

Activity, habitat use, feeding behavior, and diet of four sympatric species of Serranidae (Actinopterygii: Perciformes) in southeastern Brazil

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Diplectrum formosum (the sand perch), *Diplectrum radiale* (the aquavina), *Epinephelus marginatus* (the dusky grouper) and *Mycteroperca acutirostris* (the comb grouper) are four sympatric serranid of remarkable ecological and commercial importance. This study investigated the feeding of these four species in the São Sebastião Channel, São Paulo State (southeastern Brazil), comparing their diet, habitat utilization and morphological features related to foraging. These four serranids are opportunistic visual predators that use a total of nine different tactics to capture their preys, feed mostly on crustaceans during the day and twilight, and keep stationary and quiescent at night. The ecomorphological study was conducted to test its predictive value to infer lifestyles. It was verified that such analysis should be used carefully and must be complemented by field observations. Although morphologically and behaviorally very similar, *D. formosum* and *D. radiale* showed different preferences to the substratum type used by large individuals, which are exclusively sit-and-wait predators. On the other hand, *E. marginatus* displayed more sedentary habits than *M. acutirostris*, the most versatile predator from the studied species. The studied species of *Diplectrum* and *E. marginatus* can be regarded as benthic serranids, while *M. acutirostris* could be viewed as a nektobenthic species.

Diplectrum formosum, *Diplectrum radiale* (micholes-da-areia), *Epinephelus marginatus* (garoupa-verdadeira) e *Mycteroperca acutirostris* (badejo-mira) são quatro espécies simpátricas que pertencem à família Serranidae, de reconhecida importância ecológica e comercial. Este estudo analisou a alimentação destas quatro espécies de peixes no Canal de São Sebastião, Estado de São Paulo (sudeste do Brasil), comparando suas dietas, o uso do habitat e algumas características morfológicas relacionadas ao comportamento alimentar e a distribuição vertical na coluna d'água. Estes quatro serranídeos são predadores oportunistas que utilizam um total de nove táticas diferentes para capturar suas presas, alimentando-se principalmente de crustáceos durante o dia e crepúsculo, e permanecendo estacionários e inativos durante a noite. Um estudo ecomorfológico foi empregado para testar seu valor preditivo. Foi verificado que tal abordagem deve ser utilizada com cautela e sempre complementada com observações diretas no ambiente. Apesar de morfológicamente e comportamentalmente muito semelhantes, *D. formosum* e *D. radiale* mostraram divergências com relação ao tipo de substrato preferido pelos maiores indivíduos, que são exclusivamente predadores de espreita. Por outro lado, *E. marginatus* mostrou possuir hábitos de vida mais sedentários do que *M. acutirostris*, o mais versátil predador dentre as espécies estudadas. As espécies de *Diplectrum* estudadas, assim como *E. marginatus*, podem ser classificadas como serranídeos bentônicos, enquanto que *M. acutirostris* pode ser classificada como uma espécie nektobentônica.

Key words: *Diplectrum formosum*, *Diplectrum radiale*, *Epinephelus marginatus*, *Mycteroperca acutirostris*, Ecomorphology.

Introduction

Serranidae (Perciformes) is a monophyletic group of fishes that includes about 475 species, which range from a few centimeters to 3 m long and 400 kg in weight (Johnson, 1983; Nelson, 2006). Most serranids inhabit tropical marine ecosystems and live associated to rocky shores or coral shelves from shallow water to 200 m deep (Robins & Ray, 1986).

Serranidae is a large and important fish group, consider-

ing their diversity, biomass and role as top predators (Parrish, 1987; Randall, 1998). Most serranid species have solitary and territorial habits and feed on fish and crustaceans, although the group also includes small-sized species that live in large schools and feed on plankton (Randall, 1983).

Diplectrum formosum, *Diplectrum radiale*, *Epinephelus marginatus* and *Mycteroperca acutirostris* are four serranid species common in shallow waters (up to 10 m) of southeastern Brazil. The sand perch, *D. formosum*, and the aquavina, *D.*

radiale, are small benthic serranids (adults about 250 and 300 mm total length [TL], respectively) that inhabit shallow sand and sandy mud bottoms, two relatively poorly studied habitats. The dusky grouper *E. marginatus* is a middle to large benthic serranid (adults up to 1500 mm TL) inhabitant of reefs. The comb grouper *M. acutirostris* is a middle to large sized serranid (adults up to 800 mm TL) that lives associated to reefs, seagrass beds and estuaries (Figueiredo & Menezes, 1980; Carvalho-Filho, 1999; Humann & DeLoach, 2003a).

Epinephelus marginatus and *M. acutirostris* have considerable importance for sport (e.g. spear fishing) and commercial fisheries and are highly vulnerable to overexploitation (Sluka *et al.*, 1994; Linde *et al.*, 2004). Such species are also very appreciated as food, and are well represented in southeastern Brazil mainly by juvenile individuals (up to 400 mm TL), which is, probably as a consequence of overexploitation. The dusky grouper is cited in the “Brazilian list of aquatic invertebrates and fish species overexploited or threatened by overexploitation” – an official publication of the Brazilian Ministry of Environment (published on 28 May 2004) (see Morris *et al.*, 2000 for the threatened status of the members of the genera *Epinephelus* and *Mycteroperca*).

To date, information on the feeding biology of these four species in their natural habitats are based mostly on: 1) material collected with trawl nets or other fishing techniques (e.g., Bortone, 1971; Azevedo *et al.*, 1995; Meurer & Andreta, 2002; Reñones *et al.*, 2002) and 2) anecdotal or secondhand observations (e.g., Figueiredo & Menezes, 1980; Carvalho-Filho, 1999; Humann & DeLoach, 2003a).

Underwater studies with emphasis on the feeding biology, habitat and behavior of the dusky grouper are mainly from the Mediterranean Sea, Azores Archipelago (Portugal) and South Africa (e.g., Smale, 1986; Derbal & Kara, 1995; Barreiros & Santos, 1998; but see Machado *et al.*, 2003). Previous studies on *M. acutirostris* in Brazil, which employed a naturalist approach (see Sazima, 1986; Bonaldo *et al.*, 2004; Gibran, 2004), provided additional information on the feeding tactics and opportunism in this species.

This paper contains detailed information on activity, habitat use, feeding behavior, and diet of these four sympatric species of serranids, taken in a coastal stretch of southeastern Brazil through a combination of direct observation with scuba diving, stomach contents and ecomorphological analyses. The central focus of an ecomorphological study (see e.g. Karr & James, 1975; Motta *et al.*, 1995) is the interaction of morphological and ecological diversity among organisms both in the present and over evolutionary time (Motta & Kotschal, 1992). Underlying the study of ecomorphology is the premise that a species' morphology is related to its ecology (Keast & Webb, 1966; Casatti & Castro, 2006).

Material and Methods

Study area. Field work was carried out in seven bimonthly 10-day trips from January 1999 to February 2000, at São Sebastião Channel, a 25 km long stretch on the coast of São Paulo,

southeastern Brazil, and its surroundings (23°41' to 23°54'S and 45°19' to 45°30'W). The study area includes rocky shores and reefs as well as sandy and muddy beaches (see Rodrigues & Rocha, 1993 for map). During the study, water surface temperature varied from 18 to 31°C (average 24°C) and horizontal visibility from 0.5 to 5 m (average 2 m).

Field-work. Underwater observations and collecting activities were conducted in depths up to 20 m (average of 7 m). A total of 60 hours (34 diurnal, 13 nocturnal and 13 twilight) of scuba observations (using *ad libitum* and focal animal samplings; cf. Altmann, 1974) were conducted, and 52 hours of collecting activities using hand nets, hook-and-line or spear guns were performed at many spots of the study area (sampling all seasons).

During each observational session, it was recorded the number of individuals of each species found, the substratum types where they were, their respective positions in the water column, feeding tactics, feeding places, as well as the types of shelters or hiding places used during feeding strategies or quiescent phases. Activity was assessed based on food searching, feeding tactics, swimming, and agonistic behavior vs. inactive (*i.e.*, quiescent or “sleeping”; cf. Collette & Talbot, 1972). When “inactive”, the studied serranids could be touched and exhibited a more pale body color than the bright pattern exhibited when “active”.

