Feeding ecology of two sympatric species of large-sized groupers (Perciformes: Epinephelidae) on Southwestern Atlantic coralline reefs

Matheus O. Freitas[1,2], Vinicius Abilhoa[2], Henry L. Spach[1], Carolina V. Minte-Vera[3], Ronaldo B. Francini-Filho[4], Les Kaufman[5] and Rodrigo L. Moura[6]

Red and black groupers are large-bodied opportunistic ambush predators commonly found in Southwestern Atlantic tropical reefs. We investigated the diet of both species in order to detail ontogenetic, spatial and temporal trends, and to assess the extent of overlap in resource use between these two sympatric predators on the Abrolhos Bank, Brazil. Decapods and fishes were the main food items of *Epinephelus morio* while fishes were the main prey of *Mycteroperca bonaci*. Both diets were significantly influenced by body size and habitat, but only smaller individuals of *E. morio* feed almost exclusively on crustaceans. While the two groupers rely on many of the same prey types, coexistence may be facilitated by *E. morio* feeding more heavily on crustaceans, particularly the blackpoint sculling crab *Cronius ruber*, while black grouper take comparatively few crustaceans but lots of fish prey. Predators like red and black groupers could trigger indirect effects in the community and influence a large range of ecological processes, such as linkages between top and intermediate predators, and intermediate predators and their resources.

Keywords: Abrolhos Bank, Diet, *Epinephelus morio*, Feeding overlap, *Mycteroperca bonaci*.

A garoupa e o badejo-verdadeiro são predadores oportunistas de grande porte, com estratégia de emboscada, comumente encontrados em recifes tropicais do Atlântico Sul. A dieta das duas espécies foi investigada, avaliando influências ontogenéticas, espaciais e temporais, assim como a sobreposição no uso de recursos entre estes dois predadores co-orrentes no Banco dos Abrolhos, Brasil. Decápodes e peixes foram os principais itens alimentares de *Epinephelus morio*, enquanto que os peixes foram as principais presas de *Mycteroperca bonaci*. Ambas as dietas foram significativamente influenciadas pelo tamanho corporal e habitat, mas apenas indivíduos menores de *E. morio* alimentaram-se quase que exclusivamente de crustáceos. Como as duas espécies utilizam muitas presas semelhantes, a coexistência parece ser facilitada pelo fato de *E. morio* se alimentar principalmente de crustáceos, particularmente do caranguejo *Cronius ruber*, enquanto que o badejo-verdadeiro consome relativamente poucos crustáceos e grande quantidade de peixes. Predadores como as espécies estudadas podem causar efeitos indiretos na comunidade e influenciar uma grande variedade de processos ecológicos, como conexões entre predadores de topo e intermediários e predadores intermediários e seus recursos.

Palavras-chave: Banco dos Abrolhos, Dieta, *Epinephelus morio*, *Mycteroperca bonaci*, Sobreposição alimentar.

Introduction

Epinephelids are demersal predatory fishes found in shallow to mesophotic waters of all tropical and subtropical oceans, especially in hard bottom habitats (Heemstra, Randall, 1993; Craig *et al.*, 2011). The 160 or so species in the family encompass a wide range of body sizes and food habits, ranging from small zooplanktivores to some of the largest predators in tropical and subtropical reef ecosystems (Claro *et al.*, 2001).

The red grouper *Epinephelus morio* (Valenciennes, 1828) and black grouper *Mycteroperca bonaci* (Poey, 1860) are large (maximum sizes of 125 and 150 cm, respectively) carnivores that inhabit rocky and coralline

[1]Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal do Paraná, 81531-990 Curitiba, PR, Brazil. (MOF) serranidae@gmail.com (corresponding author), (HLS) henry@ufpr.br
[2]Grupo de Pesquisa em Ictiofauna, Museu de História Natural Capão da Imbuia. Rua Prof. Benedito Conceição, 407, 82810-080 Curitiba, PR, Brazil. (VA) vabilhoa@uol.com.br
[3]Inter-American Tropical Tuna Commission. 8901 La Jolla Shores Drive, La Jolla CA 92037-1509 EE.UU. - USA. cminte@iattc.org
[4]Universidade Federal da Paraíba, Centro de Ciências Aplicadas e Educação, Campus IV - Litoral Norte, Av. Santa Elizabete, 160, 58297-000 Rio Tinto, PB, Brazil. rbfrancinifilho@gmail.com
[5]Boston University Marine Program, 5 Cummington Street, Room 431, Boston, MA, USA. 02215. lesk@bu.edu
[6]Instituto de Biologia, Departamento de Biologia Marinha, Universidade Federal do Rio de Janeiro. Av. Carlos Chagas Filho, 373, Bloco A, Edifício do Centro de Ciências da Saúde, Ilha do Fundão, Cidade Universitária, 21941-902 Rio de Janeiro, RJ, Brazil. moura@biologia.ufrj.br

reefs (Crabtree, Bullock, 1998). They are among the most common epinephelids in the Tropical Western Atlantic and support important fisheries throughout their range (Burgos *et al*., 2007; Crabtree, Bullock, 1998; Freitas *et al*., 2011b) from Massachusetts (EUA) to Southeastern Brazil (Heemstra, Randall, 1993). In the Abrolhos Bank, the largest and richest coralline reefs in the South Atlantic (Moura *et al*., 2013), groupers have been heavily targeted since at least the mid 16th Century (Bueno, 1999).

Black and red groupers are important predators in hard-bottom communities of the tropical Western Atlantic (Brulé, Canché, 1993; Brulé *et al*., 1994; Brulé *et al*., 2005). In the Abrolhos Bank, they are the two most abundant epinephelids, representing more than three times the biomass of all other groupers combined, and 20% of large carnivore's biomass, a category that also includes sphyraenids, lutjanids and carangids (Francini-Filho, Moura, 2008a). In the Northern Hemisphere, fishes, crustaceans, gastropods and cephalopods are important dietary components of both species (Moe, 1969; Bullock, Smith, 1991; Brulé, Canché, 1993; Brulé *et al*., 1994; Brulé *et al*., 2005), but there is no information on their food habits for the entire Southwestern Atlantic.

Groupers are predators thought to play important roles in ecosystem function through either direct or indirect interactions (Huntsman *et al*., 1999; Dulvy *et al*., 2004; Campbell, Perdede, 2006; Rizzari *et al*., 2014). Therefore investigations on the relationships among such large-bodied marine predators, their predator-prey interactions and the environment are important for an overall understanding of the mechanisms that structure populations and communities of reef fishes (Hixon, 1991; Hixon, Beets, 1993). Food partitioning among closely related co-occurring predators is crucial for their coexistence (Davies *et al*., 2007).

