ANALYSIS OF TROPHIC ONTOGENY IN *EPINEPHELUS MARGINATUS* (SERRANIDAE)

by

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ABSTRACT. - Ontogenetic diet shifts of the dusky grouper, *Epinephelus marginatus* (Lowe, 1834), in the Balearic Islands (western Mediterranea) were studied using the stomach contents of 203 specimens ranging between 134 to 1056 mm total length. A total of 64.5% of the examined stomachs contained food. Diet composition, characteristics of ingested preys (average number and average weight), feeding strategy and niche overlap in relation to fish size were evaluated. There were statistical differences (Redundancy Analysis) for the proportions of the main food categories related to size. A high proportion of crustaceans was characteristic of the diet of smaller fishes, while the proportion of cephalopods increased for the larger sizes. Nevertheless, this pattern only represented a low percentage (5.5%) of the variation in diet composition. For growth, the dusky grouper increased the ingestion of larger preys rather than catch a greater number of preys. In proportion to a larger mouth size there was an increased ability to catch voluminous cephalopods and, as a result, the grouper developed from a generalist to a more specialised type of feeding. Shifts in diet composition could be related to behavioural changes. When size is a good predictor of diet composition, the function derived from Redundancy Analysis could be used to estimate the representative diet of a stock in relation to its size structure.

RÉSUMÉ. - Analyse de l'alimentation en fonction de la taille chez *Epinephelus marginatus* (Serranidae).

Les changements ontogénétiques du régime alimentaire du mérou brun, *Epinephelus marginatus* (Lowe, 1834), dans les îles Baléares (ouest Méditerranée) ont été étudiés par l'analyse des contenus stomacaux de 203 spécimens, de longueur totale comprise entre 134 à 1056 mm. Au total, 64,5% des estomacs contenaient des aliments. La composition du régime alimentaire, les caractéristiques des proies (nombre et poids moyens) ainsi que la stratégie alimentaire et la nature de la niche trophique en fonction de la taille ont été évaluées. Les principales catégories de proies diffèrent statistiquement (Analyse de Redondance) en fonction de la taille des individus. Le prédominance des crustacés caractérise le régime des plus petits individus, tandis que la proportion de céphalopodes est plus importante pour les mérous de plus grandes tailles. Cependant, cette remarque concerne seulement un faible pourcentage (5,5%) de la variation dans la composition du régime alimentaire. Les besoins énergétiques pour la croissance du mérou brun impliquent l'accroissement de la taille des proies, et non l'augmentation de leur nombre. L'aptitude à capturer des proies de grande taille (céphalopodes) est proportionnelle à la taille de la bouche, par conséquent, le régime alimentaire du mérou, généraliste au début, évolue vers un type plus spécialisé avec le temps. Les changements alimentaires pourraient être liés à des modifications comportementales. Lorsque la taille est un bon indicateur de la composition du régime, la fonction dérivée de l'Analyse de Redondance peut être utilisée pour estimer le régime alimentaire représentatif d'un stock en fonction de la structure de taille.

Key words. - Serranidae - *Epinephelus marginatus* - MED - Balearic Islands - Trophic ontogeny - Diet - Mouth size - Ecological modelling.

The dusky grouper *Epinephelus marginatus* (Lowe, 1834) lives in warm and temperate waters. It is present in the Mediterranean Sea and in the Atlantic Ocean (Ringuelet and Aramburu, 1960; Heemstra, 1991). This particular species inhabits the irregular rocky bottoms, which offer many shelters (e.g., caves, holes, tunnels and crevices) along the continental shelf, but preferentially from the shore to a depth of 50 m in the Mediterranean Sea (Chauvet, 1991).

In Balearic waters, *E. marginatus* is a target species for the long-line artisanal fishery and game fishing (spearfishing). The species is classified as being at lower risk on the International Union for Conservation of Nature world red list (IUCN, 1994) and is in the subcategory of species that are close to being qualified as vulnerable. In the Balearic Islands, despite the relative abundance of juveniles, *E. marginatus* is still threatened because the abundance of the large specimens has decreased considerably in the last fifty years due to fishing pressure (Mayol *et al*., 2000). The high efficiency of spearfishing in the capture of certain littoral species has led to the development of regulation measures by the regional government for game fishing catches. These measures limit the catch for fisherman to 5 kg/person/day and establish a minimum catch size for certain specified species (for the dusky grouper specifically a total length of 45 cm has been established). Despite the present unbalanced condition of the demographic structure of *E. marginatus* populations caused by fishing pressure, this sedentary species has shown a positive response in the protected marine areas of the Balearic Islands (Coll *et al*., 1999; Reñones *et al*., 1999) and other sites in the Mediterranean Sea (Zabala *et al*., 1997a).

