Diet and feeding strategy of the dusky grouper *Mycteroperca marginata* (Actinopterygii: Epinephelidae) in a man-made rocky habitat in southern Brazil

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The dusky grouper (*Mycteroperca marginata*) is a marine species usually associated with rocky bottoms and reefs. The present work investigated the diet and feeding strategy of a dusky grouper population inhabiting a 4.5 km long pair of rocky jetties located in the mouth of Patos Lagoon estuary. No prior research has been conducted in such man-made habitat and the current study provides a basis for comparative studies on the diet of the dusky grouper populations inhabiting natural vs. man-made rocky habitats. Similarly with previous studies on natural substrates, crabs and fishes were the main food categories consumed (%IRI = 85.1 and %IRI = 12.6, respectively), whereas shrimps and mollusks had lower importance in the diet (%IRI = 1.9 and 0.4, respectively). As previously reported for dusky grouper populations inhabiting reefs and rocky bottoms, the present work revealed conspicuous size related dietary shifts. Blue crabs and fishes become increasingly important food items in the diet of larger individuals (> 500 mm, TL). Finally, it was found that the studied dusky population has a generalist feeding strategy with a high between-individual variation in prey consumption. Such strategy remained similar across the size increment of the species. Our findings suggest that man-made rocky substrates provide suitable feeding grounds for the dusky grouper in southern Brazil and could be used as an additional tool in the conservation efforts of this endangered species.

**Key words:** Endangered species, *Epinephelus marginatus*, Jetties, Patos Lagoon, Stomach content analysis.

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Introduction

The dusky grouper *Mycteroperca marginata* (formerly *Epinephelus marginatus*) (Actinopterygii, Epinephelidae) has a wide geographical distribution, occurring from the British Isles to South Africa, Mozambique in the Indian Ocean and in the Mediterranean Sea (Heemstra & Randall, 1993). In the western Atlantic, its range is restricted to the southern coast of South America, from Rio de Janeiro State south to Argentina (Figueiredo & Menezes, 1980; Rico & Acha, 2003; Luiz Jr. *et al.*, 2004). The ‘Molhes da Barra de Rio Grande’ (hereafter ‘MBRG’), a man-made rock substrate (rocky jetty) 4.5 km long located at Rio Grande City in southern Brazil connecting a large coastal lagoon with the Atlantic Ocean, probably constitutes the southernmost limit of this species along the Brazilian coast (Condini *et al.*, 2007).
The dusky grouper is usually found in relatively shallow waters (up to 80 m deep), especially in coastal rocky substrates and reefs (Heemstra & Randall, 1993; Paiva & Andrade-Tubino, 1998). In southern Brazil, *M. marginata* is exploited by fishermen in rocky bottoms along the coastline (Haimovici et al., 1994). The rocky substrates of the MBRG harbors a population of dusky groupers that has been regularly exploited by sport and commercial fisheries and represents a significant source of income to local artisanal fishermen (Condini et al., 2007).

The dusky grouper *M. marginata* is currently considered as an endangered species by the International Union for Conservation of Nature (IUCN) (Cornish & Harmelin-Vivien, 2004) and, in Brazil, the dusky grouper is considered overexploited (Brasil, 2004). Some of its biological features such as sedentary and territorial behavior (La Mesa et al., 2002), low growth rate, late maturation and protogynous hermaphrodite mode of reproduction (Fennessy, 2006) make this species particularly vulnerable to anthropogenic threats such as fishery. Accordingly, overexploitation from commercial fishing is considered the primary threat affecting this species (Cornish & Harmelin-Vivien, 2004).

Prior research on the biological and ecological aspects of the dusky grouper *M. marginata* has been concentrated on populations of the Mediterranean (Marino et al., 2001; Reñones et al., 2002; Linde et al., 2004) and the African western coast (Fennessy, 2006). In Brazil, although have been recorded in São Paulo and Rio de Janeiro States (Begossi & Silvano, 2008), previous studies have been focused on populations of Santa Catarina State, where the dusky grouper is commonly found in reefs and coastal rocky bottoms (Bertoncini et al., 2003, Gerhardinger et al., 2006; Machado et al., 2008). Previous studies regarding the diet and feeding behavior of this species in natural habitats such as reefs and coastal rocky bottoms have shown that the dusky grouper is a carnivorous fish preying upon mainly on crustaceans, cephalopods and fishes (López & Orvay, 2005; Gibran, 2007; Machado et al., 2008). *Mycteroperca marginata* has crepuscular feeding habits and increases their hunting activities at twilight. They hid into the deepest region of the rocky shelters or crevices and tend to stay close to their shelters, particularly their juveniles (Gibran, 2007).