Several modes of space and food utilization enable reef fishes inhabiting structurally complex habits to generate differential patterns of resource partitioning (Jones, 1968; Smith, Tyler, 1972; Shpigel, Fishelson, 1989; Gibran, 2007). Resource partitioning includes food, habitat and/ or temporal segregation (Pianka, 1973; Schoener, 1974), and has been extensively documented among reef and rocky fishes (*e.g.* Clarke, 1977; Hixon, 1980; Larson, 1980; Gladfelter, Johnson, 1983; Bouchon-Navaro, 1986; Sala, Ballesteros, 1997; Pratchett, 2005; Gibran, 2007). The degree of overlap in the use of available resource among grouper species is variable, and interactions are associated, for example, with seasonal and diel changes (Brulé *et al*., 1994), habitat use (Sierra *et al*., 2001; Craig *et al*., 2011) and ontogenetic shifts (Machado *et al*., 2008; Freitas *et al*., 2015). Food segregation seems to play a more important role than habitat or temporal separations within many fish assemblages (Ross, 1986).

In the present study we investigated food habits of the black and red groupers obtained from eight years of artisanal fisheries monitoring program in the Abrolhos

Bank region in Brazil. This comprehensive dataset included stomach contents from groupers collected from a variety of habitats and seasons, and therefore presumably reflects the general feeding habits of species examined. Information provided here represents one of the most extensive databases assembled over a relatively large period of time, particularly for a coralline reef environment, and provides a uniquely large amount of information to investigate ecological interactions among large-bodied marine predators, and to understand the role of predation in the regulation of reef fish communities. Specifically, our objectives were to determine important prey groups in the diets of these groupers and estimate their relative importance, identify any spatial, temporal or ontogenetic shifts in their diets, and assess the extent of overlap in the diet between these two sympatric predators. Data provided here is the first information on the feeding ecology of the red and black groupers in the Southwestern Atlantic.

Material and Methods

Study area. The study was carried out in the Abrolhos Bank (16º40'- 19º40' S; 39º10'- 37º 20' W), a region with 42,000 km² and depths rarely exceeding 30 m, with a shelf edge at about 70 m depth. Abrolhos harbors an extensive mosaic of benthic megahabitats (Moura *et al*., 2013). Rhodolith beds comprise the largest megahabitat (~21,000 km²), followed by unconsolidated sediments (~20,000 km²) and reefs (~9,000 km²). The two groupers studied are predominantly found on reefs and less often on rhodolith beds, being absent from unconsolidated bottoms. Most reefs in this region assume the characteristic and highly peculiar form of mushroom-shaped pinnacles (chapeirões), which rise 5 to 25 m height above the bottom and extend from 20 to 300 m across their tops (Francini-Filho, Moura, 2008a,b).

There are four marine protected areas (MPAs) in the region, all of them poorly enforced. The Extractive Reserve of Cassurubá (ERC; 1,006 km²) includes large mangroves in which fishing is small-scale artisanal or for subsistence. The other three MPAs encompass reefs: the no-take National Marine Park of Abrolhos (NMPA; 913 km²), the multiple-use Marine Extractive Reserve of Corumbau (MERC; 895 km²), and the Environmental Protected Area Ponta da Baleia/Abrolhos (EPA; 3,460 km²).

Samples were obtained in two cross-shelf strata, Inner Shelf (IS) and Outer Shelf (OS) (Fig. 1). The IS includes a no-take zone of the NMPA (Timbebas Reefs) and other unprotected reefs such as the Parcel das Paredes (the largest continuous reef in the South Atlantic), Sebastião Gomes, Coroa Vermelha and Viçosa. Reefs in this IS arc consist of banks with flat and exposed tops, and mushroom-shaped pinnacles, with depths reaching up to 20 m. This area is subjected to the highest fishing pressure in the region, with ~200 boats operating regularly with hand lines,

spears and various types of nets (Francini-Filho, Moura, 2008a). Siliciclastic (= terrigenous) contents in peri-reefal sediments are higher in the IS, while the carbonate fraction is higher in the OS. The OS includes the best-enforced area of the NMPA, including the Abrolhos islands and the Parcel dos Abrolhos. Besides this protected area with emerging pinnacles, the OS as also encompasses a large realm of mesophotic reefs, rhodoliths beds and seasonal fleshy algal pavements, from 25 to 90 m depths (Moura *et al.*, 2013). The OS also harbors non-emergent pinnacles and coalesced reef structures (drowned reefs), paleo valleys and channels, as well as depressions (similar to sinkholes but formed differently) locally known as "buracas" (Bastos *et al.*, 2013; Moura *et al.*, 2013).

Sampling and analytical procedures. Specimens were obtained monthly through a fish landing monitoring program that target fleets on hook and line, longline and spear fishing in the Cities of Nova Viçosa, Caravelas, Alcobaça, and Prado (Fig. 1), between June 2005 and September 2012. After capture, fishes were immediately stored on ice on board, and transferred to the laboratory where they were kept until processing. Fishes were measured (Total Length - TL cm; Standard Deviation - SD), weighed, and their stomachs were immediately fixed in 10% formalin for 24 h, and subsequently transferred and stored in 70% alcohol. Voucher specimens were deposited in the ichthyological collection of Museu de História Natural Capão da Imbuia (MHNCI 12657 for *E. morio* and MHNCI 12658 for *M. bonaci*).
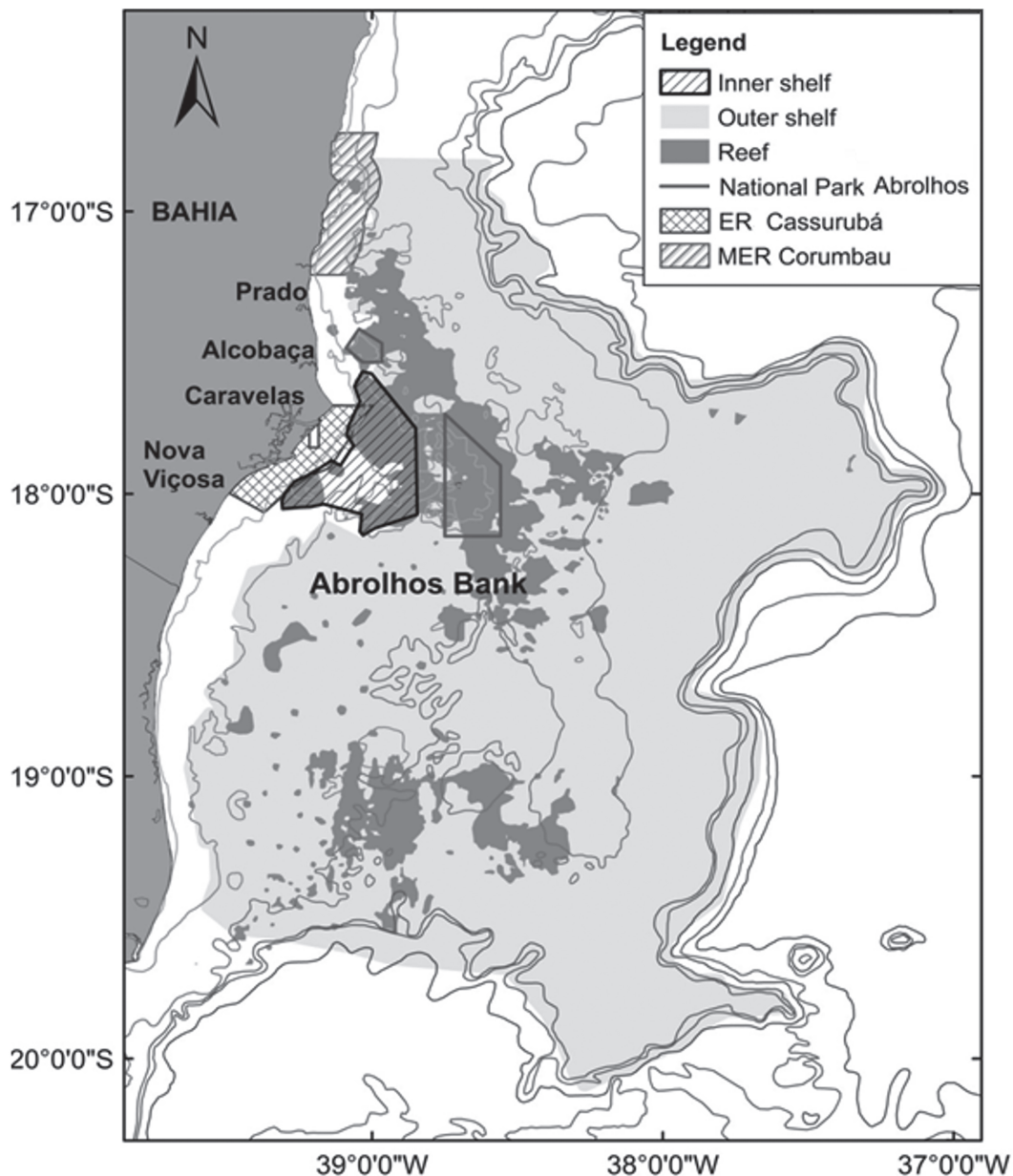