Fishery research is being developed to allow the elabora-

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tion of management plans in an ecosystem context (Pauly *et al.*, 2000). This implies the construction of models that can describe the biomass flows between the different pools of exploited ecosystems. These models can be used to explore the ecological implications of specific fishery management plans.

Dietary studies provide us with information about the trophic interactions between species and constitute basic knowledge for the application of ecosystem models that represent the food webs of natural environments. However, large fishes frequently change their feeding habits as they grow, and a single species may contain individuals that have different ecological roles. Analyses of trophic ontogeny can detect dietary shifts related to predator size, and this information has to be incorporated into ecological modelling in order to obtain more realistic representations of what is happening in nature (Stoner and Livingston, 1984).

Several studies have focused on the food habits of *E. marginatus* in the Mediterranean Sea (Derbal and Kara, 1996; Reñones *et al.*, 2002) and in the Atlantic Ocean (Smale, 1986; Azevedo *et al.*, 1995, for juvenile fishes; Barreiros and Santos, 1998, for adult specimens). In these studies, differences in diet composition between size classes have been attributed qualitatively to fish size. However, predator size is only one of the factors that can determine the total abundance of the prey in gut contents, and other factors, such as prey availability, competition between predators and the digestibility of preys, could influence diet composition. Nevertheless, the actual percentage of the total variation in diet composition that could be related to fish size is not known.

In the present study, we investigated trophic ontogeny quantitatively in *E. marginatus* by testing and quantifying the effect of size on diet composition, and analysing complementary aspects of food preferences, in order to clarify the importance of fish size on feeding habits. We also propose the use of a function to predict the representative diet of a stock in relation to its size structure.

MATERIAL AND METHODS

Stomach contents were obtained from specimens captured during game fishing competitions held on the islands of Majorca and Minorca (Fig. 1), from 1998 to 2000 in summer and autumn. A total of 157 individuals whose size ranged from 285 to 1056 mm total length were collected from the competitions. In conjunction with the competitions, 46 juveniles (134 to 504 mm total length) were captured by speargun or trammel nets. Captures were carried out between depths of 0 and 45 m.

The fishes were measured (± 1 mm) and their stomachs were dissected, conserved on ice during their transport to the laboratory, and subsequently frozen. In the laboratory, the stomach contents were extracted and analysed. The preys were identified to the lowest possible taxon and weighed (± 0.01 and ± 0.001 g). The hard parts of the more digested preys were measured using an ocular micrometer or a calliper, according to their size. Crustacean fragments and cephalopod beaks, as well as the otoliths and jawbones of fish preys were identified by comparing them with material from a reference collection, deposited in the Port d'Andratx aquaculture center (Majorca, Spain).

Variations in gravimetric measurements resulting from differential digestion were minimized by the use of regression equations (Macpherson, 1978) both from fresh specimens captured in Majorca waters (see appendix) and the scientific literature (Clarke, 1986; Petrarkis and Stergiou, 1995; Dulčić and Kraljevic, 1996; Gordoa and Molí, 1997; Merella *et al.*, 1997; Froese and Pauly, 1998; Quetglas *et al.*, 1998). Due to the difficulty in obtaining some decapod species, the less digested decapods found in the stomachs were included for the regression analysis in these cases.

The estimated weight of food consumption seemed to be adequate for the dusky grouper diet because the majority of food categories consumed by this fish possessed hard body parts that resisted digestion and therefore did not lead to overemphasis of any resistant prey. Moreover, these hard pieces allowed good regression equations to be obtained. The utilisation of the real weight undervalues the importance of the cephalopods, which are usually very metabolised.

Diet composition was analysed by employing the following traditional indices (Hyslop, 1980): *frequency of occur-*

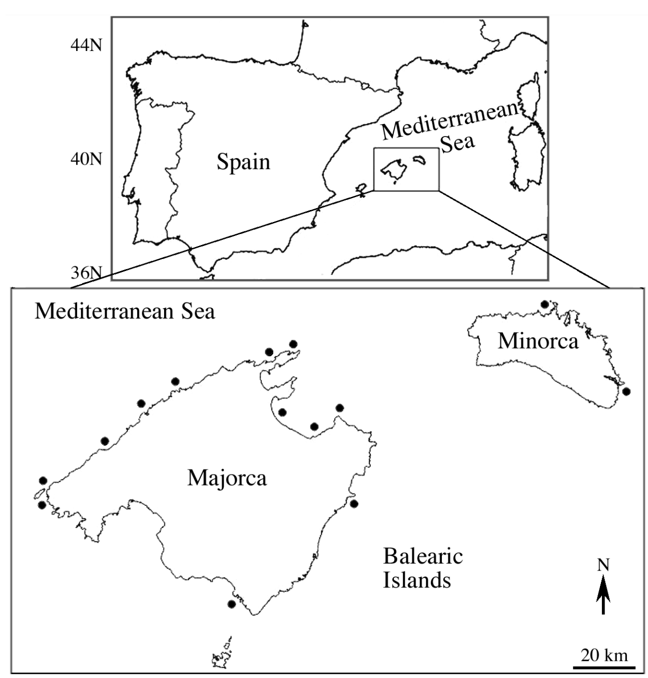

Figure 1. - Location of the sampling stations (●) in the Balearic Islands.

