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José de Anchieta Cintra da Costa Nunes

Influência da exposição de ondas, tamanho de grupo e complexidade do habitat no forrageio e densidades de peixes do gênero *Halichoeres* (Labridae) em costões rochosos tropicais

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Dissertação apresentada ao Instituto de Biologia da Universidade Federal da Bahia, para obtenção do título de Mestre em Ecologia e Biomonitoramento.

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Entender os efeitos da estrutura do habitat sobre a densidade de peixes é fundamental para avaliar por quais variáveis estes são influenciados. A composição do substrato é uma variável ambiental capaz de influenciar comportamento e distribuição dos peixes. A estrutura distinta e a fauna associada a diferentes tipos de substrato podem oferecer diversos tipos de recursos (*e.g.* presas e refúgios), assim as características estruturais dos substratos podem influenciar as atividades e densidades dos peixes.

O comportamento de forrageio é um aspecto importante no uso do habitat pelos peixes. Recentemente estudos realizados em campo e laboratório investigaram os efeitos do fluxo d'água sobre o comportamento e processos energéticos de peixes recifais. Exposição a ondas foi indicada por estes estudos como um dos fatores que influenciam as atividades dos peixes e as seguintes generalizações foram feitas: peixes com diferentes capacidades natatórias respondem em diferentes graus ao hidrodinamismo e em locais com intenso fluxo d'água, os peixes passam mais tempo abrigados refúgios (ex. tocas). A formação de cardumes é conhecida como um importante mecanismo anti-predador, os benefícios de 'muitos olhos' incluem a detecção rápida, além de gerar confusão, aos predadores, reduzindo sua eficiencia. Além disso, o compartilhamento de informações no cardume pode resultar em uma menor procura por comida.

Dentre as famílias de peixes recifais, Labridae é uma das mais diversas e comuns em recifes rasos com aproximadamente 600 espécies encontradas em águas tropicais, subtropicais e temperadas dos oceanos Atlântico, Índico e Pacífico. A maioria das espécies não ultrapassa 25 cm de comprimento, embora o tamanho máximo registrado alcance 2 m. Para a maioria das espécies as fases iniciais (FI) e terminais (FT) são facilmente identificados visualmente, além do sexo. As espécies maiores possuem importância econômica, pois são utilizadas na alimentação, enquanto que as menores são comercializadas com fins ornamentais.

Os labrídeos possuem grande diversidade no formato do corpo e nas adaptações voltadas para alimentação e, consequentemente, possuem grande versatilidade trófica; sendo importantes na estruturação da comunidade recifal. São comumente invertívoros, enquanto outros quando jovens, são considerados limpadores, removendo ectoparasitos e tecido necrosado de outros peixes. Apesar da família Labridae ter sido foco de estudos nos Oceanos Pacífico e Atlântico Norte, poucos são conhecidos no Atlântico Sul.

Estes peixes exibem uma diversidade de padrões comportamentais e de microhabitats preferenciais durante o forrageio, apesar dos avanços no entendimento entre o forrageio de peixes e escolha de micro-habitats da família Labridae, a maioria dos estudos foram conduzidos em ambientes com alta diversidade de corais. Estes ambientes são estruturalmente complexos e oferecem uma ampla gama de condições ambientais, como consequência esses peixes podem se especializar para viver/usar ambientes com características particulares.

Nós estudamos a influência da complexidade do habitat, tamanho do grupo e exposição as ondas sobre as densidades e atividade de forrageio, incluindo a influencia do tamanho do cardume e fase de vida sobre forrageio, de três espécies do gênero *Halichoeres* (Labridae), sendo duas endêmicas, em nove costões rochosos tropicais no Brasil. Essas espécies são influenciadas pela exposição de ondas, em geral, fases iniciais destas espécies foram mais influenciadas com a exposição do que as fases terminais, exceto *H. brasiliensis* FT que não teve influência da exposição sobre atividade de forrageio. Embora as FI tivessem associações com rugosidade e algas e FT com profundidade, a complexidade do habitat não influenciou o forrageio dessas espécies. Nós também encontramos variações no microhabitat preferencial de forrageio e diferenças no conteúdo estomacal foram observadas entre as espécies e as fases. O tamanho do cardume influenciou a atividade de forrageio, exceto para *H. brasiliensis*. Nós acreditamos que o uso comportamental de microhabitats pode ser uma grande ferramenta para investigar padrões de distribuição entre recifes de coral e costões rochosos tropicais, gerando subsídios para seu manejo e conservação.

Este trabalho será submetido para revista *Marine Biology*. Normas podem ser acessadas ao final do manuscrito.

How wave exposure, group size and habitat complexity influence fish forage and densities of the genus *Halichoeres* (Perciformes: Labridae) in tropical rocky shores?

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Abstract

Wave exposure and habitat complexity have been used for explain patterns of variation in the distribution and behavior of many reef fishes. Here we studied the influence of these factors on densities and foraging activity, including the influence of group size on foraging, of three species of the genus *Halichoeres* (Labridae) in nine tropical rocky shores in Brazil. Our study showed that *Halichoeres* species are influenced by wave exposure in tropical rocky shores, in general, Initial phases (IP) of the three species analyzed were influenced more with exposure than Terminal phases (TP), except for *H. brasiliensis* TP, where exposure had no influence on foraging. IP of the species there were associated with rugosity and algae and TP with depth, habitat complexity also influence on foraging of these species. We also found variations of microhabitat patches used for foraging between species and differences in the stomach contents were found between species and phases. Group size had influence on foraging activity, except for *H. brasiliensis* TP. We believe that behavioral use of microhabitats can be a great tool to investigate distribution patterns of fish between coral reefs and tropical rocky shores.

Key words: wave exposure, group size, habitat complexity, fish forage, densities, *Halichoeres*, Brazil

Resumo

Exposição as ondas e complexidade do habitat tem sido usado para explicar padrões de variação na distribuição de muitas espécies de peixes recifais. Nós estudamos a influência desses fatores sobre as densidades e atividade de forrageio, incluindo a influencia do tamanho do grupo sobre forrageio, de três espécies do gênero *Halichoeres* (Labridae) em nove costões rochosos tropicais no Brasil. Nosso estudo mostrou que estas espécies são influenciadas pela exposição de ondas, em geral, fases iniciais (FI) destas espécies analisadas foram mais influenciadas com a exposição do que as fases terminais (FT), exceto *H. brasiliensis* FT que não teve influência da exposição sobre atividade de forrageio. FI tiveram associações com rugosidade e algas e FT com profundidade, a complexidade do habitat também influenciou o forrageio dessas espécies. Nós também encontramos variações no microhabitat preferencial de forrageio entre as espécies e diferenças no conteúdo estomacal foram encontradas entre as espécies e as fases. O tamanho do grupo influenciou a atividade de forrageio, exceto para *H. brasiliensis*. Nós acreditamos que o uso comportamental de microhabitats pode ser uma grande ferramenta para investigar padrões de distribuição entre recifes de coral e costões rochosos tropicais.