Fig. 1. Map of the Abrolhos Bank showing the municipalities where samples were collected and emerging coralline reefs are shown in dark grey. MER= Marine Extractive Reserve; ER= Extractive Reserve.

Stomach contents were examined in the laboratory using a stereomicroscope. The identification of food items was performed as refined as possible according to literature data (Melo, 1996; Amaral *et al*., 2006) and consultation with experts. All identifiable prey items were enumerated, weighed and identified to the lowest possible taxon (LPT). If gut contents were too digested for identification, the material was weighed and classified as "remains". Frequency of occurrence (%FO) (*i.e*., percentage of stomachs in which a food item occurred), proportion by weight (%W) (*i.e*., percentage participation of each item in the total food weight), as well as the proportion in number (%N) (*i.e*., percent of each item within total food items) were determined (Hyslop, 1980; Bowen, 1996). These variables were used to calculate the Index of Relative Importance (IRI) (*cf*. Pinkas *et al*., 1971), which establishes the order of importance of food items in the diet. IRI values were standardized to percentages (Cortés, 1999) and were calculated according to the equation IRI = FO (%W + %N). Feeding strategy diagrams (Amundsen *et al*., 1996) were used to examine the dietary importance of a particular prey item. These diagrams allow for a visual assessment of niche width and the importance of different prey items, as well as the predators' strategies (specialization *vs*. generalization), using occurrence and prey-specific weight.

Variations on diet were visualized with respect to cross-shelf strata (IS and OS), size classes (*E. morio*: juveniles 15-50.0 cm TL and adults 50.5-90 cm TL; *M. bonaci*: juveniles 26.1-62 cm TL and adults 68-147 cm TL; according to sex and reproductive development presented in Freitas, 2014) and seasons (cool and warm). Seasons were characterized from sea surface temperature (SST) historical data (November 1981- January 2008; http://nomad3.ncep.noaa.gov). The cool season has median SSTs < 26°C and spans from June to November (min. SST 24.5^{o}C, August). The warm season has median SSTs >26°C, spanning from December to May (max. SST 28°C, February). The warm season is characterized by prevailing NE winds and higher water visibility, while the cold season is characterized by polar front intrusions causing strong sediment re-suspension (Segal *et al*., 2008).

A two-way crossed permutational multivariate analysis of variance (PERMANOVA) using a population-wide dissimilarity metric was employed to examine the effects of habitat, ontogeny and season (factors) on the standardized and transformed (Logx+1) weight contribution of each prey item (LPT). Significant factors were further analyzed using PERMANOVA pair-wise comparisons. The Bray-Curtis dissimilarity was used in all tests, with 999 permutations under a reduced model. Similarity of percent contribution (SIMPER) analysis was used to examine the prey categories that are most responsible for between-factors separation (Clarke, Gorley, 2001). All analyses were performed using the PRIMER/PERMANOVA 6.0 software (Plymouth Marine Laboratory, Plymouth, England).

Results

A total of 361 stomachs from *Epinephelus morio* (mean 51.2 cm; range: 15-96 cm TL; SD: ± 13.5) were obtained between May 2005 and September 2012, and only 180 (49.9%) stomachs contained prey items (mean 49.2 cm; range: 23.2-90 cm TL; SD: ± 9.7). Identifiable prey items included decapods, cephalopods, stomatopods and teleosts (Tab. 1). Crustaceans (59.9% IRI) and teleosts (38.1% IRI) were the most important items, while cephalopods, stomatopods and other invertebrates collectively represented 4.2% IRI.

Diet of juveniles (60.6% of the stomachs analyzed, mean 43.4 cm; range: 23.2-50 cm TL; SD: ±9.7) was dominated by fish (43.7% IRI) and brachyuran remains (24.1% IRI). Blackpoint sculling crab *Cronius ruber* (15.0% IRI) was the third most important item (Tab. 1). Diet included several teleosts (*e.g.* Blackbar soldier fish *Myripristis jacobus*, spotted moray *Gymnothorax moringa* and parrotfishes, *Scarus* spp.), common octopus *Octopus vulgaris*, shrimps, stomatopods, and a wide variety of decapods (13 species). The diet of adults (39.4% of the stomachs analyzed) was dominated by *C. ruber* (40.4% IRI), followed by brachyuran (23.8% IRI) and fish remains (23.2% IRI). Seven teleost species were registered as prey of adults, including greenback parrotfish *Scarus trispinosus* and *Scarus* spp., the ocean surgeon *Acanthurus bahianus*, the burrfish *Chilomycterus spinosus* and the seadevil *Ogcocephalus vespertilio*. Filamentous algae, bivalve remains, gastropods and echinoderms were also present in low quantities.