rence (%F = [number of stomachs with determinate prey taxon / number of stomachs containing food] x 100); *numerical composition* (%N = [total number of determinate prey taxon / total number of individuals of all food items] x 100), and *weight composition* (%W = [total weight of determinate prey taxon / total weight of all food items] x 100).

Differences in the weight proportion of the three main groups (decapods, fishes and molluscs) as a function of size were evaluated statistically by applying a Redundancy Analysis (RDA), after measuring the length of the gradient by Detrented Correspondence Analysis (DCA). This method allows the existence of any correlation between two sets of variables (explanatory and response variables) to be analysed. The RDA could be interpreted as the multivariate generalisation of regression analysis. The test of the significance of the ordination axis was carried out by Monte Carlo permutation based on 999 iterations.

One-way ANOVAs were calculated to detect size related variations in the mean number and the mean weight of prey items. Due to the low number of preys per stomach obtained, fishes were placed into four size classes (< 41 cm, 41-50 cm, 51-60 cm, > 60 cm, with n = 29, 38, 42 and 22, respectively) taking into account that the classes were well represented. Before running the ANOVAs the assumptions of normality of data and homogeneity of variance were tested using the Kolmogorov-Smirnov (Lilliefors probability) and Cochram's tests, respectively. When these assumptions were not met data were log transformed, and the assumptions were tested again. One-way ANOVA was performed despite the fact that the variables did not meet the prerequisites to perform the analysis, but in these cases a more conservative significance level (99%, $p < 0.01$) was adopted. The post-hoc Tukey's test was performed to determine pair-wise differences.

The feeding strategy for the size classes was determined following the graphical method described by Tokeshi (1991). In this method, the mean feeding diversity (D_I) is plotted against the population feeding diversity (D_P) and the feeding strategy is interpreted from the position of the data points on the graph (Fig. 4A). The values of D_I and D_P, based on the Shannon-Wiener diversity index, H, were calculated in the following manner:

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

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

where N = total number of fish of a determined size class, P_{ij} = the proportion of prey-type i in the jth fish, P_i = the proportion of the prey-type i in the whole size class. These diversity indexes were calculated by using the weight proportions.

A multivariate cluster analysis was performed in order to determine the similarity in the diets between the size classes, based on the Bray-Curtis distance applied to the abundance matrix and using the Unweighted Pair-Group Method (Arithmetic Average), UPGMA, as the linking algorithm. The Bray-Curtis analysis was chosen because, in contrast to the ordination techniques, it reflects the differences in the dominance of the prey items rather than their lack of similarity (Marshall and Elliott, 1997). This aspect seems to be most important to distinguish intraspecific variation in the diet of *E. marginatus*. The cophenetic correlation between the cophenetic value matrix and the dissimilarity matrix obtained with the Bray-Curtis distance was calculated to determine the degree of representation of the cluster analysis.

RESULTS

Diet composition

A total of 203 stomachs of *E. marginatus* specimens ranging from 134 to 1056 mm total length were analysed. Of these, 32.5% stomachs were empty and 3% were everted. There were 309 prey items recorded that belonged to nine major prey categories: algae, phanerogams, polychaetes, crustacean stomatopods, crustacean decapods, molluscs, echinoderms, fishes and miscellaneous (Tab. I). The weight was estimated for 21.4% of the preys.

In reference to the frequency of occurrence (% F) and the numerical composition (% N), the most important food was the decapods, which were present in 60.31% of the stomachs and represented 50.19% of the total ingested preys. The decapods were mainly represented by brachyurans (50.38% F, 37.74% N). Next in importance were fishes (44.27% F, 26.46% N) then molluscs (31.30% F, 19.46% N), although these were mainly cephalopods (29.01% F, 16.73% N).

At the species level, the most important decapod was *Liocarcinus corrugatus* (15.27% F, 10.51% N), followed by species from the genus *Pilumnus* (12.21% F, 7.39% N). None of the fish species were dominant within the diet spectrum, and all were represented by similar abundance, however, high values were obtained for undetermined fishes (12.21% F, 6.23% N). *Chromis chromis* (6.87% F, 3.89% N), *Scorpaena* sp. (5.34% F, 2.73% N), *Serranus* sp. (3.82% F, 1.95% N) and *Coris julis* (3.05% F, 1.56% N) displayed slightly larger indices. The most important cephalopods found in the stomach contents were *Octopus vulgaris* and *Sepia officinalis*, and both showed the same index value for % F (10.69) and % N (5.84).