Because of the absence of referential spots during dives over soft bottoms (necessary to observe *D. formosum* and *D. radiale*), concentric transects with a radius varying from 1-10 m were used (derived from the common “search-in-circles” scuba diving procedure; cf. Shreeves *et al.*, 1991). The transects were centered in the observer's diving partner, who kept stationary while the observer performed each transect, meter by meter. During night and twilight observations, a dive light with a red filter was used to reduce the disturbance caused by white-light (cf. Helfman, 1992).

Diet analysis. Stomach content analysis was performed to 20 individuals of *D. formosum* (nine collected at night and 11 during the day); 30 of *D. radiale* (three collected at night and 27 during the day); 30 of *E. marginatus* (20 collected during the evening twilight, six during the day, and four at night); and 30 of *M. acutirostris* (28 collected during the night and two at the beginning of the evening twilight). The collected specimens were weighted (0.1 g of precision) and fixed in 10% formalin on capture. Voucher specimens are deposited in the fish collection of the Laboratório de Ictiologia de Ribeirão Preto (LIRP), Departamento de Biologia (FFCLRP), Universidade de São Paulo, in Ribeirão Preto, Brazil (*D. formosum* LIRP 4297-4304; *D. radiale* LIRP 4305-4315; *E. marginatus* LIRP 4316-4324 and *M. acutirostris* LIRP 4325-4332).

For each broad category of food item the “frequency of occurrence” (cf. Bowen, 1992) and the “percent composition” (cf. Hynes, 1950) were calculated. Bait was easily recognized and discarded. Food overlap between each pair of species was also calculated, based on the formula of Morisita (1959), modified by Horn (1966 *apud* Zaret & Rand, 1971: 340).

Morphology and ecomorphological analysis. Some morphological features, such as body shape, general body coloration, caudal fin form, dentition, and number of pyloric caeca were considered to ascertain if they were in accordance with the mode-of-life of the studied serranids (such as position in the water column, habitat use, feeding behavior, feeding habits, and diet). These morphological features were also compared to each other. Additionally, the following six ecomorphological attributes, which were chosen based on their biological interpretations, were calculated to each studied species (Gatz, 1979):

a) Compression index (CI): maximum body depth divided by maximum body width. High values indicate a laterally compressed fish. No-benthic fishes have compressed bodies compared to benthic forms. CI indicates the fish position in the water column.

b) Relative body depth (RBD): maximum body depth divided by standard length (SL). Low values indicate an elongated fish. It is assumed to be directly related to the capacity for making vertical turns. A fish with a high RBD value has great maneuverability.

c) Relative head length (RHL): head length divided by SL. RHL should be high for predatory species.

d) Relative mouth width (RMW): interior lateral dimension of the opening when the mouth is fully opened, divided by SL.

e) Relative mouth height (RMH): interior dorsal-ventral dimension of the opening when the mouth is fully opened, divided by SL. Mouth dimensions would indicate, like head length, the relative size of prey.

f) Intestinal ratio (L_{DT}/L_S index): ratio digestive tube length/standard length. The relative gut length is expected to be related to feeding habits and diet composition.

All measurements were conducted with a plastic rule and calipers (to 1 mm of precision) in recently fixed specimens. A rectangular data matrix containing the mean values of the six ecomorphological attributes calculated for each of the four studied species (Table 1) was transformed into a cross-products matrix (variance/covariance) and submitted to a Principal Component Analysis (PCA), using the PC-ORD MjM Software (McCune & Mefford, 1999). The same rectangular matrix was also submitted to a Cluster Analysis to verify the morphological distance (or similarities) among the studied serranids (Gauch, 1982; Ludwig & Reynolds, 1988).

Results

Activity and habitat use. A total of 289 individuals of *D. formosum* (215 observed during the daytime, 37 at night, and 37 at twilight), 234 of *D. radiale* (222 during the daytime, seven at night, and five at twilight), 522 of *M. acutirostris* (385 during the daytime, 96 at night, and 41 at twilight), and 246 of *E. marginatus* (193 during the daytime, 21 at night, and 32 at twilight) were recorded during this study. These individuals were active only during the day and twilight hours (see details below). In contrast, all individuals were “inactive” or quiescent during the night (cf. Collette & Talbot, 1972), and could be easily captured with hand nets. During the twilight, individuals of *E. marginatus* and *M. acutirostris* > 200 mm SL appeared “excited”: they were outside their hiding places and were swam actively searching/sizing at prey (see “Feeding behavior and intra/interspecific associations”).

Diplectrum formosum: individuals < 130 mm SL were found both over sand/muddy and sandy/gravel bottoms, positioned in the water column and oriented against the water flux (Fig. 1a). Individuals < 100 mm SL were also near rocky reefs or inside depressions on soft bottom, associated with organic matter, benthic sessile invertebrates, or green algae (e.g., *Caulerpa* spp.). Individuals > 130 mm SL were found exclusively associated with sandy/gravel bottoms, stationary on their pelvic fins (Fig. 1b) (Table 2). Individuals were always stationary at night, resting on the bottom inside soft substratum depressions with organic matter or sessile organisms.

Diplectrum radiale: activity and habitat use was equal to the sand perches’ (Fig. 1c-d), but individuals > 130 mm SL were found exclusively associated with sand-muddy/muddy substrata (Table 2).

Epinephelus marginatus: always associated with rocky shores or reefs (Table 2). One hundred and eleven individuals were in contact with the bottom, inside rocky shelters or crevices (mostly individuals > 200 mm SL, that were rarely seen outside hiding places) (Fig. 1e), or among rocks (mostly individuals < 200 mm SL) (Fig. 1f). Thirty individuals were outside their shelters and patrolling the substratum, probably searching for benthic preys (mainly at twilight) (Fig. 1g). At night, dusky groupers hid into the deepest region of the rocky shelters or crevices and were more difficultly seen. The

Table 1. Ecomorphological attributes (average \pm standard deviation) calculated for *Diplectrum formosum* (n=12; SL \geq 130 mm); *D. radiale* (n=27; SL \geq 130 mm); *Epinephelus marginatus* (n=13; 200-305 mm SL); and *Mycteroperca acutirostris* (n=11; 180-247 mm SL). CI = compression index; RBD = relative body depth; RHL = relative head length; RMW = relative mouth width; RMH = relative mouth height; L_{DT}/L_S index = intestinal ratio (intraspecific variations of the gut length were mainly related to the amount of food and/or feces present).

Species	CI	RBD	RHL	RMW	RMH	L_{DT}/L_S index
<i>D. formosum</i>	1.38 \pm 0.104	0.24 \pm 0.025	0.33 \pm 0.023	0.15 \pm 0.014	0.16 \pm 0.028	0.98 \pm 0.153
<i>D. radiale</i>	1.29 \pm 0.085	0.25 \pm 0.010	0.34 \pm 0.013	0.16 \pm 0.015	0.16 \pm 0.024	0.97 \pm 0.135
<i>E. marginatus</i>	1.69 \pm 0.123	0.33 \pm 0.010	0.41 \pm 0.019	0.19 \pm 0.016	0.19 \pm 0.021	1.06 \pm 0.101
<i>M. acutirostris</i>	2.16 \pm 0.182	0.31 \pm 0.013	0.37 \pm 0.021	0.18 \pm 0.017	0.20 \pm 0.025	0.96 \pm 0.110

few individuals outside hiding places were always nearby shelter entrances.

Mycteroperca acutirostris: found on rocky shores, reefs, depressions in the soft substrata (n=16), and transition areas between hard and soft bottoms (Fig. 1h-l; Table 2). Individuals 200-300 mm SL (n=3) were on the bottom, inside bottom depressions with organic matter (Fig. 1h). Twenty five individuals were inside or nearby rocky shelters or crevices; individuals > 200 mm SL were hidden mainly during the night (n=7), and small individuals (n=18) were hidden during the day. When active, most of the large individuals were swimming in mid water (Fig. 1k-l), except for individuals inside bottom depressions (n=15) (Fig. 1h-i) or just stationary on the bottom (n=3) (Fig. 1j), performing a sit-and-wait strategy. Individuals < 300 mm SL that were stationary in the water column remained in an inclined posture, with the anterior part of the body turned upward toward the water surface. At night they were inactive (n=96), resting on the bottom and positioned in parallel with the rock walls (n=78) and were rarer inside rocky holes, crevices (n=12), or inside soft bottom depressions (n=6).