The diet of *E. morio* individuals from the IS was dominated by the portunid (swimming) crab *C. ruber* (30.5% IRI), followed by fish remains (29.2% IRI), while that of individuals from the OS was dominated by fish (64.9% IRI) and unspecified brachyuran remains (14.3% IRI). In the cold season, the *E. morio* diet was dominated by *C. ruber* (53.7% IRI), fish (15.5% IRI) and brachyuran remains (11.4% IRI), while in the warm season the most representative prey were brachyuran (40.3% IRI) and fish remains (31.4% IRI), followed by *C. ruber* (10.7% IRI).

A total of 162 stomachs from *Mycteroperca bonaci* (mean 70.9 cm; range: 26.1-147 cm TL; SD: ±24.4) were obtained between May 2005 and September 2012, and only 47 (29.1%) stomachs contained prey items (mean 68 cm; range: 36-117 cm TL; SD: ±20.5). Identifiable prey items included teleosts, stomatopods and Caribbean spiny lobster (*Panurilus argus*) (Tab. 1). Fish remains (92.4% IRI) were the most important prey category. Collectively, Tomtate grunt *Haemulon aurolineatum* (2% IRI), Brazilian wrasse *Halichoeres brasiliensis* (1.9% IRI) and *S. trispinosus* (1.2% IRI) were the most prevalent identifiable items.

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Tab. 1. Diet composition of *Epinephelus morio* and *Mycteroperca bonaci* showing number percentage (N), frequency of occurrence (FO), weight percentage (W) and percentage of Index of Relative Importance (IRI) of food items consumed in two different size classes (Juvenile=J and Adult=A) from the Abrolhos Bank, Brazil. T= Total.

Item	Epinephelus morio %N J	A	T	%FO J	A	T	%W J	A	T	%IRI J	A	T	Mycteroperca bonaci %N J	A	T	%FO J	A	T	%W J	A	T	%IRI J	A	T
TELEOSTEI	27.94	24.61	26.65	50.94	46.49	48.81	32.47	50.08	43.58	43.70	27.97	38.13	96.43	96.43	96.42	99.15	114.27	104.22	98.34	99.61	99.48	99.79	99.61	99.87
Acanthostracion polygonius Poey, 1876	0.53	---	0.30	0.96	---	0.55	0.58	---	0.23	0.04	---	0.01	---	3.57	1.79	---	4.76	2.12	---	0.05	0.05	---	0.36	0.06
Acanthurus bahianus Castelnau, 1855	---	0.75	0.30	---	1.41	0.55	---	2.11	1.23	---	0.13	0.03	---	---	---	---	---	---	---	---	---	---	---	---
Acanthurus coeruleus Bloch, Schneider, 1801	0.53	---	0.30	0.96	---	0.55	0.42	---	0.17	0.03	---	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Acanthurus spp.	0.53	1.49	0.91	0.96	2.82	1.67	0.16	7.40	4.39	0.02	0.85	0.33	---	---	---	---	---	---	---	---	---	---	---	---
Aluterus monoceros (Linnaeus, 1758)	---	---	---	---	---	---	---	---	---	---	---	---	---	3.57	1.79	---	4.76	2.12	---	23.59	21.16	---	2.70	0.75
Blenniidae	0.53	---	0.30	0.96	---	0.55	0.07	---	0.03	0.02	---	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Carangidae	---	---	---	---	---	---	---	---	---	---	---	---	3.85	3.57	3.57	6.98	4.76	4.25	---	5.57	5.72	0.42	0.91	0.61
Chilomycterus spinosus (Linnaeus, 1758)	0.53	0.75	0.60	0.96	1.41	1.11	1.70	1.86	1.75	0.08	0.12	0.10	---	---	---	---	---	---	---	---	---	---	---	---
Engraulidae	0.53	---	0.30	0.96	---	0.55	0.12	---	0.05	0.02	---	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Gobiidae	0.53	---	0.30	0.96	---	0.55	0.12	---	0.05	0.02	---	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Gymnothorax moringa (Cuvier, 1829)	0.53	---	0.30	0.96	---	0.55	2.39	---	0.94	0.10	---	0.02	---	---	---	---	---	---	---	---	---	---	---	---
Gymnothorax spp.	---	1.49	0.60	---	2.82	1.11	---	13.50	7.89	---	1.43	0.35	---	3.57	1.79	---	4.76	2.12	---	0.71	0.63	---	0.43	0.10
Haemulon aurolineatum Cuvier, 1830	---	---	---	---	---	---	---	---	---	---	---	---	---	17.86	8.93	---	14.29	6.38	---	13.40	12.02	---	9.32	2.06
Halichoeres brasiliensis (Bloch, 1791)	---	---	---	---	---	---	---	---	---	---	---	---	3.57	7.14	5.36	3.85	9.52	6.38	14.46	14.82	14.79	0.73	4.36	1.98
Halichoeres poeyi (Steindachner, 1867)	0.53	---	0.30	0.96	---	0.55	0.22	---	0.09	0.02	---	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Myripristis jacobus Cuvier, 1829	0.53	---	0.30	0.96	---	0.55	2.76	---	1.10	0.11	---	0.03	---	---	---	---	---	---	---	---	---	---	---	---
Ogcocephalus vespertilio (Linnaeus, 1758)	---	0.75	0.30	---	1.41	0.55	---	1.55	0.91	---	0.11	0.02	---	---	---	---	---	---	---	---	---	---	---	---
Ophichthydae	2.65	1.49	2.12	4.81	2.82	3.89	0.20	4.48	2.70	0.51	0.57	0.71	---	---	---	---	---	---	---	---	---	---	---	---
Paraclinus nigripinnis (Steindachner, 1867)	0.53	---	0.30	0.96	---	0.55	0.02	---	0.01	0.02	---	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Scarinae	1.59	2.99	2.12	2.88	5.63	3.89	0.55	4.73	2.98	0.23	1.47	0.75	3.57	3.57	3.57	3.57	4.76	4.25	6.64	0.72	1.32	0.41	0.43	0.32
Scarus spp.	0.53	---	0.30	0.96	---	0.55	0.31	---	0.12	0.03	---	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Scarus trispinosus Valenciennes, 1840	---	0.75	0.30	---	1.41	0.55	---	0.55	0.32	---	0.06	0.01	3.57	7.15	5.36	3.57	9.52	6.38	12.51	7.04	7.60	0.65	2.82	1.27
Sparidae remains	---	0.75	0.30	---	1.41	0.55	---	0.43	0.25	---	0.05	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Sparisoma spp.	---	---	---	---	---	---	---	---	---	---	---	---	---	3.57	1.79	---	4.76	2.12	---	5.81	5.21	---	0.93	0.23
Synodus spp.	0.53	---	0.30	0.96	---	0.55	2.88	---	1.13	0.12	---	0.30	---	---	---	---	---	---	---	---	---	---	---	---
Unidentified fish	16.81	13.40	15.80	30.77	25.35	28.89	19.97	13.47	17.24	42.33	23.18	35.39	81.87	42.86	62.47	84.03	52.38	68.10	57.75	27.90	30.98	97.58	77.35	92.49
ALGAE																								
Filamentous algae	---	1.49	0.60	---	2.82	1.11	---	0.10	0.06	---	0.15	0.03	---	---	---	---	---	---	---	---	---	---	---	---
MOLLUSCA																								
Octopus vulgaris Cuvier, 1797	3.17	1.49	2.42	5.77	2.82	4.45	9.66	0.46	4.07	2.75	0.18	1.09	---	---	---	---	---	---	---	---	---	---	---	---
BIVALVE	---	1.49	0.60	---	2.82	1.11	---	0.12	0.07	---	0.15	0.03	---	---	---	---	---	---	---	---	---	---	---	---
GASTROPODA	1.59	2.99	2.12	2.88	5.63	3.89	0.12	1.51	0.93	0.18	0.85	0.45	---	---	---	---	---	---	---	---	---	---	---	---
ECHINODERMATA																								
Echinoidea	---	1.49	0.60	---	2.82	1.11	---	2.62	1.53	---	0.39	0.10	---	---	---	---	---	---	---	---	---	---	---	---
CNIDARIA - CORAL	1.59	1.49	1.51	2.88	2.82	2.78	0.29	0.24	0.26	0.20	0.16	0.18	---	---	---	---	---	---	---	---	---	---	---	---