Regarding the weight composition (% W), the cephalopods (77.47% W) were clearly the predominant food in the diet. They were mainly represented by both the species *Octopus vulgaris* (43.91% W) and *Sepia officinalis* (25.34% W). These were followed by fish (10.66% W) and decapods (10.42% W).

Food in relation to fish size

A relationship was found between diet composition and

Table I. - Prey recorded in the stomach contents of *Epinephelus marginatus*. % F = Frequency of occurrence; % N = Numerical composition; % W = Weight composition.

Prey	% F	% N	% W
Algae total	*12.98*	-	*0.261*
Phanerogams total	*24.43*	-	*0.651*
Posidonia oceanica	24.43	-	0.651
Annelida Polychaetes total	*0.76*	*0.39*	*0.011*
Unidentified Aphroditidae	0.76	0.39	0.011
Crustacea	*61.80*	*51.75*	*10.55*
Decapoda total	*60.31*	*50.19*	*10.42*
Anomura total	7.63	3.89	0.32
Dardanus sp.	0.76	0.39	0.129
Galathea spp.	4.58	2.33	0.185
Pagurus anachoretus	0.76	0.39	0.001
Pagurus sp.	0.76	0.39	<0.001
Unidentified Anomura	0.76	0.39	0.004
Brachyura total	*50.38*	*37.74*	*7.94*
Dromia personata	3.05	1.56	0.551
Ebalia sp.	0.76	0.39	0.001
Herbstia condylata	4.58	2.33	0.623
Ilia nucleus	0.76	0.39	0.010
Lissa chiagra	0.76	0.39	0.120
Maja sp.	0.76	0.39	0.003
Maja verrucosa	3.05	1.56	1.265
Paractnea monodi	0.76	0.39	0.038
Pilumnus spp.	12.21	7.39	0.450
Pisa corallina	1.53	0.78	0.039
Pisa muscosa	0.76	0.39	0.012
Pisa nodipes	1.53	0.78	0.056
Pisa sp.	2.29	1.17	0.046
Pisa tetraodon	3.05	1.56	0.276
Liocarcinus corrugatus	15.27	10.51	3.749
Liocarcinus sp.	2.29	1.17	0.159
Xantho incisus granulicarpus	1.53	0.78	0.044
Xantho poressa	0.76	0.39	0.008
Xantho sp.	0.76	0.39	0.075
Unidentified Maiidae	0.76	0.39	0.002
Unidentified Portunidae	0.76	0.39	0.062
Unidentified Xanthidae	0.76	0.39	<0.001
Unidentified Brachyura	7.63	3.89	0.351
Macrura Natantia total	*7.63*	*4.28*	*0.08*
Alpheus dentipes	0.76	0.39	0.002
Athanas nitescens	0.76	0.39	<0.01
Brachycarpus biunguiculatus	2.29	1.17	0.052
Gnatophyllum elegans	2.29	1.17	0.019
Lysmata seticaudata	1.53	0.78	0.003
Thoralus cranchii	0.76	0.39	<0.001
Macrura Reptantia total	*6.87*	*3.50*	*2.07*
Palinurus elephas	0.76	0.39	1.664
Scyllarus arctus	4.58	2.33	0.314
Scyllarus sp.	1.53	0.78	0.092
Unidentified Decapoda	1.53	0.78	0.016
Stomatopoda total	*2.29*	*1.17*	*0.086*
Unidentified Squillidae	2.29	1.17	0.086
Unidentified Crustacea	0.76	0.39	0.045