Palavras Chave: exposição de onda, tamanho do grupo, complexidade do habitat, forrageio de peixe, densidades, *Halichoeres*, Brasil

Introduction

One of the most important questions in reef ecology is the understanding of how fish communities are structured by environmental variables (Jones and Syms 1998; Bellwood and Wainwright 2002). In fact several studies have examined the effect of these and also of biotic variables on the structure of fish communities (Gladfelter and Gladfelter 1978, Luckhurst and Luckhurst 1978; Chabanet et al. 1997; Ornellas and Coutinho 1998; Arbutus-Oropeza and Balart 2001; Ferreira et al. 2001).

According to Chaves and Monteiro-Neto (2009), habitat type and availability can influence the distribution, richness, density and biomass of fish. Thus, the habitat complexity can be an important factor explaining richness and diversity of species, providing shelter from predators (Hixon and Beets 1993) and potentially changing competitive interactions and survival (Jones 1988; Syms and Jones 2000).

Reef fishes in tropical rocky shores had little attention, probably because in this region studies are focused in corals reefs. Ferreira et al. (2001) showed that many studies investigated the factors that can influence reef fishes communities, but the great majority of these have been carried out on corals, few have focused on rocky shores, especially in tropical areas (Ferreira et al. 2001). Despite their low complexity when compared to coral reefs, tropical rocky shores and adjacent environments can support a rich reef fauna and flora (Ferreira et al. 1998; Guimaraes and Coutinho 1996; Ornellas and Coutinho 1998).

Understanding the effects of habitat structure on the density of fish is essential to assess which variables are important and if current predictions (e.g. the influence of algae and corals on fish densities) can be also applied to different reef environments, like rocky reefs. Habitat complexity, as composition of the substratum, can influence behavior and distribution of fish (Jones and Syms 1998, Floeter et al. 2007, Krajewski et al. 2010). According to Krajewski et al. (2010), distinctive structure and fauna associated with different types of substratum can offer different types of resources (e.g. prey and shelter) and can influence the activities of fish.

Wave exposure has been considered one of the key factors in shaping coral reef fish assemblages, thus, fish with different swimming abilities will be affected by hydrodynamics. Field and laboratory studies investigated the effects of water flow on the behavior and energy processes of reef fishes (Bellwood and Wainwright 2001, Fulton et al. 2001; Fulton and Bellwood 2002). In places with an intense water flow, the fish spend more time in refuges (Bellwood and Wainwright 2001, Fulton and Bellwood 2002a; Fulton et al. 2005; Floeter et al. 2007; Johansen et al. 2007).

Foraging behavior is a key aspect of habitat use by animals, including fish (Fulton and Bellwood 2002). The optimal foraging theory considers the distribution of prey within patches of microhabitats and continuous compensation, associated with excursions between or within patches, as important factors that affect foraging (MacArthur and Pianka 1966, Schoener 1971, Norberg 1977). Studies suggested that foraging depends on the distribution and size of patches of preferred habitat (Covich 1976; Fulton and Bellwood 2002).

Aggregation with other foragers is a common risk-reduction strategy, allowing more time to be spent foraging without incurring a higher probability of being eaten (White and Warner 2007), thus foraging in a group has been suggested as a way to reduce risk and to enhance the amount of information regarding where to find food and how long to stay in a patch of a certain quality (Steinberg and Persson 2005). Aggregation to forage is a common strategy among coral reef fishes (Connel and Gillanders 1997), for example, surgeonfish (Acanthuridae) and parrotfish (Labridae) forage more efficiently in large groups (Wolf 1987; Clifton 1991). By contrast, fish in high-density aggregations may forage less effectively or simply to spend less time foraging and they may also experience interference competition while foraging (Buckel and Stoner 2004).

The fishes of the Labridae family have a great variety of body shapes and several morphological adaptations for feeding and, consequently, have trophic versatility, being important in structuring reef communities (Randall 1967; Hobson 1974; Deloach and Humann 1999). Although these fishes have been the focus of studies in the Pacific Ocean and in the North Atlantic (Thresher 1979; Bellwood and

Wainwright 2001; Jones 2005; Jones 2006), few have been conducted in the South Atlantic (Sazima et al. 1998; Francini-Filho et al. 2000; Sazima et al. 2005; Coni et al. 2007; Coni et al. 2010).

Wrasse fish exhibit a variety of behavioral patterns and preferred microhabitats for foraging, a generalization is the existence of a positive relationship between swimming ability and foraging distance (Fulton and Bellwood 2002; Jones 2002). Most studies involving foraging micro-habitats of the family Labridae were conducted in coral reef environments. These are structurally complex environments and offer a large amount of environmental conditions, as a consequence of these fish can specialize to live and use fairly specific habitats (Krajewski et al. 2010).

The genus *Halichoeres* is considered highly diverse and widely distributed in the Atlantic Ocean (Barber and Bellwood 2005). These wrasses are diurnal, perform opportunistic behavior and feed invertebrates (Randall 1967; Sazima et al. 1998; Carvalho Filho 1999, Sazima et al. 2005). In Brazil there are eight species of this genus, of which five are endemic (Rocha et al. 2010; Froese and Pauly 2012).

In general, most of the studies involving *Halichoeres* species in the Atlantic Ocean were developed in the Caribbean region (Jones 2002; Jones 2005; Jones 2006), so the relationships between habitat characteristics, foraging activity and densities of *Halichoeres* species are poor understood in tropical rocky shores. Moreover, trophic ecology and social behavior, can change with the species development (Lukoschek and McCormick 2001; Jones 2002; Bonaldo et al. 2006), ontogenetic shifts in behavior within *Halichoeres* species were investigated in Caribbean coral reefs (Jones 2002), whereas there is no study on the Brazilian endemic species.

Here we study the relationship between exposure, group size (i.e. number of fishes in the schools) and habitat complexity (deep, rugosity and benthic cover) on the foraging and densities of three wrasses *Halichoeres poeyi* (Steindachneir 1867), *H. penrosei* Starks 1913 and *H. brasiliensis* (Bloch 1791) in tropical rocky shores in Brazil. The hypotheses were i) that there would be a negative relationship between wave exposure on foraging of this species in different ontogenetic phases, ii) that there would be a positive relationship between habitat complexity on foraging of these species and iii) there would be a positive relation between foraging activity and group size. We also investigate the variables that are correlated with fish densities, the preferred species to form schools, the preference of foraging patches and diet of these species.

Materials and Methods

Study Area

The study was done in rocky shores located in the city of Salvador, Bahia, Brazil. These rocky shores were assessed through free diving between September 2011 and February 2012. We developed our study in nine rocky shores (Figure 1). These are shallow (max. 6 m depth) and the hard substrata is composed predominantly by filamentous algae, macroalgae, and zoanthids (*Palythoa caribaeorum* and *Zoanthus sociatus*). The black sea urchin, *Echinometra lucunter*, ascidians and colonies of corals *Favia gravida*, *Montastrea cavernosa, Mussismilia hispida* and *Siderastrea* spp. are also found. During our study, horizontal visibility ranged from 5 to 12 m, and water temperature was around 27º C.