Tab. 1. (continued)

Item	*Epinephelus morio* %N J	%N A	%N T	%FO J	%FO A	%FO T	%W J	%W A	%W T	%IRI J	%IRI A	%IRI T	*Mycteroperca bonaci* %N J	%N A	%N T	%FO J	%FO A	%FO T	%W J	%W A	%W T	%IRI J	%IRI A	%IRI T
CRUSTACEA	65.71	64.95	65.5	119.23	122.57	118.79	57.46	44.87	49.50	53.17	70.15	59.98	3.57	3.57	3.58	3.85	4.76	4.24	1.66	0.39	0.52	0.21	0.39	0.13
Callinectes spp.	0.53	---	0.30	0.96	---	0.55	0.40	---	0.16	0.03	---	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Cronius ruber (Lamarck, 1818)	6.88	14.90	9.99	12.50	28.17	18.33	25.37	27.47	26.42	15.02	40.42	26.42	---	---	---	---	---	---	---	---	---	---	---	---
Cycloes bairdii var. atlantica Verrill, 1908	---	0.75	0.30	---	1.41	0.55	---	0.04	0.13	---	0.04	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Family Inachoidinae	0.53	0.75	0.60	0.96	1.41	1.11	0.03	0.22	0.14	0.02	0.04	0.03	---	---	---	---	---	---	---	---	---	---	---	---
Leptopisa setirostris (Stimpson, 1871)	---	0.75	0.30	---	1.41	0.55	---	0.06	0.04	---	0.04	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Lithadia sp.	---	0.75	0.30	---	1.41	0.55	---	0.02	0.01	---	0.03	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Macrocoeloma camptocerum (Stimpson, 1871)	0.53	---	0.30	0.96	---	0.55	0.23	---	0.10	0.02	---	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Majiidae	---	0.75	0.30	---	1.41	0.55	---	0.10	0.06	---	0.04	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Malacostraca – Shrimps remains	3.70	2.99	3.32	6.73	5.63	6.11	0.44	0.40	0.41	1.03	0.64	0.86	---	---	---	---	---	---	---	---	---	---	---	---
Microphrys antillensis Rathbun, 1901	5.82	2.99	4.53	10.58	5.63	8.34	1.71	0.50	0.97	2.96	0.66	1.74	---	---	---	---	---	---	---	---	---	---	---	---
Microphrys spp.	1.06	---	0.60	1.92	---	1.11	0.02	---	0.01	0.07	---	0.02	---	---	---	---	---	---	---	---	---	---	---	---
Mithraculus forceps Milne-Edwards, 1875	6.39	1.49	3.63	9.62	2.82	6.67	2.48	0.49	1.26	3.17	0.19	1.23	---	---	---	---	---	---	---	---	---	---	---	---
Mithrax braziliensis Rathbun, 1892	3.70	0.75	2.42	6.73	1.41	4.45	2.87	0.54	1.44	1.64	0.06	0.65	---	---	---	---	---	---	---	---	---	---	---	---
Mithrax forceps Milne-Edwards 1875	2.65	---	1.51	4.81	---	2.78	2.32	---	0.91	0.89	---	0.25	---	---	---	---	---	---	---	---	---	---	---	---
Mithrax hemphilli Rathbun, 1892	1.06	---	0.60	1.92	---	1.11	0.90	---	0.36	0.14	---	0.04	---	---	---	---	---	---	---	---	---	---	---	---
Mithrax hispidus (Herbst, 1790)	---	2.24	0.92	---	4.23	1.66	---	2.30	1.34	---	0.65	0.14	---	---	---	---	---	---	---	---	---	---	---	---
Mithrax spp.	1.59	---	0.92	2.88	---	1.66	1.00	---	0.40	0.27	---	0.08	---	---	---	---	---	---	---	---	---	---	---	---
Mithrax tortugae Rathbun, 1920	2.12	0.75	1.51	3.85	1.41	2.77	1.79	1.59	1.64	0.56	0.11	0.33	---	---	---	---	---	---	---	---	---	---	---	---
Notolopas brasiliensis Miers, 1886	---	0.75	0.30	---	1.41	0.55	---	0.02	0.01	---	0.03	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Odontodactylus havanensis (Bigelow, 1893)	1.65	2.99	2.8	4.81	5.63	5.00	1.08	0.45	0.70	0.48	0.65	0.65	---	---	---	---	---	---	---	---	---	---	---	---
Panurius argus Latreille, 1804	0.53	---	0.30	0.96	---	0.96	0.43	---	0.17	0.10	---	0.10	3.57	---	1.79	3.85	---	2.12	1.66	---	0.17	0.21	---	0.06
Parthenope serrata Schmidt, 1857	1.06	0.75	0.60	1.92	1.41	1.11	0.23	0.09	0.09	0.11	0.04	0.03	---	---	---	---	---	---	---	---	---	---	---	---
Persephona sp.	1.06	---	0.60	1.92	---	1.11	0.59	---	0.23	0.11	---	0.03	---	---	---	---	---	---	---	---	---	---	---	---
Pilumnus dasypodus Kingsley, 1879	---	0.75	0.30	---	1.41	0.55	---	0.05	0.05	---	0.04	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Portunidae remains	1.06	2.24	1.51	1.92	4.23	2.77	3.24	0.42	1.52	0.30	0.38	0.32	---	---	---	---	---	---	---	---	---	---	---	---
Portunus ventralis (Milne-Edwards, 1879)	---	0.75	0.30	---	1.41	0.55	---	0.06	0.03	---	0.04	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Pseudosquilla ciliata (Fabricius, 1787)	2.12	---	1.21	3.85	---	2.22	1.16	---	0.46	0.47	---	0.14	---	---	---	---	---	---	---	---	---	---	---	---
Stenorhynchus seticornis (Herbst, 1788)	1.06	3.73	2.12	1.92	7.04	3.89	0.20	0.65	0.24	0.09	1.04	0.38	---	3.57	1.79	---	4.76	2.12	---	0.39	0.35	---	0.39	0.07
Stomatopoda	3.17	2.24	2.8	5.77	4.23	5.00	1.07	0.24	1.07	1.18	0.35	0.718	---	---	---	---	---	---	---	---	---	---	---	---
Superfamily Dromioidea	---	0.75	0.30	---	1.41	0.55	---	0.47	0.28	---	0.06	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Unidentified Brachyura	15.85	16.41	16.98	28.85	30.99	30.00	6.62	6.33	6.49	24.15	23.87	25.00	---	---	---	---	---	---	---	---	---	---	---	---
Unidentified Decapoda	2.12	2.24	2.24	3.85	4.23	4.44	1.33	1.58	1.50	0.49	0.54	0.65	---	---	---	---	---	---	---	---	---	---	---	---
Xanthidae	0.53	1.49	0.91	0.96	2.82	1.66	0.89	0.49	0.64	0.05	0.19	0.10	---	---	---	---	---	---	---	---	---	---	---	---