Prey	% F	% N	% W
Molluscs total	*31.30*	*19.46*	*77.70*
Gastropoda total	*4.58*	*2.72*	*0.23*
Columbela rustica	0.76	0.39	0.003
Haliotis lamellosa	3.05	1.56	0.211
Lima hians	0.76	0.78	0.016
Cephalopoda total	*29.01*	*16.73*	*77.47*
Loligo vulgaris	0.76	0.39	0.217
Octopus spp.	1.53	0.78	0.332
Octopus macropus	5.34	3.11	7.550
Octopus vulgaris	10.69	5.84	43.912
Sepia officinalis	10.69	5.84	25.337
Unidentified Cephalopoda	1.53	0.78	0.120
Echinoderma total	*0.76*	*0.39*	*0.023*
Ophiura sp.	0.76	0.39	0.023
Teleostei total	*44.27*	*26.46*	*10.66*
Atherina sp.	0.76	0.78	0.061
Centracanthus cirrus	0.76	0.39	0.124
Chromis chromis	6.87	3.89	0.808
Coris julis	3.05	1.56	0.336
Diplodus annularis	1.53	1.56	1.219
Diplodus vulgaris	0.76	0.39	1.229
Gobius sp.	1.53	0.78	0.093
Labrus sp.	0.76	0.39	0.388
Labrus viridis	0.76	0.39	0.350
Mullus surmuletus	0.76	0.39	0.330
Muraena helena	0.76	0.39	1.100
Parablennius trigloides	0.76	0.39	0.066
Parophidion vassali	1.53	0.78	0.193
Sardinella aurita	1.53	0.78	0.098
Scorpaena porcus	1.53	0.78	0.970
Scorpaena scrofa	0.76	0.39	0.331
Scorpaena sp.	3.05	1.56	0.618
Serranus cabrilla	0.76	0.39	0.177
Serranus scriba	1.53	0.78	0.486
Serranus sp.	1.53	0.78	0.802
Spicara smaris	0.76	0.78	0.323
Syngnathus typhle	0.76	0.39	0.028
Unidentified Clupeidae	0.76	0.39	0.050
Unidentified Congridae	0.76	0.39	0.101
Unidentified Labridae	0.76	0.39	0.001
Unidentified Muraenidae	0.76	0.39	0.036
Unidentified Teleostei	12.21	6.23	0.345
Miscellaneous	*3.76*	-	*0.137*
Unidentified matter	0.76	0.39	0.103
Wood	1.53	-	0.007
Sand	0.76	-	0.005
Stones	2.29	1.17	0.022

fish length. Figure 2 shows the ordination of three main food categories (crustaceans, fishes and molluscs) along a canonical axis obtained by Redundancy Analysis (F = 6.88; p < 0.005). The biplot shows that a high proportion of crustaceans was characteristic of the diet of smaller fishes, while higher proportions of molluscs appeared in the diet of larger fishes. The fish category seemed to have some importance for a narrow interval in the intermediate sizes, when the other food categories were a long way from their respective maxima. However, predator size only explained 5.5% of the variation of food composition.

No differences between size classes were detected with respect to the mean number of prey items ingested (F = 1.749; df (3:125); p = 0.160) (Fig. 3). However, a small number of prey corresponded specifically to the larger size class, but these differences were not significant (Tukey's test). One way ANOVA showed differences in the mean weight of food between size classes (F = 7.868; df (3:125); p < 0.001). The pair-wise comparisons revealed differences between the smaller size class (≤ 40 cm), which corresponded to the lower mean weight, and the other three groups (Fig. 3). According to these observations, the increase of food weight in fishes larger than 40 cm was related to the ingestion of more voluminous preys and not to the capture of a larger number of preys.

The Tokeshi graphical method revealed differences in the feeding strategy as a function of size (Fig. 4A). There were three groups below 60 cm corresponding to a generalist strategy with heterogeneous feeding, while the larger size class (> 60 cm) corresponded to a specialist strategy. According to this representation, the stomachs of fishes

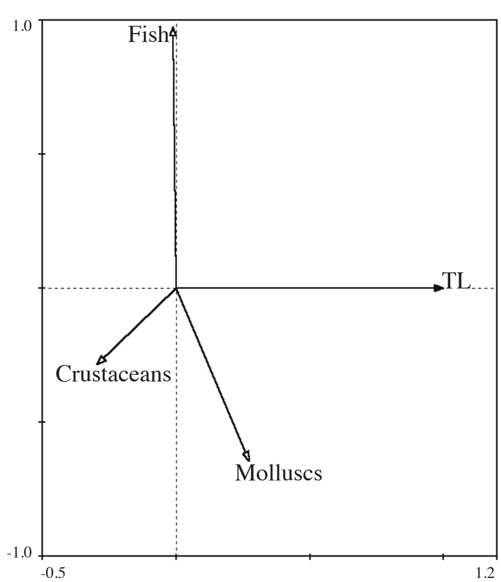

Figure 2. - Redundancy Analysis: ordination biplot of weight proportions for the three main food categories explained by total fish length (TL).