INSERT FIGURE 1 HERE

Visual census for densities

We used stationary visual censuses adapted from Bohnsack and Bannerot (1986), with 4 m radius and 5 min of duration for measure densities of fishes. We used the color to determine the life phase of each individual (e.g. Initial phases – IP and Terminal phases TP), there is considerable difference in colour among these labrids as well as the life intervals within each species (Jones 2002). Terminal phases (TP) were easily distinguished from Initial phases (IP) because of their bolder colour patterns (except *H. poeyi*) and changes in morphology. A total of 10 visual censuses were performed in each rocky shore, data were recorded on plastic clip boards. Identifications of all species, including species that belonging to others genus, were done using specialized literature (Humman and DeLoach 2002; Sampaio and Nottigham 2008).

Foraging activity

The foraging activity, ie feeding frequency (bites / min), and selection of the substrate, was obtained by the method "focal animal" where we counted the number of bites invested on each substratum (Lehner 1979). We conducted a total of 540 focal animals. For each of the nine sampling sites were conducted 60 focal observations, being 20 for each species (10 TP and 10 IP) with 3 minute duration, where all occurrences were recorded in plastic clipboards, between 09:00 - 16:00 pm. When a *Halichoeres* were found, we waited 1 minute before start "focal animal". In each observation the species and number of fish (max. 1 m distance) in the schools were recorded. We avoid record fishes of the same school, thus in the end of each observation we move away at least 5 m.

Habitat complexity

For each visual census there were two measurements of rugosity, benthic cover and depth, totalizing 60 measurements of habitat complexity for each site. Rugosity was measured using the link-chain method proposed by Luckhurst and Luckhurst (1978). Benthic cover was obtained using replicates of a 25 x 25 cm quadrats (100% cover) and depth was measured using dive computer. Only higher taxonomic levels of benthic organisms were discriminated: macroalgae, turf algae (epilithic algae and macro algae recruits less than 5 mm), coralline algae and corals.

Depth, benthic cover (algae and corals) and rugosity were chosen as habitat complexity variable in this study because: i) depth may have an influence on the association of wrasses with different habitats (Morton and Gladstone 2011), ii) *Halichoeres* species are found in habitats with corals (Jones 2002),

iii) algal habitat provides opportunities to feed (Morton et al. 2008) and iv) high rugosity indicates protection against large-sized predators and high diversity of microhabitats for feeding (Tuya et al. 2009).

Wave Exposure

We used a similar scale of wave exposure proposed by Krajewski et al. (2011), where wave exposure was classified within an arbitrary scale from 1 to 9. The score 9 is the highest exposure recorded among the sites. In this classification Krajewski et al. (2011) used previous dive experience of the authors to classify wave exposure. Additionally we used plaster dissolution method (Jokiel and Morrissey 1993; Angradi et al. 1998), to check the exposure gradient. Sites with high exposure were expected to have greater weight loss of plaster objects. Three plaster balls with size and weight previously known were placed in each rocky shore studied and removed after 24 hours. We found a strong relationship (r^2 = 0.81) between the arbitrary exposure gradient and the data obtained by the plaster dissolution method.

Diet

A total of 102 fishes were collected, being 15 *H. brasiliensis* IP, 10 *H. brasiliensis* TP, 25 *H. penrosei* IP, 15 *H. penrosei* TP, 21 *H. poeyi* IP and *H. poeyi* 16 TP. Collections were made between 9 AM and 4 PM, the active time for the species, using a handspear or handnets while snorkeling. Fish were preserved in formaldehyde (10% concentration) in order to prevent digestion of the components in the gastrointestinal tract. When instantly injecting the formaldehyde was not possible, fish were kept on ice. Items were identified and placed in 5 different categories: Polychaetes, Bivalves, Gastropods, Crustaceans and Echinoids.

Data analysis

Fish densities and habitat relationships were analyzed with Canonical Correspondence Analysis (CCA). Monte Carlo permutation test was used to check if the axis were significant. Principal Component Analysis (PCA) was utilized for dimension reduction of the environmental variables (rugosity, depth, coralline algae, macro algae, turf and coral cover) with data log (x+1) transformed and normalized. Linear regressions were conduced to investigate the influence of habitat complexity (using PCA scores) on fish foraging. The influence of wave exposure and group size on fish foraging were also investigated with Linear regressions. To achieve statistical tests requirements, foraging data were log (x+1) transformed.

The Electivity Index was used to identify preferences of substrate to forage. It was calculated according to the following formula: $E_i = (r_i - n_i)/(r_i + n_i)$, where E_i is the value of electivity for the type of substrate *i;* r_i is the percentage of feeding bites in the substrate *i* and n_i is the percentage of substrate *i* in the studied location. The IVLEV's Electivity Index varies from -1 to 1. Values near -1 show low preference or rejection while values near +1 indicate high preference for a particular substrate (Krebs 1989). The preferences of group formation also was investigated using a Electivity index. In this case r_i was the percentage of encounters with a species *i* and n_i was the relative density. ANOSIM analysis was utilized to compare diets of the species and ontogenetic phases.

Results

Influence of habitat complexity on foraging activity

The data of four groups of the benthic cover variables (turf, macroalgae, coralline algae and corals) used in PCA analysis were responsible for 71 to 97% of the total benthic cover in the studied sites. PCA results showed that rugosity (r= 0.57) and coralline algae (r= 0.47) were positively correlated with the axis of habitat complexity (axis from PCA analysis: PC1 with 41.7 % of data variation) and coral (r= -0.30) and depth (r= -0.58) were negatively correlated with the habitat complexity axis.

Regression analysis showed that habitat complexity influenced foraging activity, except for *H. brasiliensis* TP (Table 1).

INSERT TABLE 1 HERE

Influence of habitat complexity and wave exposure on densities

Monte Carlo Permutation test showed that the axes from CCA analysis were significant (p=0.006) and the first two axes accounted respectively for 40% and 33% of the variance between species and variables. The IP densities of *H. poeyi* and *H. penrosei* were correlated positively with rugosity and coralline algae, respectively. *Halichoeres* species in the terminal phases were correlated positively with depth and wave exposure (Figure 2).

INSERT FIGURE 2 HERE

Influence of wave exposure on foraging activity

There was a change of foraging activity for all species in the exposure gradient, forage activity decrease in rocky shores with higher degree of wave exposure (Figure 3). In general, IP of the three species analyzed were influenced more with exposure than TP, results of Regression analysis showed significant differences in the foraging activity for: *Halichoeres penrosei* IP, *H. poeyi* IP, *H. brasiliensis* IP, *H. penrosei* TP and *H. poeyi* TP.

INSERT FIGURE 3 HERE

Influence of group size on foraging and preference of group formation

Linear Regressions showed a positive relation between foraging activity and group size (Figure 4). Except for *H. brasiliensis* TP where this relation was not significant. The species that showed the highest degree of sociability were *H. penrosei* (87.7% IP and 42.2 % TP found in schools) and *H. poeyi* (75.5% IP and 51.1% TP), while *H. brasiliensis* was found more solitarily (31.1% IP and 17.7% TP).

INSERT FIGURE 4 HERE

Within the observed schools the majority of them had others *Halichoeres* species (74%). The species *H. poeyi* and *H. penrosei* were found foraging together in 53 % of the observations involving these two species. IP and TP of *H. penrosei* and *H. poeyi* had preference to forage with *Acanthurus bahianus* (Acanthuridae) and *Pseudupeneus maculatus* (Mullidae) (Figure 5 A and B). IP of *H. penrosei* also selected *Thalassoma noronhanum*. IP of all species selected *Sparisoma axillare* (Labridae). IP of *H. brasiliensis* also selected *A. coeruleus* (Acanthuridae) and *A. bahianus* (Figure 5 C).