Feeding behavior and intra/interspecific associations. The studied serranids employed several tactics to capture their preys after visual detection. The visual detection could be realized by the movements of their eyes, which frequently

performed a series of target-acquiring and tracking movements accompanying free drifting items and moving organisms close to the bottom. The serranids also presented inquisitive behavior, with visual inspection of the surroundings and attention to anything that moved. *Mycteroperca acutirostris* captured small schooling fish, fish larvae and mysid shrimps at twilight and in the morning hours; *Diplectrum* specimens ate small benthic organisms during the day and twilight; and *E. marginatus* fed on decapods disturbed by the diurnal foraging activity of the goldspotted eel *Myrichthys ocellatus* (Anguilliformes: Ophichthidae; cf. Gerhardinger *et al.*, 2006). This kind of association was observed at least three times in the study area, and sometimes, comb grouper individuals also acted as followers together with the dusky groupers (Table 2).

The following nine feeding tactics were recorded during the study period (Table 2):

- "Picking at relatively small prey" (cf. Keenleyside, 1979).
- "Following behavior" (see Sazima, 1986; Gibran, 2002).
- "Sit-and-wait predation" (cf. Sazima, 1986).
- "Nibbling" (modified from Sazima, 1986); can be considered as a sub-category of "picking at relatively small prey"; used by opportunistic fishes that search the substratum to bite algae or organic matter to feed on their associated fauna.
- "Drift feeding" (cf. Grant & Noakes, 1987).
- "Ambush hunting" (modified from Keenleyside, 1979);

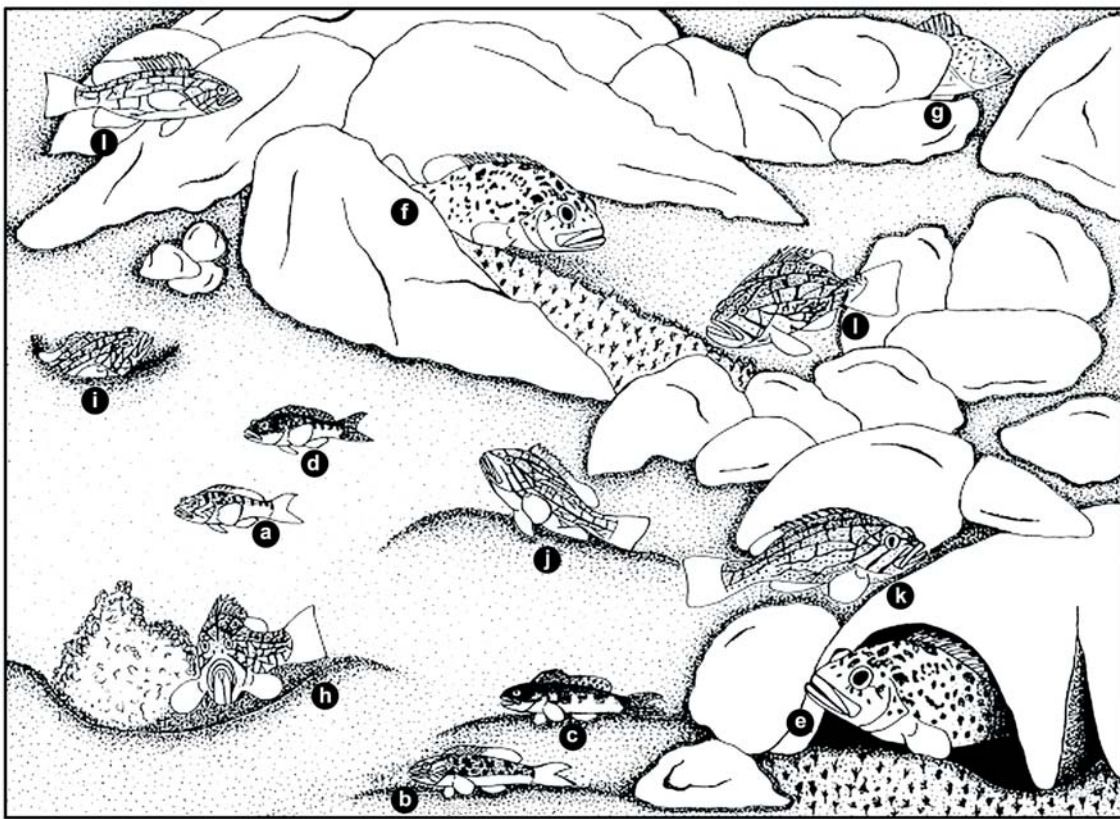


Fig. 1. Habitat partitioning by the four studied serranids during their feeding activity phases. *Diplectrum formosum* (a-b); *Diplectrum radiale* (c-d); *Epinephelus marginatus* (e-g); and *Mycteroperca acutirostris* (h-l). There is no scale among the fishes or between them and the environment.

the fish keeps stationary and inconspicuous on the bottom, by hiding and/or camouflage, thus surprising its preys (invertebrates or fish).

g) “Roving or patrolling” (modified from Sazima, 1986); used by fishes that swim actively in mid-water or just above the bottom, visually inspecting the surroundings and sizing their preys (invertebrates or fish). This tactic is a very commonly employed by Epinephelinae serranids during the changeover time (*i.e.*, at twilight hours, when they have peaks of activity; pers. obs.).

h) “Stalking predation” (*cf.* Sazima, 1986).

i) “Dying or illness feigning” (*cf.* Gibran, 2004); an unusual behavior that seems to be a modification of the stalking tactic.

Individuals of *D. formosum* and *D. radiale* > 100 mm SL, *E. marginatus* > 200 mm, and *M. acutirostris* 200-300 mm SL were solitary, while and *D. radiale* or *D. formosum* individuals < 100 mm SL were usually in groups (probably promoting the protection of the small sized fish group). *Epinephelus marginatus* and *M. acutirostris* < 200 mm SL were also found in groups of up to three individuals and *M. acutirostris* > 300 mm SL were usually in groups, patrolling (Table 2).

Diplectrum formosum: 252 individuals were engaged in feeding activities. Most of them (202) were < 130 mm SL and swam about 10 cm over the bottom, dispersed in the water

column and occasionally touching the bottom with their pelvic fins. On the other hand, individuals > 130 mm SL were always stationary on their pelvic fins (n=50). The species displayed the following feeding tactics: picking relatively small prey (n=12); stalking (n=1); nibbling (n=6); drift feeding (n=13) and following behavior (n=2). Individuals > 130 mm SL were exclusively sit-and-wait-predators (Table 2). During two occasions, when a small hunting individual had encountered a large one, the smaller individual was chased away by a short horizontal lunge. Also, some of the individuals that were swimming actively momentarily rubbed one side of their bodies against the substratum (n=7), probably performing “chafing behavior” (*cf.* Baerends & Baerends van Roon, 1950). This behavior is usually used to scrap parasites or fungus from the skin, but can also represent an “intimidating display”.

Diplectrum radiale: the 227 individuals engaged in feeding activities during the day and twilight presented the same behavioral pattern of *D. formosum*: individuals > 130 mm SL (n=13) were stationary on their pelvic fins employing sit-and-wait predation (n=4), alternatively with active feeding (n=2) through short lunges, and sizing prey on the substratum just ahead (picking at relatively small prey; n=9). A single individual was observed nibbling the substratum twice (algae or organic matter). On the other hand, individuals < 130 mm SL (n=173) were in the water column, up to 10 cm over the bot-

Table 2. Synthesis of the results obtained during the underwater observations. Each line of the group formation, habitats and microhabitats is in accordance to each size category of the standard length column (SL).