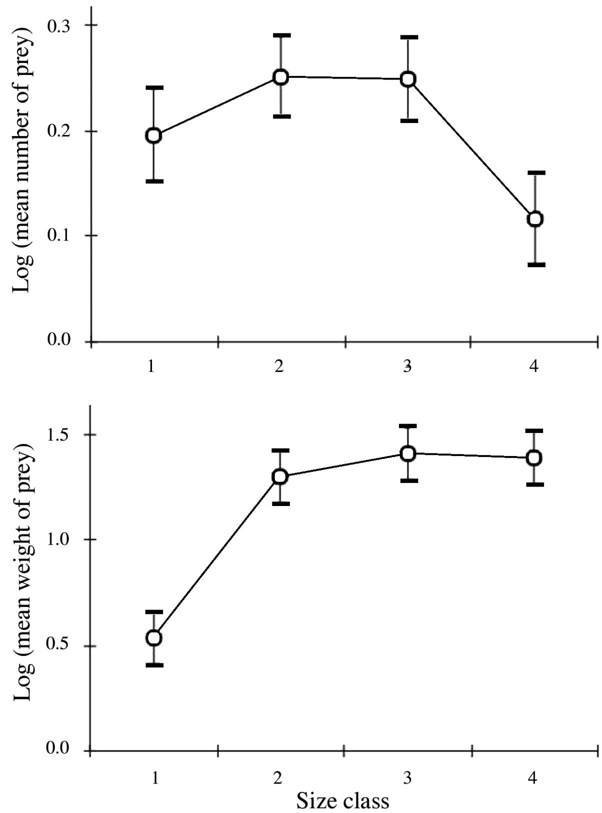

Figure 3. - Mean number and mean weight of preys (± standard error) in stomach contents for the size classes (1: ≤ 40 cm; 2: 41-50 cm; 3: 51-60 cm and 4: > 60 cm).

measuring less than 60 cm TL had a high individual mean diversity (i.e., they contained a variety of items in similar proportions, and, consequently, had a high group diversity), whereas the stomach contents of the larger size were dominated by only one particular prey item.

The cluster analysis carried out to detect diet similarity in relation to size showed a high degree of representation (r = 0.888). It discriminated three well-differentiated groups (Fig. 4B). The first dichotomy separated the larger size class (> 60 cm) from the other three length groups with a 71.5% dissimilarity. The second dichotomy had a 65.7% dissimilarity and separated the smaller size class (≤ 40 cm) from the fishes of intermediate size (41-60 cm).

DISCUSSION

Epinephelus marginatus is a necto-benthic species that predates on a wide spectrum of decapod and fish species frequenting rocky bottoms, as well as on the littoral cephalopods. Vegetable matter has also been found in their stomachs, but it is possible that the groupers ingest this with their preys, especially with brachyurans because algae has frequently been found entangled between their legs. Our findings concerning the main importance of decapods, fishes and cephalopods in the diet composition of *E. marginatus* agree with those obtained by other studies for a similar size range on the South African coasts (Smale, 1986) and in the western Mediterranean (Derbal and Kara, 1996; Reñones *et al*., 2002).