Diet of juveniles (55.3% of the stomachs analyzed) was dominated by fish remains (98.0% IRI) and *H. brasiliensis* (0.79% IRI) (Tab. 1), besides several species of teleosts (*e.g.* parrotfish *S. trispinosus*, Scarinae and jacks represented collectively 1.48% IRI). The diet of adults (44.7% of the stomachs analyzed) was dominated by fish remains (77.3% IRI), followed by *H. aurolineatum* (9.3% IRI), *H. brasiliensis* (4.3% IRI), *S. trispinosus* (2.8% IRI) and unicorn leather jacket filefish *Aluterus monoceros* (2.7% IRI).

The diet of *M. bonaci* from the IS was composed by fish remains (97.3% IRI), and fish species more abundant were *Acanthurus* spp. (1.2% IRI), *H. brasiliensis* (0.4% IRI) and *S. trispinosus* (0.35% IRI), while the diet of individuals from the OS was dominated by fish remains (76.4% IRI), *H. aurolineatum* (9.5% IRI) and *H. brasiliensis* (4.5% IRI). During the cold season, diet was dominated by fish remains (84.1% IRI), *A. monoceros* (6.5% IRI) and *H. aurolineatum* (3.3% IRI), similarly to the warm season, when fish remains (91.5% IRI), *H. brasiliensis* (2.5% IRI) and *H. aurolineatum* (2.1% IRI) were the most representative items.

For *E. morio* several less abundant taxa clustered in the lower left quadrant of the feeding strategy diagram, representing items with low contribution to the diet in terms of prey-specific weight. For juveniles (Fig. 2a), the main prey items were *C. ruber*, fish remains, brachyuran remains, *O. vulgaris*, and several decapods (*Leptopisa setirostris*, *Macrocoeloma camptocerum*,

Mithraculus forceps, *Notolopas brasiliensis* and *Microphrys antillensis*). Among adults (Fig. 2b) the dominant identifiable items included *Gymnothorax* spp., *Acanthurus* spp. and Scarinae. For *M. bonaci* juvenile samples the feeding strategy diagram showed a dominance of fish remains in the upper right portion (Fig. 2c), which suggested a more specialized feeding strategy than that of *E. morio*. This is also supported by the presence of other fish species (*S. trispinosus* and *H. brasiliensis*), and also of *P. argus* in the lower left quadrant. Adult samples of *M. bonaci* were similar, with presence of *A. monocerus* and *H. aurolineatum* (Fig. 2d).

The diet of the red and black groupers was significantly influenced by body size and habitat (PERMANOVA *P*=0.001 and *P*=0.015, respectively; Tab. 2). We also found significant dietary differences in pairwise comparisons between cross shelf strata (PERMANOVA, *P*= 0.026) and species/stages of juvenile and adult *E. morio* (PERMANOVA, *P*= 0.011), juvenile *E. morio* and *M. bonaci* (PERMANOVA, *P*= 0.001), adult *E. morio and* juvenile *M. bonaci* (PERMANOVA, *P*= 0.001) and adult *E. morio* and *M. bonaci* (PERMANOVA, *P*= 0.016). Fish as prey were the main contributors to the dietary dissimilarities between species, with a greater importance for *M. bonaci* diet (Tab. 3). SIMPER analyses showed that fish remains (23.86%), *C. ruber* (12.18%) and brachyura remains (11.5%) (Tab. 4), where the main contributions to the dietary dissimilarities between IS and OS cross-shelf strata.
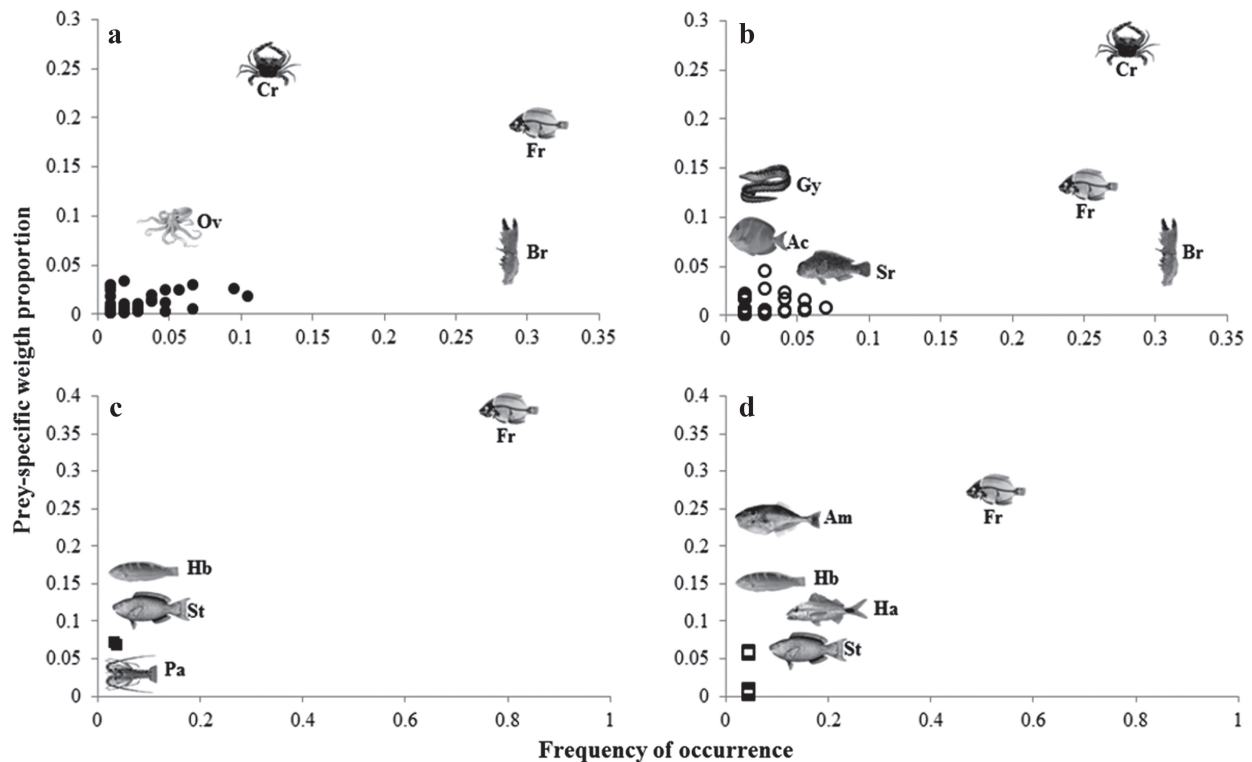