Species	SL (mm)	Group formation (number of individuals)	Habitats	Microhabitats	Feeding activity	Feeding tactics	Feeding associations
<i>Diplectrum formosum</i>	<100	1 to 10	soft bottoms	interface soft bottoms-hard	diurnal and crepuscular (feed mainly during daytime)	picking at relatively small prey; stalking; nibbling; drift feeding; sit-and-wait predation	following behavior with a sea star
	100-130	solitary	soft bottoms	substrata; inside soft bottoms depressions or associated to organic matter mass or algae			
<i>Diplectrum radiale</i>	>130	solitary	sandy or gravel bottoms	in the open, on the soft bottom	diurnal and crepuscular (feed mainly during daytime)	picking at relatively small prey; stalking; nibbling; drift feeding; sit-and-wait predation	following behavior with a sea star
	<100	1 to 10	soft bottoms	interface soft bottoms-hard			
<i>Epinephelus marginatus</i>	100-130	solitary	soft bottoms	substrata; inside soft bottoms depressions or associated to organic matter mass or algae	diurnal and crepuscular (feed mainly at twilight hours)	patrolling; ambush hunting	following behavior with the goldspotted eel
	>130	solitary	sand-muddy or muddy bottoms	in the open, on the soft bottom			
<i>Mycteroperca acutirostris</i>	<200	1 to 3	hard substrata	nearby algae and shelters; among rocks or inside hiding places	diurnal and crepuscular (feed mainly at twilight hours)	patrolling; ambush hunting; stalking; dying or illness feigning	following behavior with the goldspotted eel
	>200	solitary	hard substrata	among rocks or inside hiding places			
<i>Mycteroperca acutirostris</i>	<200	1 to 3	hard substrata and boundaries	nearby algae and shelters; over hard substrata	diurnal and crepuscular (feed mainly at twilight hours)	patrolling; ambush hunting; stalking; dying or illness feigning	following behavior with the goldspotted eel
	200-300	solitary	hard substrata and boundaries	inside soft bottoms depressions; over the bottom and in the water column			
	>300	1 to 15	hard substrata and boundaries	in the water column			

tom, moving actively their paired fins (like *D. formosum*) (Table 2). Three individuals < 130 mm SL were stationary on the substratum on their pelvic fins. Individuals < 100 mm SL were also observed together nearby rocky shores, and most of them were inside depressions on the soft bottom in groups of about six individuals. One 200 mm SL individual exhibited the same “chafing behavior” or “intimidating display” observed in *D. formosum*. Five individuals < 130 mm SL were capturing drift feeding items (nine times).

Two 150 mm SL *D. radiale* individuals were stationary on their pelvic fins on sand/muddy bottom during the evening twilight, performing sit-and-wait predation. One of these individuals was seizing an unidentified prey and afterwards was attracted by a moving sea star *Luidia senegalensis* (Echinodermata: Asteroidea), which it followed for up to 10 s (Table 2; see Gibran, 2002). It also performed “chafing behavior” or “intimidating display”.

Epinephelus marginatus: individuals > 200 mm SL were rarely seen outside hiding places, which they seem to leave just for a few minutes while they capture prey in the surroundings. Individuals < 200 mm SL used to leave their shelters to investigate observers when stationary and positioned in front of them (*i.e.*, “inquisitive behavior”). In three natural encounters, large individuals chased smaller ones. Another agonistic behavior observed was the use of the spines of the dorsal fin against other fish (*e.g.*, conspecifics and *Stegastes* species (damselfishes, Pomacentridae), promoting repulse. Individuals also used their fin spines as anchors, impeding their easy removal from hiding places. Additionally, some individuals exhibited expanded and conspicuous dorsal fin spines in an apparent intimidating behavior.

Mycteroperca acutirostris: individuals > 300 mm SL (n=122) were frequently in groups, patrolling the surroundings of the rocky shores (n=120), actively swimming about 2 m over the bottom and capturing prey in mid water (n=9), or more rarely (n=2) stationary on the gravel, solitary in the open. Individuals < 200 mm SL were the most inquisitive of the four studied serranids, followed by *E. marginatus* of the same size class. The larger *M. acutirostris* individuals were always more unconcerned than the smaller ones. Six individuals were capturing prey in the water column through a vertical lunge from the bottom to the surface (nine captures; see Fig. 1 of Bonaldo *et al.*, 2004: 104 for a photo of the initial posture of this serranid in an ambush). Two individuals were stalking and lunging prey items and one of them was performing dying or illness feigning (*cf.* Gibran, 2004: it captured five small fishes < 30 mm TL). Some *M. acutirostris* individuals 200-300 mm SL were also observed roving or patrolling, actively searching for prey (Table 2).

Similar to the two *Diplectrum* species, seven *M. acutirostris* individuals exhibited “chafing behavior” or “intimidating display” (10 times). In a unique natural encounter, the larger individual chased the smaller one, which was also observed during an interspecific encounter involving a hidden and larger *E. marginatus* and a small *M. acutirostris*.

Diet and food overlap. In the study area, the studied serranids can be considered crustacean feeders (Table 3; Fig. 2). Significant value of food overlap was found only between the *Diplectrum* species (Table 4).

Morphology and ecomorphological analysis. The studied serranids have small conic jaw teeth disposed in parallel series. Teeth are also present on the vomer, palate and pharynx. The guts of the four species are relatively short (Table 1), and pyloric caeca related to the protein richness of the diet were also found: *D. formosum* and *D. radiale* have an average of six caeca each, *E. marginatus* 20; and *M. acutirostris* 10. They have cryptic or disruptive body colors, which enables them to blend with the background (*cf.* Helfman *et al.*, 1997). They are also able to change their body color from pale to bright, providing crypticity or for intra- and interspecific communication (Randall, 1998).

Diplectrum formosum and *D. radiale* have elongated and cylindrical bodies, with relatively smaller mouths, and are very similar both morphologically and ecologically. On the other hand, *E. marginatus* and *M. acutirostris* have a more compressed and relatively taller body, with increased maneuverability, and relatively larger mouths. The basic morphological differences between *E. marginatus* and *M. acutirostris* are that the dusky grouper has a more robust body, with a greater mouth and head (head about 41% of SL). The dusky grouper has also a comparatively longer gut and is a benthic species (like the two *Diplectrum* species), while the comb grouper is the most compressed among the studied species, and an explorer of both the bottom and the water column. The comb grouper could be viewed as a nekto-benthic species (*cf.* Lincoln *et al.*, 1982; see Table 5 and Figs. 3-4).

Discussion

Activity and habitat use. The studied serranids are diurnal and crepuscular predators, but the *Diplectrum* species feed mostly during the daytime, as showed by this and previous studies (*e.g.* Bortone *et al.*, 1981; Meurer & Andreatta, 2002). These two species also showed spatial segregation related to the kind of substratum explored by their adult individuals (SL>130 mm), and *D. formosum* was always in areas with a greater transparency of water. In a study on blood parameters and abiotic conditions of different habitats, it was found that *D. formosum* prefers well oxygenated waters over a sandy bottom, while *D. radiale* lives in poorly oxygenated waters over muddy-clay bottoms and has higher oxygen affinity and number of erythrocytes (Mundaray & Pérez, 1988). *Diplectrum radiale* occurs more frequently on coastal habitats than *D. formosum* (Figueiredo & Menezes, 1980). Such bathymetrical distribution may be related to the distribution of marine substrata; since the sea bed at the São Sebastião Channel is mainly muddy, with just a few isolated sandy or gravel areas associated with some of its beaches, and at the proximities of rocky habitats.

During this study, *E. marginatus* and *M. acutirostris* were always found together and, on a larger spatial scale, these

Table 3. Frequency of occurrence (%) of food items of *Diplectrum formosum* (n=20); *D. radiale* (n=30); *Epinephelus marginatus* (n=30); and *Mycteroperca acutirostris* (n=30). A = average; SD = standard deviation; “-” indicates the absence of the correspondent item. *All of the porcelain crabs found in the dusky groupers’ stomach were *Petrolisthes galathinus*.

	<i>D. formosum</i>	<i>D. radiale</i>	<i>E. marginatus</i>	<i>M. acutirostris</i>
SL (mm)	37-170	53-202	140-305	105-247
SL: A±SD	117±46.8	165±40.7	201±41.4	169±34.5
Weight (g)	0.9-113.9	2.9-208.5	73.6-700	24.5-318.4
Weight: A±SD	52±42.3	126±55.8	232±143	118.4±72.4
n (with food items)	16	24	17	24
Food items	Frequency of occurrence (%)			
Crustacea	87.5	95.83	94.12	100
Decapoda	81.25	91.67	88.24	29.17
Natantia	75	79.17	23.53	29.17
Penaeidea	56.25	75	11.76	25
Caridea	18.75	4.17	-	-
Brachyura	25	37.5	35.29	-
Portunidae	18.75	25	-	-
Xanthidae	-	8.33	29.41	-
Leucosiidae	-	8.33	-	-
Calappidae	-	8.33	-	-
Majidae	-	-	5.88	-
Anomura	25	20.83	64.7	8.33
Porcellanidae	-	12.5	64.7*	-
Callianassidae	18.75	4.17	5.88	8.33
Hippidae	12.5	-	-	-
Mysidacea	25	4.17	-	87.5
Amphipoda	31.25	4.17	-	-
Caprellidae	31.25	-	-	-
Stomatopoda	-	4.17	-	-
Mollusca	18.75	16.67	-	4.17
Polychaeta	6.25	-	17.64	-
Ophiuroidea	-	12.5	-	-
Teleostei	37.5	54.17	5.88	4.17