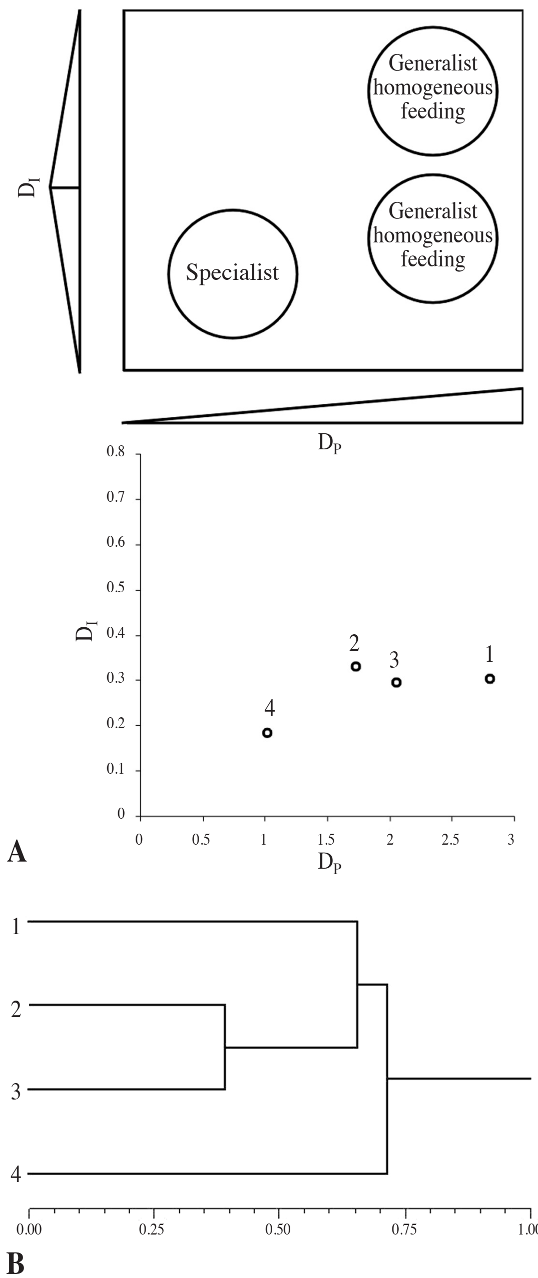

Figure 4. - **A**: Scheme for the interpretation of the Tokeshi graphical method (after Tokeshi, 1991) (top) and scatterplot of *Epinephelus marginatus* size classes according to this method (1: ≤ 40 cm; 2: 41-50 cm; 3: 51-60 cm and 4: > 60 cm) (bottom). **B**: Dendrogram representing cluster of dissimilarity based on diet (abundance matrix) between size classes (Bray-Curtis distance-UPGMA) (1: ≤ 40 cm; 2: 41-50 cm; 3: 51-60 cm and 4: > 60 cm).

An effect of predator size on the mass percentage of the three main preys of the grouper diet was detected. According to the pattern found, crustacean decapods are important preys of smaller groupers. However, as predators grow fishes and cephalopods are incorporated into the diet, which together with crustaceans, are the principal preys of intermediate fishes. Cephalopods were the preferred prey for larger fishes. This pattern agrees with the observations of Smale (1986) and Derbal and Kara (1996) on food segregation with growth in the dusky grouper, although these authors pointed out a major contribution of fish prey in the diet of smaller specimens. Our results also coincided with those obtained by Reñones *et al*. (2002) based on isotope data. However, the pattern found only represents 5.5% of the total variation of the grouper's diet. Other factors that could determine the diet composition of species, such as the prey availability, competition between predators and the digestibility of preys would explain the variation of the prey composition in gut contents.

However, groupers from the 0+ age group seem to possess a different diet. These juveniles feed predominantly on small crustaceans (amphipods, crabs and isopods), which were rare preys in the stomach contents of groupers larger than 13 cm (Azevedo *et al*., 1995). Furthermore, *Octopus vulgaris* clearly represented the preferred prey for groupers between 90 and 138 cm total length (Barreiros and Santos, 1998). Possibly, the food segregation of *E. marginatus* in relation to size is not a gradual process but a marked change at the level of both the 1+ age class and long-lived specimens.

For growth, groupers satisfied their nutritional requirements through the capture of large prey, and not by the ingestion of a great number of preys. As the dusky grouper begins to catch larger preys, its moves from heterogeneous to specialist feeding, with the diets of the smaller and larger fishes showing the lowest niche overlap, and the intermediate sizes the largest.

Wainwright and Richard (1995), based on the similarity of the corporal morphology and the strong interspecific relationship between size and diet composition in serranids, claim that the changes in the diet associated with fish size are probably due to the effects of size on a common functional morphology rather than to changes in the capture mechanism. As these authors suggested, *E. marginatus* follows the interspecific pattern of changes in the diet as a function of size described for the tropical serranids, which would be expected if the changes in the diet were dependent on a factor related to the size of the predator (e.g., the mouth size). In the model described by Wainwright and Richard (1995), while smaller species feed on copepods and other components of small zooplankton, and intermediate sizes feed on shrimps and crabs, the largest species feed on fish and cephalopods. As a result, the smaller sized *E. margin-*

atus individuals feed on small crustaceans, such as amphipods, small crabs and isopods (Azevedo *et al.*, 1995). The intermediate individuals feed on crabs, cephalopods and fishes (Smale, 1986; Derbal and Kara, 1996; Reñones *et al.*, 2002), and the larger individuals feed fundamentally on cephalopods (Barreiros and Santos, 1998).

The dusky grouper is an ambush predator of cephalopods and fishes (Smale, 1986; Barreiros and Santos, 1998). However, it seems probable that for the predation of other prey types, such as the non-evasive brachyurans or other less mobile preys, the grouper does not necessarily lie in wait but actively seeks out its prey. If this were so, the changes in the proportion of the non-evasive prey would indicate changes in the feeding behaviour. Small to medium sized fishes can supply their energetic requirements with the capture of brachyurans, and they can adopt a patrolling behaviour that can be used to find new shelter sites. When the fishes reach a certain size, they have a mouth dimension that allows them to capture voluminous cephalopods successfully. Due to their foraging strategy, the capture of this evasive prey implies they must adopt a more sedentary behaviour.

The differences in predation described above would represent different adaptabilities to the effort of reproduction for both sexes. In a protogynous hermaphrodite species, like *E. marginatus*, the reproductive effort of dominant males (the largest fishes of the population) seems to be greater than for females, so they expend a large amount of energy tirelessly patrolling a territory in order to defend it from other males and to maintain frequent interactions with neighbouring females (Zabala *et al.*, 1997b). Females can probably allocate most of their time and energy budgets on reproduction since they have a diet based on less energetic preys (brachyurans) compared to males. To do this they adopt a more passive feeding behaviour (ambush predation) to prey on more profitable preys (cephalopods), which may help to increase their energetic gains according to their elevated energetic investment during the reproductive period.