Fig. 2. Feeding strategy diagram incorporating the preys taxa of red (**a, b**) and black (**c, d**) groupers and their feeding strategy classification in the Abrolhos Bank for juveniles (**a, c**) and adults (**b, d**). Images of select items are offset to the right of symbols for visual interpretation. Abbreviations: Cr= *Cronius ruber*; Fr= Fishes remains; Br= Brachyura remains; Gy= *Gymnotorax* spp.; Ac= *Acanthurus* spp.; Ov= *Octopus vulgaris*; St= *Scarus trispinosus*; Sr= Scaridae remains; Pa= *Panurilus argus*; Hb= *Halichoeres brasiliensis*; Ha= *Haemulon aurolineatum*; Am= *Aluterus monocerus*.

Tab. 2. Results from two-way crossed PERMANOVA of red and black grouper diet data. df = Degree of freedom, SS = sum of squares, MS = mean squares.

		PERMANOVA				
Source	df	SS	MS	Pseudo-F	*P*(perm)	Unique perms
Habitat	1	8086.2	8086.2	1.9322	**0.015**	998
Species/stages	3	51555	17185	4.1063	**0.001**	998
Season	1	5243.7	5243.7	1.253	0.211	999
Habitat X Species/stages	3	12000	4000	0.95578	0.511	997
Habitat X Season	1	3224.1	3224.1	0.77039	0.704	999
Species/stages X Season	3	10017	3338.9	0.79782	0.839	997
Habitat X Species/stages X Season	2	3294.8	1647.4	0.39364	0.997	999
Res	212	8.8723E5	4185			
Total	226	9.8641E5				

Tab. 3. Results from two-way crossed similarity of percent (SIMPER) analyses for significant species/stage effects. Species contributions that summed cumulatively to >75% are shown. Juv = Juvenile, Av.Abund = Average abundance, Av.Diss = Average dissimilarity, Diss/SD = Dissimilarity Standart Deviation.

Average dissimilarity= 89.16	*E. morio* Juv	*M. bonaci* Juv				
Taxon	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contribution %	Cumulative %
Fish remains	0.45	0.87	27.27	1.23	30.58	30.58
Brachyura remains	0.25	0.00	8.40	0.51	9.42	40.01
Cronius ruber	0.32	0.00	8.01	0.36	8.99	49.00
Acanthurus spp.	0.01	0.23	5.95	0.32	6.67	55.67

Average dissimilarity= 92.01	*E. morio* Juv	*E. morio* Adult				
Taxon	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contribution %	Cumulative %
Fish remains	0.32	0.64	17.90	0.69	19.45	19.45
Cronius ruber	0.45	0.49	13.93	0.64	15.15	34.60
Brachyura remains	0.25	0.37	10.91	0.71	11.86	46.45
M. antillensis	0.08	0.05	3.38	0.38	3.68	50.13

Average dissimilarity= 90.82	*E. morio* Adult	*M. bonaci* Adult				
Taxon	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contribution %	Cumulative %
Fish remains	0.49	1.55	28.98	1.11	31.91	31.91
Brachyura remains	0.37	0.00	6.54	0.46	7.20	39.11
Cronius ruber	0.64	0.00	5.11	0.36	5.63	44.74
Haemulon aurolineatum	0.00	0.52	4.78	0.34	5.26	50.00

Average dissimilarity= 93.76	*E. morio* Adult	*M. bonaci* Juv				
Taxon	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contribution %	Cumulative %
Fish remains	0.49	0.87	24.05	1.12	25.66	25.66
Cronius ruber	0.64	0.00	15.70	0.56	16.74	42.40
Brachyura remains	0.37	0.00	9.26	0.50	9.88	52.28

Tab. 4. Results from two-way crossed dissimilarity of percent (SIMPER) analyses for significant Habitat effects. Species contributions that summed cumulatively to >75% are shown. Av.Abund = Average abundance, Av.Diss = Average dissimilarity, Diss/SD = Dissimilarity Standart Deviation.

Average dissimilarity= 90.87	*Inner-shelf*	*Outer-shelf*				
Taxon	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contribution %	Cumulative %
Fish remains	0.49	1.05	21.68	0.86	23.86	23.86
Cronius ruber	0.44	0.06	11.07	0.50	12.18	36.04
Brachyura remains	0.26	0.18	10.45	0.63	11.50	47.54
Cycloes bairdii var. atlantica	0.00	0.04	2.72	0.22	3.00	50.54

Discussion

Several stomachs of both species caught by hook and line, longline and spear fishing were empty. Despite the fact that some fish species regurgitated their prey(s) after capture, as already stated for some large-fish species (Randall, 1967), including groupers (Randall, Brock, 1960; Nakai *et al.*, 2001; Dierking, Meyer, 2009), we suspect that epinephelids regularly experience long periods of empty stomachs (*e.g.* Condini *et al.*, 2011; López, Orvay, 2005; Reñones *et al.*, 2002), as a combined result of resource availability, digestion rates and energy balance (Arrington *et al.*, 2002). Both species are opportunistic (Smith, 1971; Randall, 1967; Sierra *et al.*, 2001), "sit and wait" ambush predators (Bullock, Smith, 1991; Brulé *et al.*, 2005), and the regular occurrence of empty stomachs provides support to the idea that they are intermittent rather than continuous feeders.