In the Rio Grande do Sul, the southernmost State of Brazil, the current knowledge regarding the dusky grouper is basically restricted to fishery aspects (Haimovici et al., 1994; Condini et al., 2007) and no prior ecological research have been done with this endangered species in this region. The main goal of the current study was to investigate diet composition, feeding strategy and size related dietary shifts of a dusky grouper population inhabiting the MBRG, which was originally built in the beginning of the twentieth-century to maintain a navigation channel between a large subtropical coastal lagoon and the sea. Our hypothesis is that diet composition and feeding strategy of dusky groupers has been conducted in such man-made habitats. The current work provides a basis for comparative studies on diet of the dusky grouper populations inhabiting natural vs. man-made rocky bottoms, regarding the use of such habitats as feeding grounds for this endangered species.

**Material and Methods**

We adopted the recent classification of the Serranidae species proposed by Craig & Hastings (2007) and Smith & Craig (2007) based on molecular genetic analyses suggesting the change from genus *Epinephelus* to *Mycteroperca*. Therefore, we used *M. marginata* instead of *E. marginatus*.

The rocky jetties of the MBRG were built in 1911 using large rocks nearly 10 ton each that summed up approximately 4.5 million tons of rock after its construction (Capítoli, 1996). They are located in the Rio Grande City (Rio Grande do Sul State) in southern Brazil (32°09′38″S 52°05′54″W) (Fig. 1A-B), and constitutes an artificial, man-made rocky habitat that harbors a local population of dusky grouper (Condini et al., 2007) (Fig. 1C). Although precise scientific records are not available, historical accounts obtained with local fishers suggested that grouper have been caught in the MBRG at least since 1970s.

Specimens were obtained directly with local fishermen operating at the MBRG from February 2007 to May 2009 mainly during night time (between 18:00 and 07:00). See Condini et al. (2007) for a detailed description of the fishing technique employed by local fishermen in the study site. There were no individuals captured during austral winter and early spring (from June to November) due to the harsh conditions during these months. This period is characterized by higher frequency of cold fronts with wind velocities ranging from 16 to 24 ms⁻¹ from S, SW and SE directions (Braga & Krusche, 2000), which disfavor capture of the dusky grouper at MBRG during this time of the year. This effect is particularly strong in the western jetty (Fig. 1C), where most of the local grouper fishery occurs and from where the specimens were obtained. Fishing tended to be higher in the western jetty compared to the eastern one because the former is closer to the main fishermen village targeting this species (Condini et al., 2007).

In the laboratory, each individual was measured (total length, TL, mm), weighted (g) and dissected to extract its stomach, which was preserved in 10% formaldehyde and stored in 70% alcohol a week later for posterior analysis. Food items found in each stomach were identified to the lower possible taxonomic level. Each stomach was weighted before and after its content being removed. For each food item found in the stomach, it was recorded their numerical abundance, weight (0.01 g precision) and TL (mm). The prey’s TL was measured only when the prey was not broken in pieces or was too digested. Food items were pooled in the following major food categories: non-blue crabs (all brachyuran crabs except *Callinectes* spp.), blue crabs (*Callinectes sapidus, C. danae*), fishes, shrimps and mollusks.
Food items and food categories were quantified using the following parameters (Hyslop, 1980): (a) frequency of occurrence (%F) that represents the number of non-empty stomachs (in percentage) that a particular food item or food category was found, (b) numerical abundance (%N) that represents the total number (in percentage) of a particular food item or food category in relation to the total number of food items or food category found in all non-empty stomachs and (c) weight (%W) that represents the total weight (in percentage) of a particular food item or food category in relation to the total number of food items or food categories found in all non-empty stomachs (Hyslop, 1980). These parameters were used to calculate the Index of Relative Importance (%IRI) proposed by Pinkas et al. (1971): %IRI = %F * [%N + %W].

In order to assess diet changes related to differences in predator’s size (TL, mm), individuals of *M. marginata* were pooled into three size classes: < 400 mm; 400-500 mm and >500 mm (adapted from Linde et al., 2004; Machado et al., 2008). The number of individuals analyzed in each size class was 29, 34 and 15, respectively. The %IRI for each food category was computed for each size class. One-way ANOVA was used to evaluate differences in the average prey’s size and biomass among the three predefined size classes and post-hoc differences were evaluated using the Newman-Keuls test (α = 0.05). ANOVA’s assumptions of normality and homogeneity of variance were assessed via the Kolmogorov-Smirnov and Cochran tests, respectively (Zar, 1994).