Microhabitat preference to forage and diet

The results of Ivlev's electivity index showed a foraging preference of *Halichoeres* species by turf and macroalgae for both phases of *H. penrosei* and *H. poeyi* (Figure. 6 A and B), however *H. brasiliensis* had preference to forage in turf, coral and coralline algae (Figure 6 C).

The stomach contents varied according to species and phases: most contents of *H. penrosei* IP were polychaetes, while in *H. penrosei* TP were gastropods. *H. poeyi* ingested more bivalves than others invertebrates in both phases. Initial phases of *H. brasiliensis* had principally crustaceans in the stomachs and TP had gastropods (Table 2). ANOSIM analysis showed differences between species and phases, except for *H. brasiliensis* IP and *H. poeyi* IP had no significant differences in the diet (Table 3).

INSERT FIGURE 5 AND 6 HERE

Discussion

Influence of habitat complexity on foraging activity

Successful foraging by animals depends largely on the spatial distribution of food resources (Bell 1991; Thums et al. 2011). Our results showed that habitat complexity had significant influence in the foraging activities of two species investigated. Jones (2006) analyzed the distribution of behaviors within home range contours and found that *Halichoeres maculipinna*, sister species of *H. penrosei* (Rocha 2004), and *H. poeyi* displayed a random distribution of feeding throughout their home range areas in St. Croix, Virgin Islands. We believe that *Halichoeres* species in general have a random distribution of feeding throughout their home range areas.

According to Krajewski et al. (2010) we could expect that foraging substratum preferences mediate behavioral responses to substratum composition, however they did not find relationships between general behavioral responses and the abundance relative of some particular substrata. Although we investigated the relationship between habitat complexity (including benthic cover, rugosity and deep) and foraging activities of the *Halichoeres* using a different way.

Influence of habitat complexity and wave exposure on densities

Our CCA ordination showed that TP of the species studied were correlated with depth and exposure, IP with rugosity and algae cover. According to Morton and Gladstone (2011) depth may have an influence on the association of wrasses with different habitats, it is likely that other habitat characteristics also contribute to these associations, as an example this authors cited that cobbles and sediment are removed from fringe and barrens by high wave energy, whereas smaller substrates accumulate in deeper sponge gardens. Recently, Krajewski and Floeter (2011) found that *H. radiatus*, sister species of *H. brasiliensis* (Rocha and Rosa 2001), had higher density in shallow and more exposed sites in the oceanic archipelago of Fernando de Noronha (Brazil). Our results indicate for *Halichoeres* species studied had a clear change in the distribution of depth strata associated with ontogenetic shifts.

The preferential use of shallow habitat rich in algae by IP of wrasses has also been observed for rocky reefs in temperate Australia (Gillanders and Kingsford 1998; Curley et al. 2002) and New Zealand (Jones, 1984; Choat and Ayling 1987). Algal habitat provides, for smaller individuals, opportunities to feed on small crustaceans and molluscs (Denny and Schiel 2001; Shepherd and Clarkson 2001; Morton et al. 2008). However, according to Fulton and Bellwood (2004) in these shallow habitats, small wrasses are susceptible to the influence of wave surge on their swimming performance and their ability to undertake daily activities. Our results corroborated with Morton and Gladstone (2011) when also cited that overhead algal canopies offer sufficient protection to allow these individuals to occupy reef areas from which wave surge would otherwise displace them.

Tuya et al. (2009) suggested two main mechanisms to explain why labrid species tend to concentrate in and around of structural elements: first, small topographic elements (i.e. small cracks, crevices, holes, etc.) may provide protection against large-sized predators; second, these topographic elements provide a range of microhabitats for potential prey items of labrids such as crustaceans. Tuya et al. (2009) also mentioned that food and shelter provided by macro algae are important resources for labrids of temperate waters, although disentangling the relative importance of food versus shelter may be difficult.

Rocha et al. (2005) studying the abundances of *Halichoeres* in different habitats found that *H. brasiliensis* had higher abundances in spur/groove, rock and patch reefs than non reef-habitats. *H.*

maculipinna had higher abundances in linear reefs and *H. poeyi* in non reef-habitats (vegetation, sea grass and rubble), although this last species was found in all habitats studied by these authors. Our study was limited to tropical rocky shores habitat, which are shallow and narrow, probably this is the reason to explain in our findings that the differences were more striking among phases than species.

Influence of wave exposure on foraging activity

Under high wave exposure, swimming demands high energy expenditure and some invertebrate feeders, as the species studied herein, seem to avoid extra energy expenditure by avoiding foraging under high wave exposure (Johansen et al. 2007a). Our results support most findings for fish behavioral responses to water flow (Fulton et al. 2001; Fulton and Bellwood 2005; Johansen et al. 2007a, 2008; Krajewski et al. 2010), where fish decrease the foraging activity in sites with high wave exposure. The exception was *H. brasiliensis* TP, this is the largest species of genus *Halichoeres* in the Brazilian coast (Sampaio and Nottinham 2008) and probably have more swimming ability than smaller species. Feeding performance is affected by locomotor abilities which are used during search and capture of prey (Colar et al. 2008) and larger size also promotes locomotion abilities, allowing movements over large reef areas and into various micro habitats, including those that are exposed to wave action (Fulton and Bellwood 2004).

Krajewski et al. (2010) studying patterns of variation in behaviour of nine common reef fish in Fernando de Noronha-Brazil, found that most studied species tended to stay close to the bottom in sites with high hydrodynamism. According to these authors, fish may save energy avoiding swimming in the higher water layers, which have higher water flux (Johansen et al. 2007b), especially in exposed sites. Krajewski et al. (2011) also showed that *H. radiatus* was significantly positive correlated between wave exposure and proximity to the bottom.

Influence of group size on foraging and preference of school formation

The present paper showed that there is an increase in the rate of *Halichoeres* foraging as the group size increases. Schooling behavior of fishes is acknowledged as a critically important anti-predator mechanism (Magurran 1990). The benefits of ‘many eyes’ include easier detection of predators and lead to greater dilution and confusion of predators which gives the school an advantage over solitary individuals (Jones 2002). Pitcher et al. (1982) showed that information sharing within a group may result in shortened search time for food. Behavioural studies of goldfish (*Carassius auratus*) and minnows (*Phoxinus phoxinus*) have shown that members of larger groups stay longer in food patches and cover larger areas than members of small groups (Magurran and Pitcher 1983).

Halichoeres poeyi and *H. penrosei* were found more in schools than solitaries, while *H. brasiliensis* was found several times solitary. Jones (2002) cited that larger individuals of *Halichoeres* invest more time swimming alone, possibly because they are more effective at escaping predation or they are more efficient at finding food. To reinforce this pattern found by Jones (2002) and corroborated herein, other *Halichoeres* population should be investigated.