Decapods and fishes were the main food items of *E. morio*, while fishes were the main prey of *M. bonaci* in the Abrolhos Bank. This pattern corroborates previous studies in the Northern Hemisphere (Gulf of Mexico and Caribbean), where red groupers also feed on brachyurans, stomatopods, molluscs, and small fishes (Randall, 1967; Moe, 1969; Brulé, Canché 1993; Brulé *et al.*, 1994), while black groupers feed mainly on fishes, and secondarily on crustaceans (Brulé *et al.*, 2005). Results were consistent with the notion that both species are important mesocarnivores on West Atlantic reefs (Randall, 1967; Parrish, 1987; Sierra *et al.*, 2001).

The diet of red grouper changed significantly with size. Smaller individuals fed almost preferentially on crustaceans (especially *Cronius ruber* and brachyurans generally), and also on a wide range of rare items including teleosts, decapods, octopuses, shrimps, and stomatopods. Reef fragments and filamentous algae were recorded in small quantities and most probably represent accidental ingestion during predation (Linde *et al.*, 2004; Brulé *et al.*, 1994; Machado *et al.*, 2008). *Cronius ruber* and brachyuran remains were also important components of the adult diet. Studies in the Northern Hemisphere (Brulé, Canché, 1993 - 12.1 to 40 cm TL; Brulé *et al.*, 1994 - 13 to 36 cm FL) also recorded such a preference for crustaceans and mollusks in addition to small fishes by juveniles, even considering size-related differences among previous studies.

The increased consumption of fishes by larger individuals may represent a general trend in groupers (Smith, 1971; Brulé, Canché, 1993), and also for other large carnivorous reef fishes (Sierra *et al.*, 2001; Linde *et al.*, 2004), observations already noted for mutton snapper and goliath grouper on Abrolhos Bank (Freitas *et al.*, 2011b, 2015). Such ontogenetic trend is clear for the more generalist red grouper, and is aligned with optimal foraging theory, *i.e.* maximum energetic return obtained when predator selects high quality prey (Gerking, 1994). Besides reducing the competition for food, or even meeting the higher energetic demand from migration and reproduction (Gerking, 1994; Sierra *et al.*, 2001), ontogenetic shifts in diet are often accompanied by shifts in habitat (Sierra *et al.*, 2001), possibly contributing to reduced niche overlap (Machado *et al.*, 2008).

Red grouper juveniles (20-40 cm) are commonly found in crevices and under ledges in 5-25 m depths, in the inner and mid shelf. At 40-50 cm adults migrate to deeper water (50-300m), where they also occur over sandy or mud bottoms (Craig *et al.*, 2011). The juvenile habitat for black grouper appears to vary geographically. Juvenile habitat in the Yucatán Peninsula mainly consists of sandy-rocky bottoms with some ridges and crevices (Renán *et al.*, 2003) while in the north Atlantic and Gulf of Mexico it is largely seagrass beds in estuarine areas and on coral reefs (Bullock, Smith, 1991; Sluka *et al.*, 1994; Ross, Moser, 1995). In our study, juveniles of *E. morio* and *M. bonaci* came from exclusively the IS while the adults mostly came from the OS. This pattern suggests that *E. morio* and *M. bonaci* exhibit size segregation according to depth, showed to dog snapper *Lutjanus jocu* (Bloch, Schneider, 1801), mutton snapper *Lutjanus analis* (Cuvier, 1828), goliath grouper *Epinephelus itajara* (Lichtenstein, 1822) and *Cephalopholis fulva* (Linnaeus, 1758), another carnivorous fish in Abrolhos Bank (Freitas *et al.*, 2011a, 2015; Moura *et al.*, 2011; Gathaz *et al.*, 2013), and as noted by Moe (1969) for the Gulf of Mexico, and by González *et al.* (1974) and Valdés, Padrón (1980) at the Campeche Bank, Mexico. On the IS, juveniles of both species inhabited chapeirões, reef structures with a characteristic mushroom-shaped form, clustered at depths of 5 to 25m. This could explain the high occurrence of crustaceans in red grouper diet and reef fishes in black grouper diet in this particular reef habitat, because such structures increase the heterogeneity and complexity of habitat types (Dutra *et al.*, 2005). In contrast, middle and outer shelf habitats comprise a much larger realm of mesophotic reefs, rhodolith beds, and fleshy algal pavement (Moura *et al.*, 2013) in depths from 25-90 m. While the two groupers rely on many of the same prey types, coexistence may be facilitated by *E. morio* feeding more heavily on crustaceans, particularly *C. ruber*, while black grouper take comparatively few crustaceans but lots of fish prey. Furthermore, prey captured by young red grouper are generally slow-moving benthic species (principally decapods) while those consumed by black grouper are less bottom-dependent, and faster-moving organisms (reef-fishes) (Brulé *et al.*, 2005), featuring a pattern similar to *E. itajara*, on Abrolhos (Freitas *et al.*, 2015).

The annual rhythm of fish feeding intensity is strongly associated with environmental conditions and their effect on the food supply (John, 2001; Sierra *et al.*, 2001). Feeding habits and diet composition of reef fishes are usually highly variable, in part because prey availability change seasonally (*e.g.* Roos, Moser, 1995; Monteiro *et al.*, 2009; Pimentel, Joyeux, 2010). The lack of dietary temporal variation in this study (*i.e.* no significant seasonal variation in diet

composition to *E. morio* and *M. bonaci*) is consistent with the results of Brulé *et al*. (1994, 2005) and others groupers (John, 2001) and we believe that the absence of major seasonal differences (*e.g.* mean and seasonal changes in SST) may explain our results. In fact, SST's along the Abrolhos Bank are very homogeneous over the year, with fluctuations not exceeding 4ºC (see Freitas *et al*., 2011b).

Red and black groupers from Abrolhos Bank did not feed heavily on other species that are commercial harvested. Their diet is likely most influenced by variation in prey availability and diversity in different areas. In marine ecosystems, trophic cascades have been observed in hard bottom environments such as coral reefs (Pinnegar *et al*., 2000). Predators like *E. morio* and *M. bonaci* could trigger indirect effects in the community (*e.g.* Heithaus *et al*., 2008, 2010; Ferretti *et al*., 2010) and influence a large range of ecological processes (Babcock *et al*., 1999; Pinnegar *et al*., 2000; Willis, Anderson, 2003; Silveira *et al*., 2015), such as linkages between top and intermediate predators, and intermediate predators and their resources (Pace *et al*., 1999). For example, the high consumption of scarines, by both *M. bonaci* and *E. morio*, illustrate how these groupers could have a controlling role in the abundance of parrotfishes, which in turn play key roles as grazers and sand producers on coral reefs.

Acknowledgments

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