The graphical analysis proposed by Amundsen et al. (1996) was employed to analyze feeding strategy and to evaluate the contribution of each individual (phenotype) to population niche width (Deus & Petrere-Junior, 2003; Garcia et al., 2005). This approach is based on a two-dimensional representation of prey-specific abundance (P) and %F of the different prey types in the diet. The ‘prey-specific abundance of prey’ (P_i = (ΣS_i/ΣS) x 100) take into account only those predators in which the actual prey occurs; where P_i is the prey-specific abundance of prey i, S_i is the stomach content (weight) comprised of prey i, and S is the total stomach content in only those predators with prey i in their stomach (Amundsen et al., 1996). We employed the Amundsen et al.’s diagram to the different size classes defined above.

**Results**

**Diet composition**

A total of 133 individuals of *M. marginata* ranging from 260 to 800 mm TL (443 ± 100.7 mm) had its stomach content analyzed and only 78 had food content. Inspection of these non-empty
stomachs revealed 31 food items belonging to the classes Gastropoda and Bivalvia and subclasses Malacostraca and Actinopterygii (Table 1). In general, crustaceans of the Brachyura infraorder were the most frequent and abundant item in the stomach content, both in terms of their volumetric and numerical contributions (Table 1). Non-blue crabs, in particular, represented an important and diverse group in the diet, especially species of the Xanthidae family. For instance, the stone crab *Menippe nodifrons* was the most important item in the diet (%IRI = 24.1), occurring in 18.2% of the non-empty stomachs. N = 78 non-empty stomachs.

**Table 1.** Numerical abundance (%N), weight (%W), frequency of occurrence (%F) and the Index of Relative Importance (IRI%) for each food item found in the stomach content of the dusky grouper *Mycteroperca marginata* individuals captured. N = 78 non-empty stomachs.

| Prey items         | %F | %N | %W | IRI% |
|--------------------|----|----|----|------|
| **Mollusca**       |    |    |    |      |
| Gastropoda         |    |    |    |      |
| *Anachis isabellei*| 1.30 | 0.56 | 0.05 | 0.03 |
| *Anachis spp.*     | 2.60 | 2.22 | 0.23 | 0.25 |
| **Bivalvia**       |    |    |    |      |
| *Mytilus edulis platensis* | 2.60 | 1.11 | 0.00 | 0.11 |
| *Perna perna*      | 1.30 | 0.56 | 0.08 | 0.03 |
| *Ostre a equestris*| 1.30 | 0.56 | 0.03 | 0.03 |
| Bivalve unidentified| 2.60 | 1.11 | 0.18 | 0.13 |
| **Crustacea**      |    |    |    |      |
| Dendrobranchiata   |    |    |    |      |
| *Solenoceridae*    | 3.90 | 3.33 | 1.07 | 0.67 |
| *Pleoticus muelleri* |    |    |    |      |
| Anomura            |    |    |    |      |
| Porcellanidae      | 1.30 | 0.56 | 0.26 | 0.04 |
| *Pachycheles chubutensis* |    |    |    |      |
| Brachyura          |    |    |    |      |
| Majidae            |    |    |    |      |
| *Lobinia spinosa*  | 5.19 | 2.78 | 0.77 | 0.72 |
| Portunidae         |    |    |    |      |
| *Araneus cribrius* | 1.30 | 0.56 | 0.06 | 0.03 |
| *Callinectes davidae* | 9.09 | 7.22 | 11.26 | 6.53 |
| *Callinectes sapidus* | 12.99 | 7.22 | 15.67 | 11.55 |
| *Callinectes sp.*  | 5.19 | 2.22 | 1.32 | 0.71 |
| Xanthidae          |    |    |    |      |
| *Eurypanopeus abbreviatus* | 5.19 | 2.22 | 6.02 | 1.66 |
| *Hexapanopeus schmidt* | 3.90 | 1.67 | 0.34 | 0.30 |
| *Hexapanopeus caribbeaus* | 1.30 | 0.56 | 0.03 | 0.03 |
| Menippe nodifrons  | 18.18 | 12.78 | 21.33 | 24.10 |
| Panopeus australis | 6.49 | 3.89 | 3.98 | 1.98 |
| Xanthidae unidentified | 7.79 | 3.89 | 1.10 | 1.51 |
| Varunidae          |    |    |    |      |
| *Cyrtograpsus altimus* | 1.30 | 0.56 | 0.03 | 0.03 |
| Pilumnidae         |    |    |    |      |
| *Pilumnus davydovus* | 5.19 | 2.78 | 0.50 | 0.66 |
| Caridea            |    |    |    |      |
| Hippolytida        |    |    |    |      |
| *Lyssna wurdemann* | 3.90 | 1.67 | 0.44 | 0.32 |
| Caridea unidentified| 6.49 | 6.11 | 1.93 | 2.03 |
| Decapoda unidentified | 23.38 | 13.89 | 9.34 | 21.10 |
| Actinopterygii     |    |    |    |      |
| *Hypleurochilus fiscicorni* | 6.49 | 2.78 | 1.90 | 1.18 |
| *Gobionellus sp.*  | 1.30 | 0.56 | 0.05 | 0.03 |
| *Umbrina canasai*  | 1.30 | 0.56 | 0.02 | 0.03 |
| *Lycogaulus grossidens* | 1.30 | 0.56 | 3.37 | 0.20 |
| *Genidens barbus*  | 1.30 | 1.67 | 4.20 | 0.30 |
| Porichthys poriissimus | 1.30 | 0.56 | 0.17 | 0.04 |
| Actinopterygii unidentified | 22.08 | 13.33 | 14.26 | 23.67 |