Jones (2006) studying in Caribbean waters *H. garnoti*, *H. maculipinna*, *H. poeyi* and *H. bivittatus*, found these species in many activities in groups. Our study reinforces the degree of sociability for *Halichoeres* species. We used IVLEV’s Electivity Index to investigate selection of school by *Halichoeres*. Although this index had been used for evaluate substrate selection to feeding by fishes (Bonaldo et al. 2006; Francini-Filho et al. 2010; Souza et al. 2011), Francini-Filho et al. (2000) used this index to identify preferred clients by cleaner *T. noronhanum.* We believe that IVLEV’s Electivity Index can be a good tool to study relationship between different species of reef fishes.

In general our results of group selection showed that parrotfishes, surgeonfishes were preferred to form schools by studied *Halichoeres* species. Although Jones (2002) found similar results where parrotfishes and surgeonfishes were presents in the schools of Caribbean *Halichoeres* species, goatfishes were not cited as present species in the schools. Goatfishes are common in the rocky shores studied probable due to near interface with unconsolidated substratum (Barros et al. 2001; Krajewsky et al. 2006), thus the characteristics of the rocky shores can explain partly the presence of goatfishes in the sites.

The schools observed were formed by species of different families and trophic levels. We believe that *Halichoeres* spp establish schools with fish from various trophic levels (e.g. invertivores and herbivores), since these species do not offer risk, they take advantage of living in groups. The 'following behaviour' is an association that occurs in shallow tropical waters, including diurnal predators and a large variety of 'nuclear species'. These species explore the substrate by disturbing soft bottoms or coral reef environments exposing potential prey to opportunist or generalist species, known as 'the followers' (Sazima et al. 2007; Maia-Nogueira et al. 2009). According to previous studies concerning this behaviour, the association benefits the follower, which has access to prey usually unavailable and might increase feeding success or decrease susceptibility to predation (Deloach 1999; Gerhardinger et al. 2006).

Other possible case of opportunistic behavior found in our study was the association between *H. penrosei* IP and *Thalassoma noronhanum* IP. These species are similar in the body shape and color, which can be a protective mimicry relationship (see Pinheiro et al. 2010; Pereira et al. 2011). It would be interesting to evaluate the proportion of opportunistic behavior played by *Halichoeres* species to better understand the relationships among these species.

Microhabitat preference to forage and diet

The species studied had preference to forage in turf. Azevedo (2009) cited that all the size classes of *H. poeyi* had preference for foraging on the Epilithic Algal Matrix (EAM). The EAM is widely known as a substrate rich in sediment and debris with quantity of invertebrates with high nutritional value (Crossman et al. 2001; Wilson et al. 2003; Azevedo 2009).

In our study, as expected, the diets of endemic species (*H. penrosei* and *H. brasiliensis*) were similar with the sister's species from Caribbean (Randal 1967). According to Azevedo (2009) larger individuals of *H. poeyi* utilize more rigid-bodied prey like decapods and echinoids, while the smaller individuals had a tendency to feed on soft-bodied prey. Although *H. brasiliensis* and *H. penrosei* followed this pattern, stomach contents of *H. poeyi* IP were dominated by bivalves. This difference may be explained by availability of preys in the sites studied. Futures studies should test if preferences in the diet of the *Halichoeres* species are correlated with available of preys in the foraging habitats.

Morton et al. (2008) showed significant changes in dietary composition with increasing body length in labrids, reflecting mainly changes in the proportional representation of different prey. They also suggested that small individuals of each species fed mainly on amphipods, followed by small decapods, bivalves and trochid gastropods and with increasing body size, fish fed on greater volumes of hard-shelled molluscs. Similar size-related shifts in diet have been demonstrated in other species of labrids of temperate Australia and New Zealand (Jones 1988; Gillanders 1995; Denny and Schiel 2001). Increasing of mouth size, greater crushing power of pharyngeal teeth, shifts in foraging microhabitats, improved locomotion and sensory abilities are the principals factors of size-related changes in dietary compositions (Wainwright 1988; Morton et al. 2008).

Halichoeres species are influenced by wave exposure and habitat complexity in tropical rocky shores, both densities and foraging activity. Group size is important factor in the foraging activity since the foraging rates increasing with group size. Behavioral use of microhabitats may determine large-scale distribution patterns (Fulton et al. 2001), we believe that behavioral use of microhabitats can be a great tool to investigate distribution patterns of fish between coral reefs and tropical rocky shores.

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Table 1. Results of Regression analysis between fish forage and habitat complexity. IP= Initial phase and TP= Terminal phase. * = Significant results.

	F	**r^2**	**p**
H. penrosei IP	7.22	0.06	0.008*
H. penrosei TP	14.68	0.13	0.000*
H. poeyi IP	12.75	0.11	0.000*
H. poeyi TP	5.75	0.05	0.018*
H. brasiliensis IP	3.93	0.03	0.050
H. brasiliensis TP	0.70	-0.03	0.403

Table 2. Diet of the *Halichoeres* species studied. Numbers correspond to mean of percentage ± S.D.

	Crustaceans	**Bivalves**	**Gastropods**	**Echinoids**	**Polychaetes**
H. penrosei IP	19±33.9	23.8±37.8	-	-	57±50.9
*H. penrose*i TP	15±12.8	18.7±26.9	37.5±23.3	-	28.7±18.9
H. poeyi IP	23±36.3	43.5±38.7	15.3±25.1	2.5±21.8	15.3±31.8
H. poeyi TP	22.7±15.9	47.7±23.0	14.7±13.2	7.9±19.0	6.8±13.8
H. brasiliensis IP	34±34.4	31.8±26.4	20.4±40.1	4.5±5.7	9±21.3
H. brasiliensis TP	8.5±12.6	27.6±24.4	57.4±26.9	4.2±9	2.1±10.5

Table 3. Results of ANOSIM analysis comparing diet of *Halichoeres* species and ontogenetic phases.

* = Significant differences.

	R Statistic	**Significance Level**
H. brasiliensis IP, *H. brasiliensis* TP	0.159	0.025*
H. brasiliensis IP, *H. penrosei* IP	0.108	0.017*
H. brasiliensis IP, *H. poeyi* IP	0.062	0.97
H. brasiliensis TP, *H. penrosei* TP	0.222	0.006*
H. brasiliensis TP, *H. poeyi* TP	0.403	0.001*
H. penrosei TP, *H. penrosei* IP	0.091	0.047*
H. penrosei TP, *H. poeyi* TP	0.411	0.001*
H. penrosei IP, *H. poeyi* IP	0.089	0.015*
H. poeyi TP, *H. poeyi* IP	0.082	0.039*