The trophic nycthemeral rhythm of the dusky grouper is not well known, but it seems to show both diurnal (Neill, 1967; Ghafir and Guerrab, 1992) and crepuscular or nocturnal habits (Abel, 1962; Derbal and Kara, 1996). Harmelin and Harmelin-Vivien (1998) point out that the presence of the nocturnal gastropods *Haliotis* in the stomachs would be indicative of the nocturnal habits of the dusky grouper. In this study, the presence of *Haliotis lamellosa* and other twilight species, such as *Scyllarus* spp., *Herbstia condylata* and *Octopus macropus*, would support the feeding activity of *E. marginatus* during or after dusk.

By applying Redundancy Analysis to gut content data, it is possible to obtain a function that could be used to estimate the mass proportions of prey items ingested by a stock based on its size structure. However, the prediction is limited to the percentage variation of the gut content associated with the evaluated factor, so one prediction would be more or less approximate to the current diet of a stock according to the magnitude of this percentage. In the studied case, the fish size explains a low percentage of diet composition, so this factor is a poor predictor of the feeding habits in *E. marginatus*. In the case that fish size would be a good predictor of the feeding habits, we propose the use of this function in order to obtain a representative diet of a stock in relation to its size structure and for recalculating the weight proportions of the prey items for species or functional groups in ecological modelling when a temporal scale is added.

This quantitative study of the trophic ontogeny of *E. marginatus* represents a solid basis for the management of rocky littoral systems in which this species would be implicated. In addition, it will be useful in ecological modelling for the better representation of the trophic flows associated with large fishes that change their feeding habits during ontogeny.

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Appendix. - Length-weigth and length-length lineal relationships from fresh specimens captured in Majorca (Balearic Islands-Spain). The regression has been used to estimate the weight of the partially digested preys found in stomach contents of *Epinephelus marginatus*.

TL: Total length; FL: Forke length; SL: Standard length; W: Weight; LRP: Length right pincer; LLP: Length left pincer; CW: Caparace width; ML: Mantle length; h: Hook length; c: Crets length; OT: Otolith length; CL: Caparace length; CephL: Cephalic length. a: Upper beak, b: Lower beak. *: p < 0.01. **: p < 0.001.

Prey	Relation	ln (a)	b	r^2	n	range	p
Chromis chromis	W-SL	-10.628	3.053	0.975	36	34 - 86 mm	**
Chromis chromis	SL-OL	2.922	-6.964	0.981	12	2 - 5 mm	**
Coris julis	TL-SL	-1.444	1.154	0.990	60	7 - 13.5 cm	**
Dardanus sp.	W-LRP	-4.306	2.560	0.975	8	13.55 - 22 mm	**
Diplodus annularis	TL-SL	0.181	0.371	0.983	105	7.4 - 18.5 cm	**
Dromia personata	W-CL	-2.629	1.527	0.981	4	26.7 - 33.3 mm	*
Galathea ssp.	W-LLP	-5.102	2.018	0.974	18	2.7 - 16.3 mm	**
Galathea ssp.	W-CW	-7.376	2.808	0.952	55	2 - 17 mm	**
Herbstia condylata	W-LLP	-4.548	2.159	0.998	6	38 - 6.3 mm	**
Licarcinus corrugatus	W-LLP	-6.263	2.823	0.941	25	39.5 - 5.5 mm	**
Licarcinus corrugatus	W-LRP	-5.278	2.505	0.967	24	37.7 - 4.6 mm	**
Licarcinus corrugatus	W-CW	-7.830	2.923	0.990	28	54.7 - 4.1 mm	**
Sardinella aurita	W-SL	-10.864	2.875	0.994	56	27 - 166 mm	**
Scyllarus sp.	W-CephL	-8.618	3.600	0.932	8	7.35 - 10.33 mm	**
Sepia officinalis	W-h[a]	-1.137	2.488	0.863	59	24.15 - 12 mm	**
Sepia officinalis	W-ML	-2.018	2.990	0.989	85	18.2 - 4.3 mm	**
Sepia officinalis	W-c[b]	-0.409	2.407	0.873	60	18 - 9.6 mm	**
Serranus cabrilla	TL-SL	1.236	-0.429	0.983	13	8.2 - 12.8 cm	**
Serranus scriba	TL-SL	1.159	0.245	0.993	69	8 - 16.6 cm	**
Spicara smaris	FL-SL	0.092	-0.349	0.984	25	11.3 - 17.2 cm	**