respectively). Aside crustaceans, fishes were another important prey in the dusky grouper’s diet, with six fish species found in the stomach content.

**Size related dietary shift**

The relative importance of food categories in the diet changed across different size classes of the dusky grouper. The relative importance of ‘non-blue crabs’ decreased steadily across size classes and ‘blue crabs’, fishes and, in lesser extent, shrimps become increasingly important food items in the diet of larger individuals, particularly in the > 500 mm size class (Fig. 2). Accordingly, prey’s size and biomass found in the stomach content changed across size classes of the dusky grouper (Fig. 3). Prey’s average sizes (TL, mm) showed significant differences across predator’s size classes (F(2, 124) = 7.292, p < 0.001), being statistically significantly higher in the larger size classes (400-500 and >500) compared to individuals of the smallest size class (<400 mm) (Newman-Keuls test, α = 0.05). A similar increasing trend was found for prey’s average biomasses, but there were no statistically differences in prey biomass among size classes (Newman-Keuls test, α = 0.05) (Fig. 3).

According to the Amundsen et al.’s diagram, the dusky grouper had a generalist feeding strategy characterized by a high variability in prey consumption between individuals (phenotypes). By and large, this feeding strategy did not change among size classes of the dusky grouper, but there were differences in the prey taxa that were opportunistically consumed in each size class (Fig. 4). Smaller dusky grouper individuals (<400 mm) preyed upon occasionally (%F < 0.20) on an array of ‘non-blue crabs’ species and only once preyed on ‘blue-crab’ (%F: 0.04) (Fig. 4A). In contrast, ‘blue-crabs’ became increasingly frequent and abundant in the diet of larger individuals of size classes 400-500 (%F: 0.32) and >500 mm (%F: 0.40). Additionally, among those preys consumed opportunistically (i.e., preys with low frequency of occurrence and higher prey-specific abundance values), larger dusky grouper individuals switched to ‘fishes’ and other ‘non-blue crabs’. For instance, individuals between 400-500 mm consumed opportunistically the Atlantic sabretooth anchovy *Lycengraulis grossidens* and the lobate mud crab *Eurypanopeus abbreviatus*, whereas individuals > 500 fed occasionally on juveniles of the white sea catfish *Genidens barbus* and the stone crab *Menippe nodifrons*. Therefore, the analysis of the feeding strategy revealed a considerable amount of variation in the prey consumption among individuals, which suggest greater partitioning of the food resources between individuals of the population. According to the Amundsen et al.’s diagram this configuration reveals a wide food niche where different individuals specialize on different resource types (Fig. 4A, inserted box).

**Discussion**

The high frequency of empty stomachs (41.3%) found in the present work is in the range of values reported in studies
elsewhere, from 17.5\% (López & Orvay, 2005) to 56.1\% (Reñones et al., 2002). This variability could be explained by the hypothesis that different fishing methods employed to obtain the fishes (e.g., speargun, hook, and line) could lead to different rates of regurgitation of captured individuals. Alternatively, these differences could be related with ecological factors as differences in food resources availability or seasonality in each site. Nevertheless, a high frequency of empty stomachs is usually higher in carnivorous fishes when compared to detritivorous and omnivorous fishes (Arrington et al., 2002).

Brachyuran crabs were the main food items in the diet of the dusky grouper individuals inhabiting the man-made rock bottoms at MBRG, which is consistent with results found in natural rocky bottom and reefs habitats elsewhere. For instance, Linde et al. (2004) showed that brachyuran crabs occurred in 50.4\% of the analyzed stomachs of the dusky grouper Mycteroperca marginata. The number of individuals analyzed in each size class is 29, 34 and 15, respectively. Mollusks did not occur in the larger size class (>500 mm TL).