species showed no marked differences on their habitat preferences. Different of the two *Diplectrum* species, at twilight *E. marginatus* and *M. acutirostris* increased their hunting activities. During this changeover time (cf. Hobson, 1965; Collette and Talbot, 1972) there is greater availability of crustaceans over the bottom, and clouds of fish larvae and young fishes are drifting and/or swimming close to the bottom. In addition, diurnal schooling fishes (e.g., anchovies and herrings) are easier to capture by stalking predators such as *M. acutirostris* in low lights. Furthermore, dusky groupers seem to take advantage of the twilight hours to prey on nocturnal crustaceans that are outside of their diurnal hiding places (pers. obs.). The crepuscular habits of the dusky groupers were also reported in other studies (e.g. Derbal & Kara, 1996) and, considering the opportunistic behavior of this species and the frequent occurrence of prey items with nocturnal habits in their guts, it may be possible that some occasional nocturnal feeding also occurs, at least under certain conditions (see Smale, 1986; Dodrill *et al.*, 1993).

Table 4. Food overlap ($C\lambda$) between each pair of the studied species (significant value is in bold type, when $C\lambda \geq 0.6$).

Pairs of species	$C\lambda$
<i>D. formosum</i> – <i>D. radiale</i>	0.83
<i>D. formosum</i> – <i>E. marginatus</i>	0.16
<i>D. formosum</i> – <i>M. acutirostris</i>	0.40
<i>D. radiale</i> – <i>E. marginatus</i>	0.30
<i>D. radiale</i> – <i>M. acutirostris</i>	0.24
<i>E. marginatus</i> – <i>M. acutirostris</i>	0.05

Dusky grouper individuals tend to stay close to their shelters. Indeed, juveniles of this species are cryptic, live closely associated with the bottom and do not stray far from crevices, an information which is in accordance to previous studies (e.g. Smith, 1961; Derbal & Kara, 1995; La Mesa *et al.* 2002). When out of such shelters, juveniles avoided visually exposed locations (such as convex substrata and very large visual fields), preferring flat or sub-horizontal rocky substrata (La Mesa *et al.*, 2002). This habitat dependency is probably more closely related to the need for shelter than for food (Parrish, 1987), and an important factor in determining the

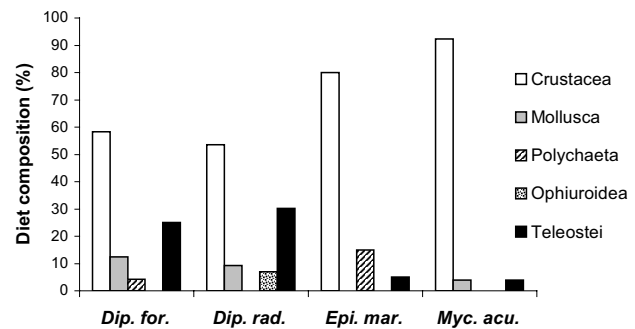


Fig. 2. Diet composition (%) of *Diplectrum formosum* (*Dip. for.*; n=16); *Diplectrum radiale* (*Dip. rad.*; n=24); *Epinephelus marginatus* (*Epi. mar.*; n=17); and *Mycteroperca acutirostris* (*Myc. acu.*; n=24), with the feeding items grouped in broad taxonomic categories.

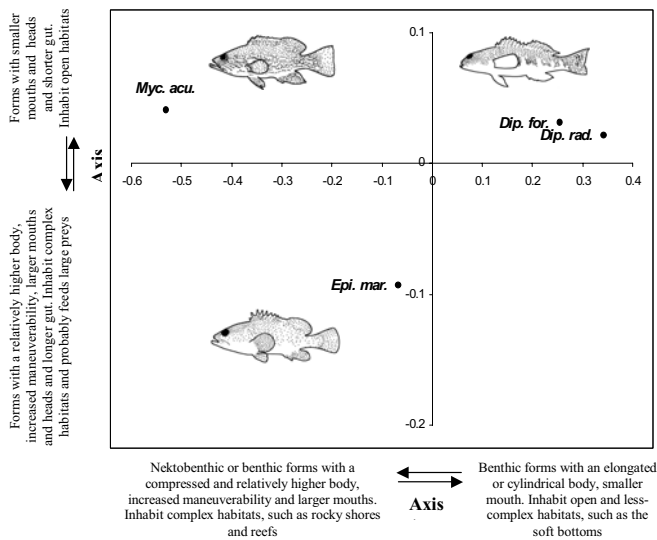


Fig. 3. Distribution of *Diplectrum formosum* (*Dip. for.*), *Diplectrum radiale* (*Dip. rad.*), *Epinephelus marginatus* (*Epi. mar.*), and *Mycteroperca acutirostris* (*Myc. acu.*) in ecomorphological space. Ordination is by the first two axes of PCA (cumulative % of variance = 99.9) (see Table 5). Line art fishes represent each genus (illustrations: Alexandre C. Ribeiro).

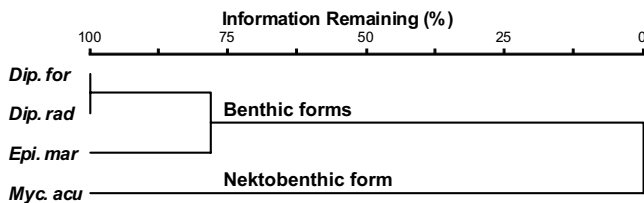


Fig. 4. Dendrogram of ecomorphological relationships (similarity) for *Diplectrum formosum* (*Dip. for.*), *Diplectrum radiale* (*Dip. rad.*), *Epinephelus marginatus* (*Epi. mar.*), and *Mycteroperca acutirostris* (*Myc. acu.*). Cluster analysis is by the Euclidean distance measure and Group Average linkage method. The principal difference between the two groups is the body form related to the vertical occupation of the water column.

microhabitat suitability for dusk groupers < 300 mm SL is certainly the availability of shelters, where the topographic variables are most important (La Mesa *et al.*, 2002; Machado *et al.*, 2003).

Previous studies have found that groupers shift to deeper depths as they grow (Derbal & Kara, 1995). At the study area, larger individuals of *E. marginatus* and *M. acutirostris* (400–600 mm SL) were frequently in waters up to 5 m depth, but only in protected sites where fishing was forbidden (pers. obs.). Thus, there is not necessarily a shift in groupers toward deeper waters with increasing size, but rather an enlargement of their bathymetric range, at least for undisturbed populations (La Mesa *et al.*, 2002), which explains this divergence between Derbal & Kara (1995) and the present study.

Feeding behavior and intra/interspecific associations. The four studied species are opportunistic predators. The *Diplectrum* species and *E. marginatus* explore prey mostly over the substratum, while *M. acutirostris* is a more versatile predator. A study on the feeding of the snowy grouper, *E. niveatus*, considered the possibility that the adults of this species are sedentary based on their stout-body and their diet, mostly composed of demersal decapods, in contrast with the slender-bodied and fast swimming serranids, such as *Mycteroperca* species (Dodrill *et al.*, 1993). Smale (1986) pointed out that *E. guaza* (= *E. marginatus*; cf. Heemstra, 1991) is a benthic reef-associated species usually found near caves. With its cryptic coloration this species is easily overlooked as it rests on the bottom. Like its congeners, they are ambush predators (see Randall, 1967; Collette & Talbot, 1972), lying in wait for prey to approach, then charging and engulfing the victim with its large mouth. All of these finds are in accordance with the present study.

Epinephelus marginatus, *M. acutirostris* and the *Diplectrum* species behaved as follower of other species in this study, a result which is in accordance to previous studies on serranids' feeding behavior, which found that such species can be considered as potential followers of substratum disturbance species (*e.g.*, Karplus, 1978; Dubin, 1982; Strand, 1988; Gibran, 2002). "Following" is a diurnal and widely distributed association, probably derived from inquisitive behavior and learning ability (see Diamant & Shpigel, 1985), that benefits the followers, which thus gain access to otherwise unavailable prey (see above-mentioned references).