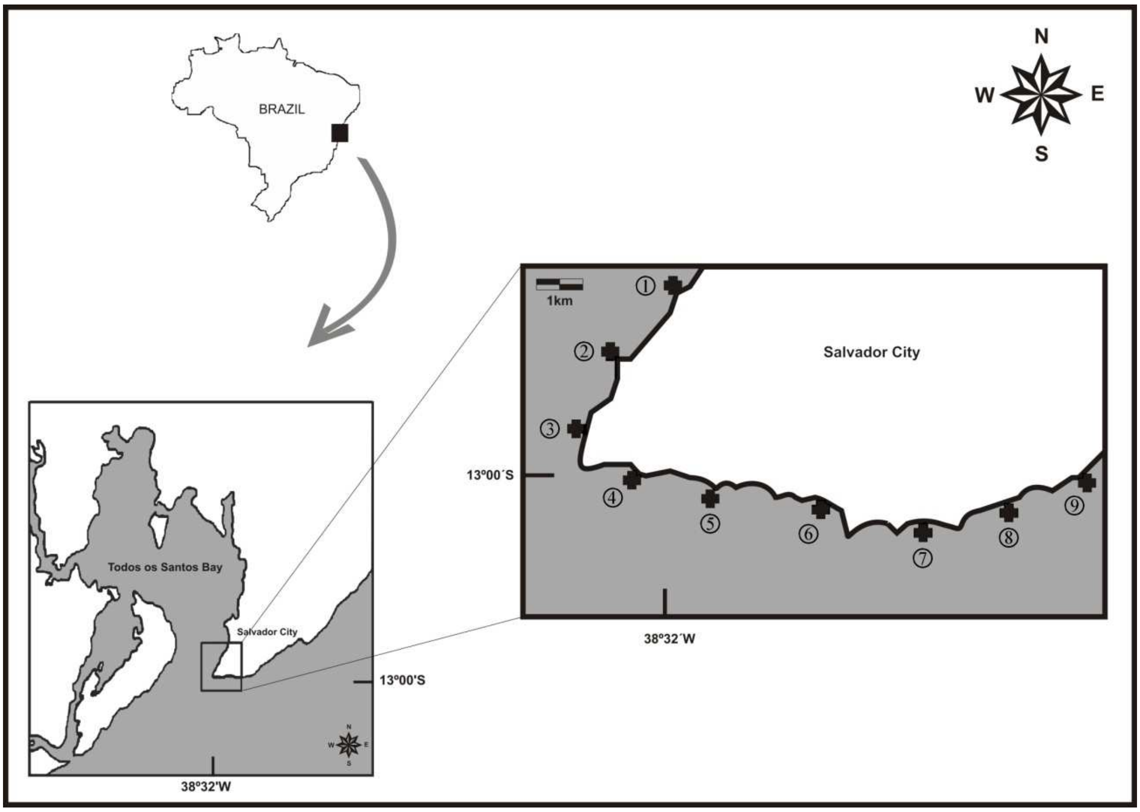


Figure 1. Map with samplings sites, rocky shores along Salvador city: 1- Solar, 2- Vitória, 3- Barra, 4- Cristo, 5- Ondina, 6- Sereia, 7- Buracão, 8- Amaralina and 9- Pituba.

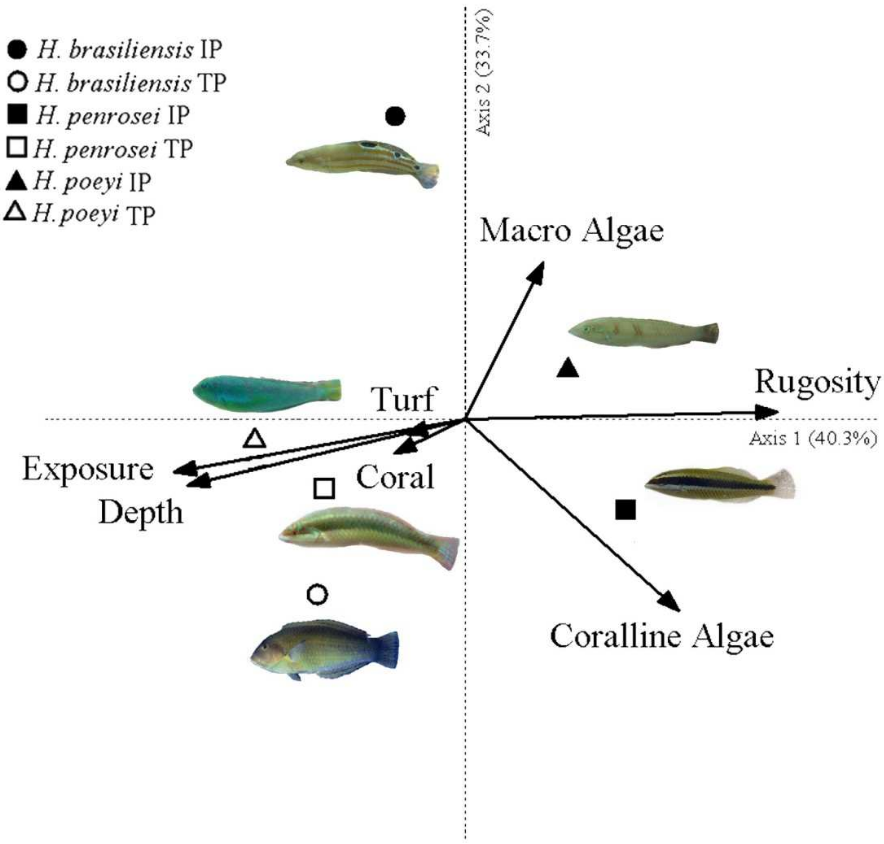


Figure 2. Correspondence Canonical Analysis between densities of *Halichoeres* species and variables of habitat complexity. IP= Initial phases and TP= Terminal phases.