Fig. 2. Components (%N, %W, %F) of the Index of Relative Importance (%IRI) for each of the five major categories of food found in the stomach content of three size classes (A: <400 mm TL; B: 400-500 mm TL; C: >500 mm TL) of the dusky grouper Mycteroperca marginata. The number of individuals analyzed in each size class is 29, 34 and 15, respectively.

Fig. 3. Average values (±SD) of prey’s size (mm, TL) and biomass (g) in the stomach content of three size classes (<400 mm TL; 400-500 mm TL; >500 mm TL) of the dusky grouper Mycteroperca marginata. The number of individuals analyzed in each size class is 29, 34 and 15, respectively.
Regarding cephalopod preys, however, there were important differences between the findings of the current work and studies on dusky grouper populations elsewhere. In contrast with most studies pointing out cephalopods as a common prey in the diet of the dusky grouper (Barreiros & Santos, 1998; Harmelin & Harmelin-Vivien, 1999; Reñones et al., 2002; Linde et al., 2004; López & Orvay, 2005), these prey taxa were not found in the stomach content of the individuals inhabiting the studied man-made rocky bottom (MBRG). In southern Brazil, squids (e.g., Illex argentinensis, Loligo sanpaulensis) and octopuses (e.g., Octopus vulgaris, O. tehuelchus) are usually found along the continental shelf and continental slope (Haimovici & Álvarez-Perez, 1990; Andriguetto & Haimovici, 1996; Santos & Haimovici, 1997; Santos & Haimovici, 2002), but they are presumably absent in the shallow waters (<10m) where the studied site (MBRG) is located. Other mollusks, such as bivalves and gastropods, were found in the stomach content of the dusky grouper at MBRG. However, these preys had very low frequency (<10%) in the analyzed stomachs, a pattern also reported by Reñones et al. (2002) and Machado et al. (2008). Some authors (Linde et al., 2004) argued that these preys, together with barnacles and vegetation, had low abundance in the dusky grouper’s stomach content because they would be accidentally ingested when they are preying upon their targeted preys such as crabs, fishes and cephalopods.

Feeding strategy analysis revealed that the studied dusky grouper population had a generalist feeding behavior characterized by a strong opportunism of some individuals in the populations towards the consumption of certain preys. The degree of opportunism, particularly in the consumption of brachyuran crabs, seemed to be greater in smaller individuals (<400 mm) than in larger individuals, which seemed to concentrate their feeding on larger preys as blue crabs.
crabs and fishes. Regardless predator size, the studied dusky population has a general feeding strategy with a high between-individual (or phenotypes) variation in prey consumption. This feeding strategy has been also found for dusky grouper populations of the Mediterranean Sea (Linde et al., 2004) and southeastern Brazil (Machado et al., 2008). Individual-level niche variation only recently has been considered as a feeding strategy to avoid conspecific competition (Bolnick et al., 2003). Future studies should evaluate the importance of individual feeding specialization in controlling food resource partitioning among individuals of dusky grouper populations.

As previously reported for dusky grouper populations inhabiting reefs and rocky bottoms, the present work revealed conspicuous size related dietary shifts. However, whereas prior studies have shown that cephalopods are usually found in the stomach of intermediate and larger sizes individuals (Reñones et al., 2002; Machado et al., 2008), the current work showed that larger preys as blue crabs and fishes become increasingly important food items in the diet of larger individuals. According to Linde et al. (2004), the dusky grouper’s efficiency in capturing larger and more mobile preys such as blue crabs seemed to increase proportionally with its increment in size (TL). This presumably higher efficiency in capturing larger preys by larger specimens could compensate the greater demand for energy expected to occur in adult individuals involved with reproduction and/or territorial patrolling activities.

In summary, our findings reveals that a dusky grouper population inhabiting a man-made rocky habitat has a similar feeding ecology in terms of diet composition, feeding strategy and size related dietary changes when compared with populations studied in reefs and natural rocky bottoms. Differences in the consumed preys were observed mainly at the species level, which could be related with differences in geographic distribution or local abundance patterns of consumed preys. Regarding feeding strategy, the studied dusky population has a general feeding strategy with a high between-individual (or phenotypes) variation in prey consumption that remained similar across their life time. These findings suggest that man-made rocky substrates as the MBRG in southern Brazil could provide suitable feeding grounds for this endangered species. Future studies should investigate the ecological role played by other rocky jetties for dusky grouper populations elsewhere.

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