Agonistic interactions frequently occurred between individuals of different life-stages, and *E. marginatus* was the only species which used its dorsal fin spines against other fishes. A raised dorsal fin is frequently used by territorial fishes as an advertisement signal (see *e.g.* Belk, 1975).

Diet. The two *Diplectrum* species fed mostly on crustaceans, including species that live associated with organic matter or algae. Infauna organisms were exclusively found in specimens collected over sand/muddy bottoms. This fact may be partially related to the feeding association between *Diplectrum* species and the sea star, since no *Diplectrum* individuals were observed ingesting mouthfuls of substratum, nor digging the bottom searching for prey. In previous studies, the sea star tube feet and its commensal porcelain crabs *Minyocerus angustus* are also potential food items of the two *Diplectrum* species (Gibran, 2002). The data comparison from the present study with previously published studies on the feeding habits of *Diplectrum* species (*e.g.*, Bortone, 1971; Bortone *et al.* 1981; Meurer & Andreatta, 2002) shows that there are few differences on food items among individuals which occur sympatrically, probably because of the local availability and abundance of prey items. Previous study found a positive correlation between the *D. radiale* length with the size and weight of its ingested preys, but a decrease in the number of prey items (Magro, 1996), which may be due to the reduction in the number of feeding tactics related to size, as

Table 5. Eigenvalues, eigenvectors, and variance extracted for the two principal axes of PCA. The correlation index values in bold type (*i.e.*, ≥ 0.6 ; negatives or positives) between each ecomorphological attribute and the correspondent axis were used to interpret the distribution of the four serranid species in the graphic of PCA (see Fig. 3).

	PCA axes	
	1	2
Eigenvalue	0.469	0.012
% of variance	97.464	2.462
Cumulative % of variance	97.464	99.926
	Eigenvectors	
CI	-0.9934	0.0708
RBD	-0.0848	-0.4522
RHL	-0.0494	-0.4763
RMW	-0.0324	-0.1948
RMH	-0.0496	-0.0994
LDT/LS	0.0039	-0.7182
	<i>r</i>	
CI	-1.000	0.011
RBD	-0.758	-0.642
RHL	-0.543	-0.833
RMW	-0.701	-0.670
RMH	-0.951	-0.303
LDT/LS	0.034	-0.987

observed herein. *Diplectrum formosum* and *D. radiale* can be regarded as generalists, although with a remarkable preference for decapod shrimps.

Diet is an indicator of habitat use. In this study, the principal food item of *E. marginatus* was the porcelain crab *P. galathinus*, an inhabitant of cracks and crevices of the rocky shores that was found inside or nearby the rocky holes where the dusky groupers obtained shelter, which corroborates the presumed sedentary habits of *Epinephelus* spp. (see Dodrill *et al.*, 1993). The importance of *P. galathinus* may suggest that it is abundant in the dusky groupers' habitat, because such serranids are opportunistic predators (*cf.* Barreiros & Santos, 1998). Previous studies had also classified juvenile dusky groupers (TL < 400 mm) as bottom crustaceans feeders (*e.g.*, Smale, 1986; Azevedo *et al.*, 1995), that explore resources exclusively from rocky substrata, where they would have simultaneously been afforded food and shelter. As they grow, fishes from rocky, seagrass and open soft-sediment habitats are consumed, which indicates an expansion of their trophic niches as the risk of predation declines (Reñones *et al.*, 2002). Indeed there are ontogenetic changes in the diet composition of the dusky grouper: crustaceans became less important with growth, while octopuses and fishes became more dominant (Smale, 1986). Furthermore, larger individuals took a wider range of preys than smaller ones, and the maximum size of prey chosen increased with growth, which is a general trend of predator-prey relationships and has been widely explained in terms of energy optimization and resource partitioning (Wootton, 1994). Similar findings were also reported in the Mediterranean (*e.g.*, Derbal & Kara, 1996; Reñones *et al.*, 2002; Linde *et al.*, 2004) and other Atlantic regions (*e.g.*, Azevedo *et al.*, 1995; Barreiros & Santos, 1998).

A study on the diet of four serranid species at the Senegalese coast found that teleostean fishes are the unique food items for the mottled grouper *M. rubra* (350-700 mm TL) (Diatta *et al.*, 2003). In the present study, *M. acutirostris* fed mostly on mysid shrimps, but it also preyed on schooling anchovies and herrings (*cf.* Hobson, 1968 found for the leopard grouper *M. rosacea*). Mysidaceans are small shrimplike peracarids often found in small clouds hovering over reefs (see Humann & DeLoach, 2003) band which are an important food resource for some serranids (see Meurer & Andreato, 2002). In the present study, the stomachs of the comb groupers with food contained hundreds of mysid shrimps < 4 mm TL and, based on the observations of *M. acutirostris* feeding behavior, it is supposed that they are captured by mouthfuls. Sazima (1986) pointed out that *M. acutirostris* (cited as *M. rubra*) is a predator species of benthic crustaceans and small fishes. The dying feigning feeding tactic described by Gibran (2004) for the comb grouper, and the behavioral observations made by Sazima (1986) and Bonaldo *et al.* (2004), corroborate the classification of this serranid as a versatile and opportunistic predator.

Food overlap. The results presented herein emphasize the ecological similarity between the two species of *Diplectrum*, but the field data showed that they present spatial segregation, at least for adult individuals (SL > 130 mm). A spatial segregation based on substratum preference, probably minimizing competition, was also found in a comparative study of *D. formosum* and the dwarf sand perch *D. bivittatum* (Bortone *et al.*, 1981). Juveniles of *D. formosum* and *D. radiale* coexist and explore a higher diversity of prey items, but use a higher number of feeding tactics in comparison with the adults. On the other hand, despite their co-occurrence, there is no overlap in diet between *E. marginatus* and *M. acutirostris*, as a consequence of their distinct use of resources, behavior, and vertical position in the water column. Many studies show that fish species with similar diets display trends to use and explore different habitats or microhabitats (see *e.g.*, Mundaray & Pérez, 1988). Schoener (1974) cites that spatial distribution and feeding resource partitioning are fundamental to community organization.

Morphological features, ecomorphology, and general considerations. Morphological features are considered as important to infer trophic ecology, since they determine how and what a fish can eat and, thus, morphology may be regarded as a predictor of the way-of-life (Wootton, 1994). In this context, species with similarities in morphology will have similarities in their diet composition. Motta (1988) compared the morphology and diet of ten species of butterflyfishes (Chaetodontidae) and concluded that morphology is not a good diet predictor, although it can infer how a fish can eat. Closely related, morphologically similar species frequently co-occur in ecological communities, and several specific mechanisms could enable the long-term presence of these potential competitors (Schmitt & Coyer, 1982). One possibil-

ity is the divergence over evolutionary time in morphology and/or behavior, which will result in the use of different resources; in this context, resource partitioning has been viewed as evidence for the existence of competition in the past (Schoener, 1974). However, it is difficult to determine whether competition or some other mechanism is responsible for shifts in resource use. While competition among sympatric species is one possibility, shifts in resource use could simply reflect the independent evolution of traits among allopatric species responding to different sets of environmental constraints (Connell, 1980).

Both morphology and behavior can influence patterns of prey capture (Schmitt & Coyer, 1982). Among fishes, morphology has often been found to determine the type of prey obtained (e.g., Keast & Webb, 1966). Some studies suggest that foraging behavior, rather than external morphology, is the critical variable accounting for the observed interspecific differences (see Schmitt & Coyer, 1982). The present study verified that the comb grouper *M. acutirostris*, in spite of a relatively large mouth, feeds on relatively smaller prey, but in great volume. Mouth size itself was not a good predictor of prey utilization (see also Hartney, 1989). A large mouth with numerous curved and pointed teeth is frequently found in carnivorous species, such as in the studied serranids. The *Diplectrum* species studied and *E. marginatus* feed on large prey items (with up to 20–37% of their SL), but the dusky groupers eat them more frequently since its diet is mainly composed of anomurans and crabs.