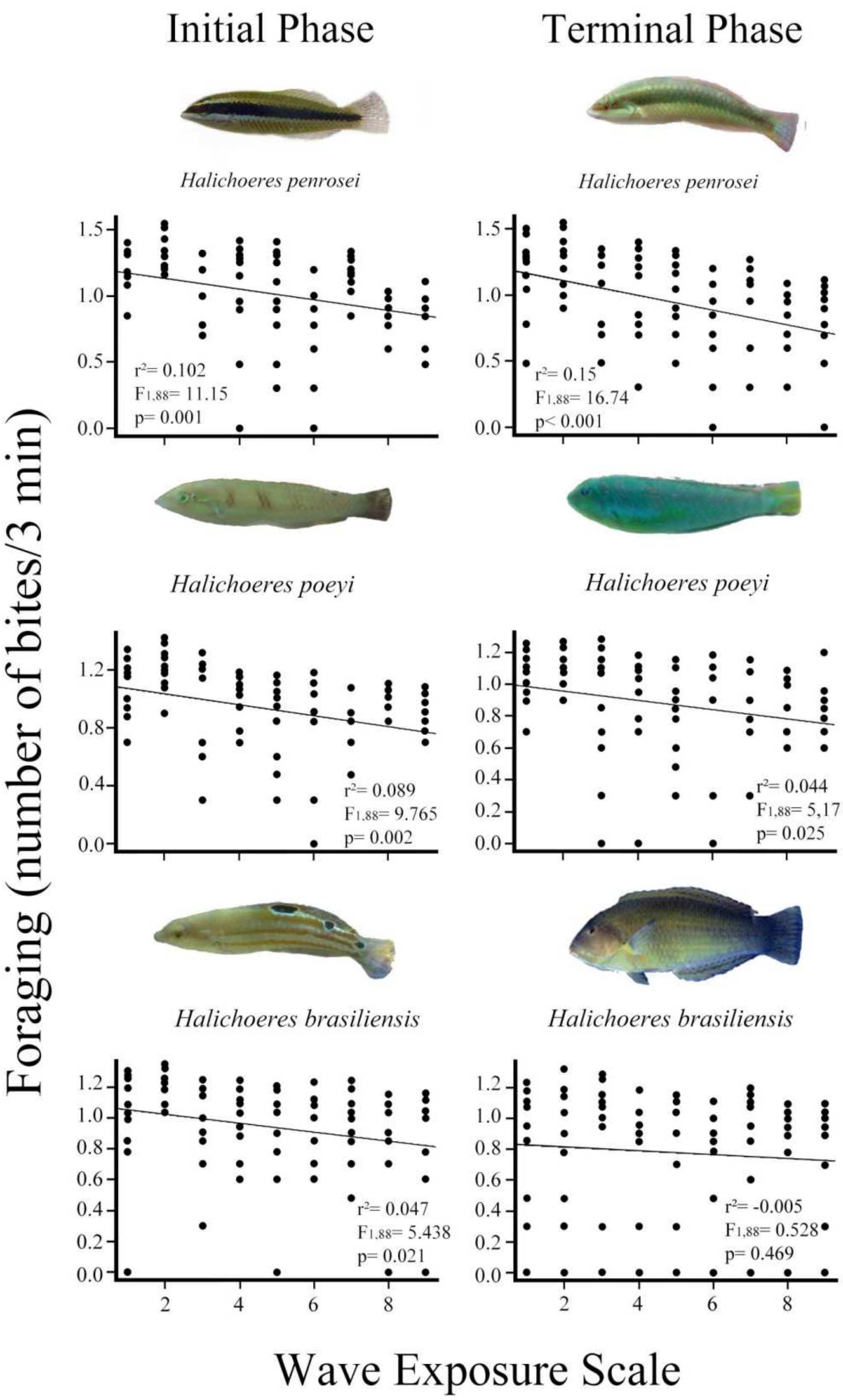


Figure 3. Relation between wave exposure and foraging activity. We used a similar scale of wave exposure proposed by Krajewski et al. (2011), where wave exposure was classified within an arbitrary scale from 1 to 9. The score 9 is the highest exposure recorded among the sites. Note that each graphic has a different scale. Data were transformed in log (*x*+1).

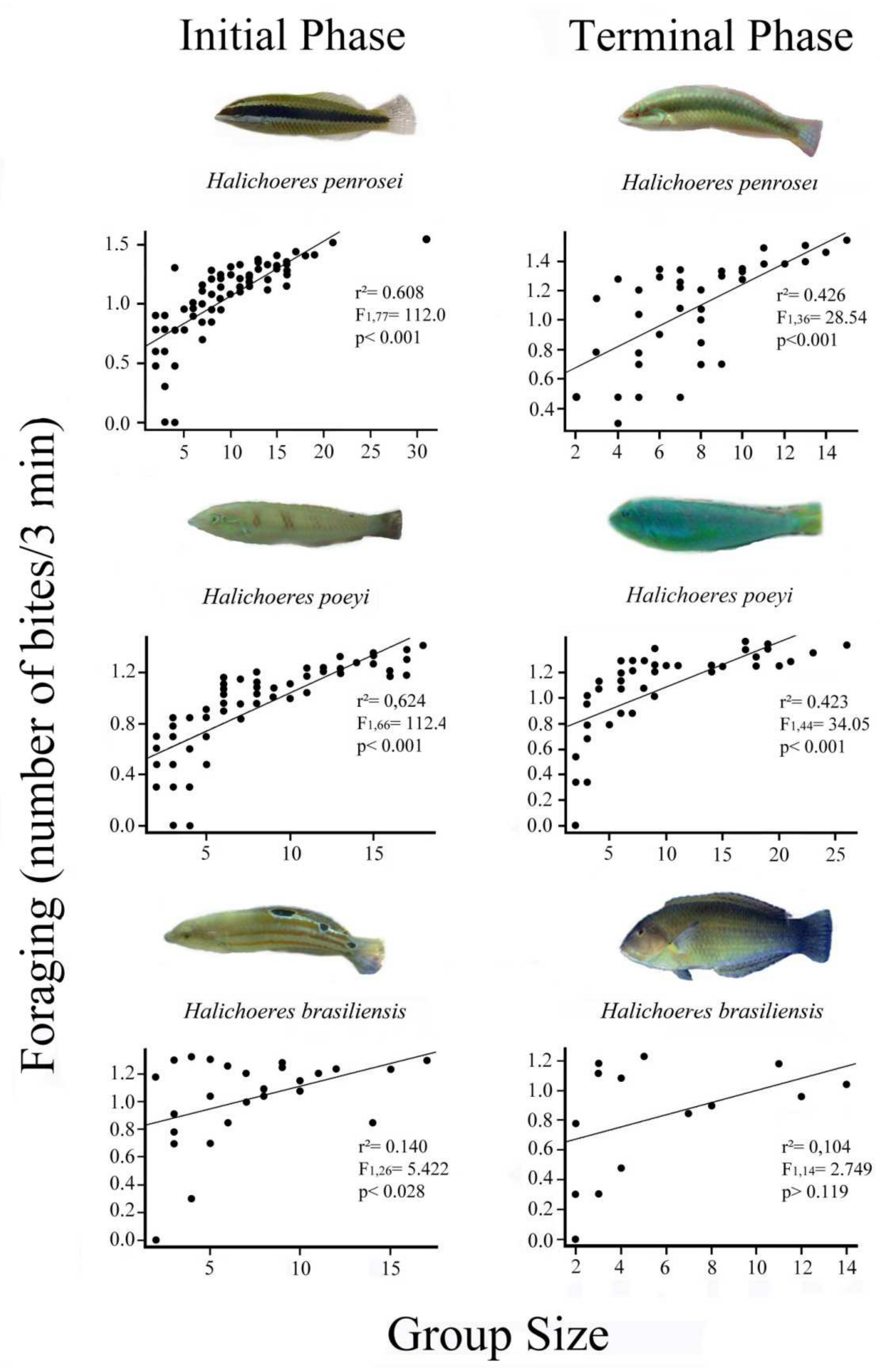


Figure 4. Relation between group size (number of fish/sample) and foraging activity. Note that each graphic has a different scale. Groups that varied in size during the 3 min. 'focal animal' samples were excluded from these analysis. Data were transformed in log (*x*+1).

