or dominant prey group during the entire life cycle. The main ontogenetic differences occur at prey species level probably as a function of habitat changes.

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