The guts of the studied serranids are relatively short, which is expected in carnivore species (cf. Wootton, 1994). The relatively longer gut of *E. marginatus* is probably related to the large and voluminous items found in it. The existence of pyloric caeca in all studied species is also related to protein digestion and carnivorous habits (Gatz, 1979), and their cryptic or disruptive body colors are a common feature shared by many lurking predators (cf. Helfman *et al.*, 1997: 334–335). The body of a disruptively colored fish has areas of contrasting color that break up the outline of the fish, making it appear unfishlike and making it more difficult to discern at low light levels (cf. Helfman *et al.* 1997), which is corroborated by the crepuscular peaks of hunting activity for the studied Epinephelinae. On the other hand, the conspicuous coloration exhibited by *D. formosum*, in contrast to *D. radiale*, may be related to its habitat: *D. formosum* inhabits sandy/gravel bottoms in which water is more transparent than over sand-muddy or muddy substrata, and coloration is almost always related to visual communication and/or camouflage.

Fast, powerful and short propulsion is another feature related to lurking. The *Diplectrum* species studied and *M. acutirostris* have truncated caudal fins, while the caudal fin of *E. marginatus* is rounded. Fish with truncated or rounded tails are comparatively slow swimmers and, although capable of sudden bursts of speed, are unable to swim for long times at high speed (cf. Norman & Greenwood, 1963). All the studied serranids are lurking predators, and the distinction of their caudal fins in truncated or rounded is also in accordance to

their life-style: the rounded fin of the dusky groupers is in accordance with its more sedentary habits, while the truncated fin shape of the *Diplectrum* species and *M. acutirostris* are in accordance with their more active feeding habits. The body shapes of the dusky groupers and the comb groupers, in contrast with the body shapes of the *Diplectrum* species, are also in accordance with their biology: the morphological design of the *Diplectrum* species is more related to a benthic lifestyle in the open, while the compressed and relatively higher body of the studied species of Epinephelinae gives them a greater maneuverability, which is closely related to their lives associated with complex habitats such as rocky shores and reefs. Considering the morphological aspects, volume, and shape of the epinepheline body, as well as their biological implications and field observations in the present study, *M. acutirostris* and all slender-bodied *Mycteroperca* species can be regarded as “fast” swimming serranids, while the *Epinephelus* groupers, such as *E. marginatus*, are more robust and sedentary forms, which is in accordance with the finds of Dodrill *et al.* (1993). Ecomorphological analyses can be useful to infer lifestyles, but it should be used with caution and always complemented by direct field observations.

During and after this study, it was verified that there is another common serranid in the study area: the twinspace bass *Serranus flaviventris* (adults about 120 mm TL), a small benthic sit-and-wait diurnal predator inhabitant of rocky shores and reefs that was also observed feeding with the use of the “picking at relatively small prey” tactic. The twinspace bass can be regarded as an ecomorphological equivalent of the *Diplectrum* species from hard substrata (FZG, unpub. data) – their similarities both in morphology and behavior may be related to a shared ancestry as members of the Serraninae (see Kendall, 1984; Smith & Craig, 2007).

Epinephelus marginatus was recently nominated as *Mycteroperca marginatus* (Craig & Hastings, 2007), although this change is not currently supported by morphological synapomorphies. Whether or not in the same genus, the dusky groupers and the comb groupers have different life strategies and diverge from the same morphological and behavioral basic body plan of their common ancestor.

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Literature Cited

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behavior*, 49(3/4): 227-265.
- Azevedo, J. M. N., J. B. Rodrigues, M. Mendizabal & L. M. Arruda. 1995. Study of a sample of dusky groupers, *Epinephelus marginatus* (Lowe, 1834), caught in a tide pool at Lajes do Pico, Azores. *Boletim do Museu Municipal do Funchal, Suplemento* (4): 55-64.
- Baerends, G. P. & J. M. Baerends van Roon. 1950. An introduction to the study of the ethology of cichlid fishes. *Behaviour Supplements*, 1: 1-242.
- Barreiros, J. P. & R. S. Santos. 1998. Notes on the food habits and predatory behaviour of the dusky grouper, *Epinephelus marginatus* (Lowe, 1834) (Pisces: Serranidae) in the Azores. *Arquipélago, Life and Marine Sciences*, 16A: 29-35.
- Belk, M. S. 1975. Habitat partitioning in two tropical reef fishes, *Pomacentrus lividus* and *P. albofasciatus*. *Copeia*, 1975(4): 603-607.
- Bonaldo, R. M., J. P. Krajewski & I. Sazima. 2004. Does the association of young fishes with jellyfishes protect from predation? A report on a failure case due to damage to the jellyfish. *Neotropical Ichthyology*, 2(2): 103-105.
- Bortone, S. A. 1971. Studies on the biology of the sand perch, *Diplectrum formosum* (Perciformes: Serranidae). Florida Department of Natural Resources, Technical Series, 65.
- Bortone, S. A., P. Rebenack & D. M. Siegel. 1981. A comparative study of *Diplectrum formosum* and *D. bivittatum* (Pisces: Serranidae). *Florida Scientist*, 44(2): 91-96.
- Bowen, S. H. 1992. Quantitative description of the diet. Pp. 325-336. In: Nielsen, L. A. & D. L. Johnson (Eds.). *Fisheries Techniques*. Blacksburg, American Fisheries Society, 468p.
- Carvalho-Filho, A. 1999. *Peixes: costa brasileira*. 3ª ed. São Paulo, Editora Melro, Ltda., 320p.
- Casatti, L. & R. M. C. Castro. 2006. Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. *Neotropical Ichthyology*, 4(2): 203-214.
- Collette, B. B. & F. H. Talbot. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *Bulletin of the Natural History Museum of Los Angeles County*, 14: 98-124.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghosts of competition past. *Oikos*, 35: 131-138.
- Craig, M. T. & P. A. Hastings. 2007. A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of the Epinephelini. *Ichthyological Research*, 54: 1-17.
- Derbal, F. & M. H. Kara. 1995. Habitat et comportement du mérour *Epinephelus marginatus* dans la région d'Annaba (Algérie). *Cahiers de Biologie Marine*, 36: 29-32.
- Derbal, F. & M. H. Kara. 1996. Alimentation estivale du mérour, *Epinephelus marginatus* (Serranidae), des cotes est algériennes. *Cybium*, 20(3): 295-301.
- Diamant, A. & M. Shpigel. 1985. Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Aqaba). *Environmental Biology of Fishes*, 13(2): 153-159.
- Diatta, Y., A. Bouaïn, F. L. Clotilde-Ba & C. Capapé. 2003. Diet of four serranid species from the Senegalese coast (Eastern tropical Atlantic). *Acta-Adriatica*, 44(2): 175-182.
- Dodrill, J., C. S. Manooch III & A. B. Manooch. 1993. Food and feeding behavior of adult snowy grouper, *Epinephelus niveatus* (Valenciennes) (Pisces: Serranidae), collected off the central North Carolina coast with ecological notes on major food groups. *Brimleyana*, 19: 101-135.
- Dubin, R. E. 1982. Behavioral interactions between Caribbean reef fish and eels (Muraenidae and Ophichthidae). *Copeia*, 1982(1): 229-232.
- Figueiredo, J. L. & N. A. Menezes. 1980. Manual de peixes marinhos do sudeste do Brasil. III. Teleostei (2). São Paulo, MZUSP, 90p.
- Gatz, A. J., Jr. 1979. Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany*, 21(2): 91-124.
- Gauch, H. G., Jr. 1982. *Multivariate analysis in community ecology*. New York, Cambridge University Press, 298p.
- Gerhardinger, L. C., M. Hostim-Silva, R. Samagaia, & J. P. Barreiros. 2006. A following association between juvenile *Epinephelus marginatus* (Serranidae) and *Myrichthys ocellatus* (Ophichthidae). *Cybium*, 30(1): 82-84.
- Gibran, F. Z. 2002. The sea basses *Diplectrum formosum* and *D. radiale* (Serranidae) as followers of the sea star *Luidia senegalensis* (Asteroidea) in southeastern Brazil. *Brazilian Journal of Biology*, 62(4A): 591-594.
- Gibran, F. Z. 2004. Dying or illness feigning: an unreported feeding tactic of the comb grouper *Mycteroperca acutirostris* (Serranidae) from the Southwest Atlantic. *Copeia*, 2004(2): 402-405.
- Grant, J. W. A. & D. L. G. Noakes. 1987. A simple model of optimal territory size for drift-feeding fish. *Canadian Journal of Zoology*, 65: 270-276.
- Hartney, K. B. 1989. The foraging ecology of two sympatric gobiid fishes: importance of behaviour in prey type selection. *Environmental Biology of Fishes*, 26: 105-118.
- Heemstra, P. C. 1991. A taxonomic revision of the eastern Atlantic groupers (Pisces: Serranidae). *Boletim do Museu Municipal do Funchal*, 43(226): 5-71.
- Helfman, G. S. 1992. Underwater methods. Pp. 349-369. In: Nielsen, L. A. & D. L. Johnson (Eds.). *Fisheries Techniques*. Blacksburg, American Fisheries Society, 468p.
- Helfman, G. S., B. B. Collette & D. E. Facey. 1997. *The diversity of fishes*. Malden, Blackwell Science, Inc., 528p.
- Hobson, E. S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia*, 1965(3): 291-302.
- Hobson, E. S. 1968. Predatory behaviour of some shore fishes in the Gulf of California. *Research Report of the United States Fish and Wildlife Service*, 73: 1-92.
- Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *American Naturalist*, 100: 419-424.
- Humann, P. & N. DeLoach. 2003a. Reef fish identification. Enlarged 3rd ed. Jacksonville, New World Publications, Inc., 481p.
- Humann, P. & N. DeLoach. 2003b. Reef creature identification. Enlarged 2nd ed. Jacksonville, New World Publications, Inc., 420p.
- Hynes, H. B. N. 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology*, 19: 36-57.
- Johnson, G. D. 1983. *Niphon spinosus*: a primitive epinepheline serranid, with comments on the monophyly and intrarelationships of the Serranidae. *Copeia*, 1983(3): 777-787.
- Karplus, I. 1978. A feeding association between the grouper *Epinephelus fasciatus* and the morey eel *Gymnothorax griseus*. *Copeia*, 1978: 164.
- Karr, J. R. & F. C. James. 1975. Eco-morphological configurations

- and convergent evolution of species and communities. Pp. 258-291. In: Cody, M. L. & J. M. Diamond (Eds.). *Ecology and Evolution of Communities*. Cambridge, Harvard University Press, 545p.
- Keast, A. & D. Webb. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *Journal of the Fisheries Research Board of Canada*, 23(12): 1845-1874.
- Keenleyside, M. H. A. 1979. *Diversity and Adaptation in Fish Behavior*. Berlin, Springer-Verlag, 208p.
- Kendall, A. W. Jr. 1984. Serranidae: development and relationships. Pp. 499-510. In: Moser, H. G. *et al.* (Eds.). *Ontogeny and Systematics of Fishes*. Ahlstrom Symposium. Special Publications No. 1. American Society of Ichthyologists and Herpetologists.
- La Mesa, G., P. Louisy & M. Vacchi. 2002. Assessment of microhabitat preferences in juvenile dusky grouper (*Epinephelus marginatus*) by visual sampling. *Marine Biology*, 140(1): 175-185.
- Lincoln, R. J., G. A. Boxshall & P. F. Clark. 1982. *A dictionary of ecology, evolution and systematics*. Cambridge, Cambridge University Press, 313p.
- Linde, M., A. M. Grau, F. Riera & E. Massutí-Pascual. 2004. Analysis of trophic ontogeny in *Epinephelus marginatus* (Serranidae). *Cybium*, 28(1): 27-35.
- Ludwig, J. A. & J. F. Reynolds. 1988. *Statistical ecology*. New York, John Wiley & Sons, Inc., 337p.
- Machado, L. F., A. B. Andrade, M. Hostim-Silva & J. P. Barreiros. 2003. Habitat use by the juvenile dusky grouper *Epinephelus marginatus* and its relative abundance, in Santa Catarina, Brazil. *Aqua, Journal of Ichthyology and Aquatic Biology*, 6(4): 133-138.
- Magro, M. 1996. Hábitos alimentares de peixes demersais da região do Saco de Mamanguá, Parati, Rio de Janeiro (Brasil). Unpublished Master Dissertation, Universidade de São Paulo, São Paulo. 235p.
- McCune, B. & M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4. Gleneden Beach, Oregon, MjM Software Design, 237p.
- Meurer, B. C. & J. V. Andreata. 2002. Hábito alimentar de *Diplacrum radiale* (Quoy & Gaimard, 1824) (Teleostei, Perciformes, Serranidae) na Baía da Ribeira, Angra dos Reis, Rio de Janeiro, Brasil. *Arquivos do Museu Nacional, Rio de Janeiro*, 60(4): 315-320.
- Morisita, M. 1959. Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science, Kyushu University, Series E, Biology*, 3: 65-80.
- Morris, A. V., C. M. Roberts & J. P. Hawkins. 2000. The threatened status of groupers (Epinephelinae). *Biodiversity and Conservation*, 9: 919-942.
- Motta, P. J. 1988. Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Environmental Biology of Fishes*, 22(1): 39-67.
- Motta, P. J. & K. M. Kotschal. 1992. Correlative, experimental, and comparative evolutionary approaches in ecomorphology. *Netherlands Journal of Zoology*, 42(2-3): 400-415.
- Motta, P. J., S. F. Norton & J. J. Luczkovich. 1995. Perspectives on the ecomorphology of bony fishes. *Environmental Biology of Fishes*, 44(1-3): 11-20.
- Mundaray, E. & J. E. Pérez. 1988. Ambiente y parametros sanguineos en dos especies sibilinas de peces. *Ecologia, Acta Científica Venezolana*, 39: 181-183.
- Nelson, J. S. 2006. *Fishes of the world*. 4th ed. Hoboken, John Wiley & Sons, Inc., 601p.
- Norman, J. R. & P. H. Greenwood. 1963. *A history of fishes*. 2nd ed. London, Ernest Benn, Ltd., 398p.
- Parrish, J. D. 1987. The trophic biology of snappers and groupers. In: Polovina, J. J. & S. Ralston (Eds.). *Tropical Snappers and Groupers: Biology and Fisheries Management*. Boulder, Westview Press, 659p.
- Randall, J. E. 1967. Food habits of reef fishes of the West Indies. *Proceedings of the International Conference on Tropical Oceanography: Studies in Tropical Oceanography*, 5: 665-847.
- Randall, J. E. 1998. Groupers, seabasses, and their allies. Pp. 195-199. In: Paxton, J. R. & W. N. Eschmeyer (Eds.). *Encyclopedia of Fishes*. 2nd ed. San Diego, Academy Press Inc., 240p.
- Renônes, O., N. V. C. Polunin & R. Goni. 2002. Size related dietary shifts of *Epinephelus marginatus* in a western Mediterranean littoral ecosystem: an isotope and stomach content analysis. *Journal of Fish Biology*, 61(1): 122-137.
- Robins, C. R. & G. C. Ray. 1986. *A field guide to Atlantic coast fishes of North America*. Boston, Houghton Mifflin Company, 354p.
- Rodrigues, S. A. & R. M. Rocha. 1993. Littoral compound ascidians (Tunicata) from São Sebastião, Estado de São Paulo, Brazil. *Proceedings of the Biological Society of Washington*, 106: 728-739.
- Sazima, I. 1986. Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *Journal of Fish Biology*, 29: 53-65.
- Schmitt, R. J. & J. A. Coyer. 1982. The foraging ecology of sympatric marine fish in the genus *Embiotoca* (Embiotocidae): importance of foraging behavior in prey size selection. *Oecologia*, 55: 369-378.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science*, 185: 27-39.
- Shreeves, K., B. Wohlers & B. Shuster. 1991. PADI adventures in diving – advanced training for open water divers. Santa Ana, PADI, 263p.
- Sluka, R., M. Chiappone & K. M. Sullivan. 1994. Comparison of juvenile grouper populations in southern Florida and the central Bahamas. *Bulletin of Marine Science*, 54: 871-880.
- Smale, M. J. 1986. The feeding biology of four predatory reef fishes off the south-eastern Cape coast, South Africa. *South African Journal of Zoology*, 21: 111-130.
- Smith, C. L. 1961. Synopsis of biological data on groupers (*Epinephelus* and allied genera) of the western North Atlantic. *FAO Fisheries Biology Synopses*, 23: 1-61.
- Smith, W. L. & M. T. Craig. 2007. Casting the percomorph net widely: the importance of broad taxonomic sampling in the search for the placement of serranid and percoid fishes. *Copeia*, 2007(1): 35-55.
- Strand, S. 1988. Following behaviour: interespecific foraging associations among Gulf of California reef fishes. *Copeia*, 1988(2): 351-357.
- Wootton, R. J. 1994. *Ecology of teleost fishes*. London, Chapman & Hall, 404p.
- Zaret, T. M. & A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology*, 52(2): 336-342.

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