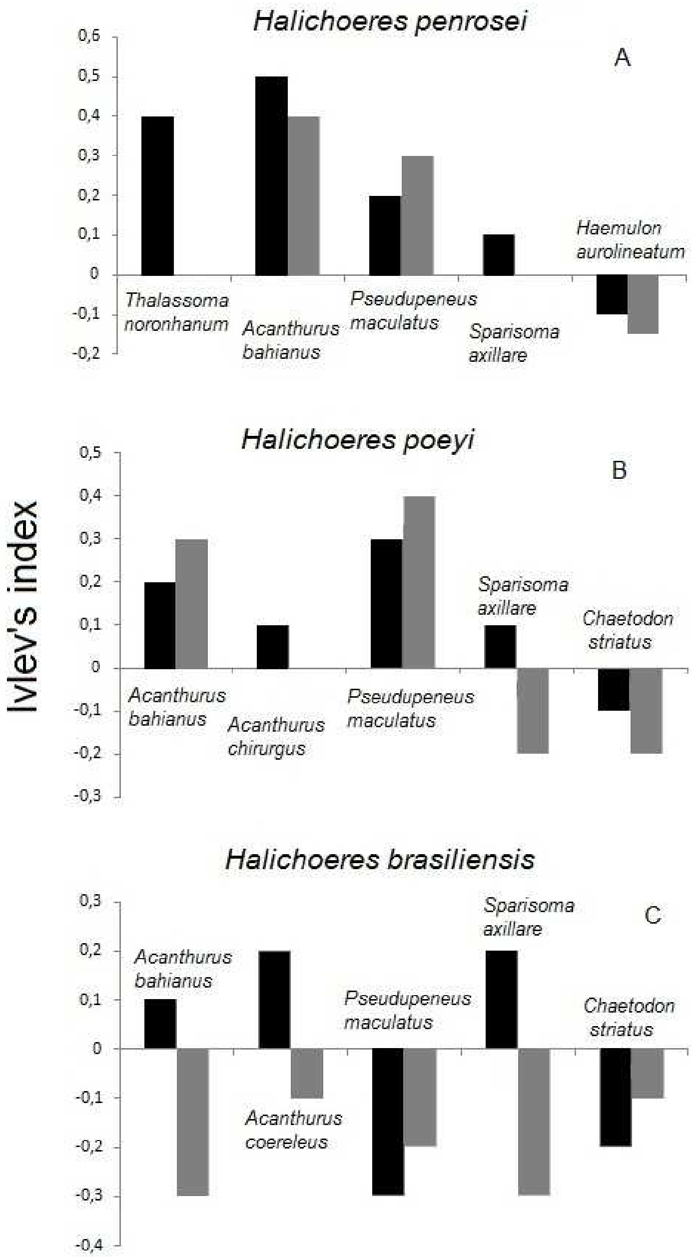


Figure 5. Results of Ivlev's index showing the species preference to forming of groups by *Halichoeres* species. Black bars= initial phases; Gray bars= terminal phases. Note that each histogram has a different scale.

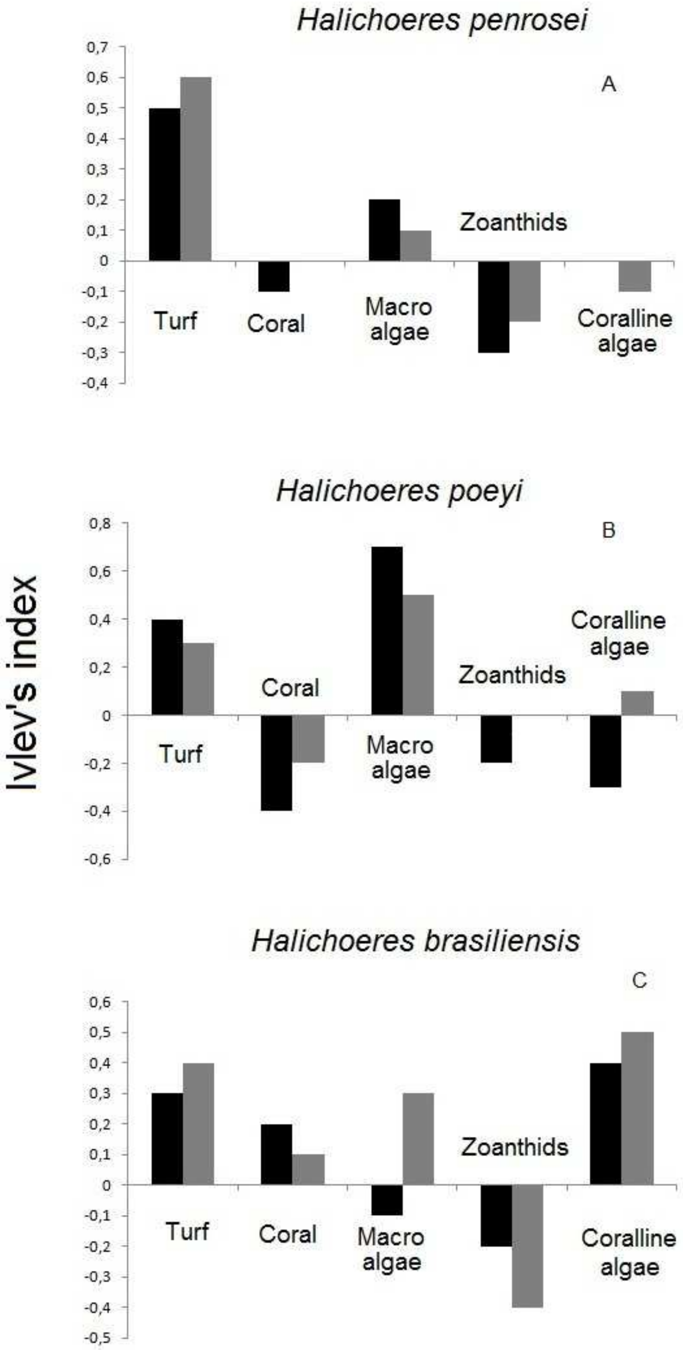
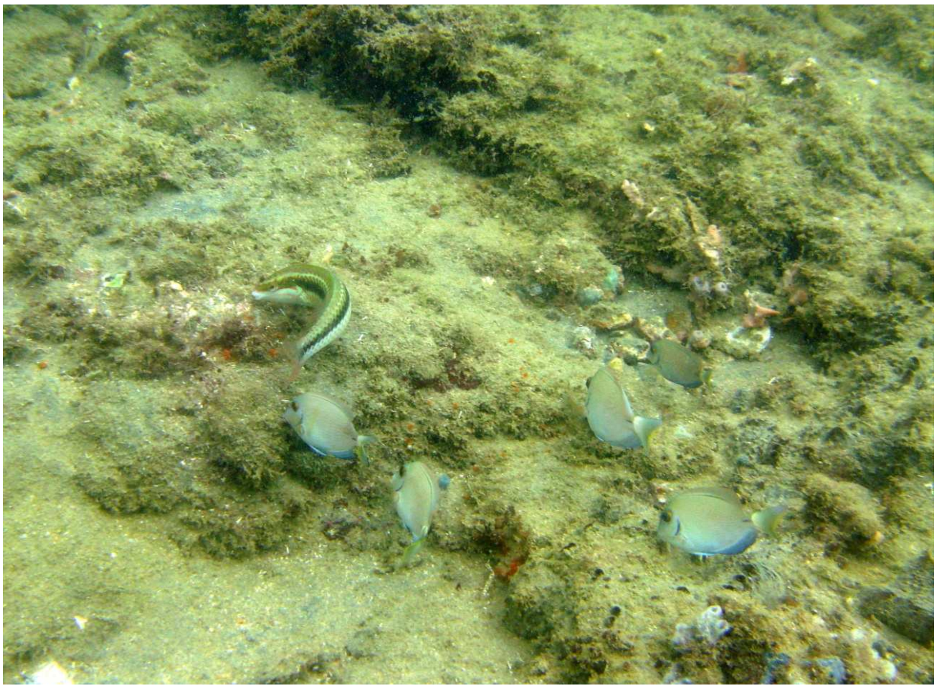


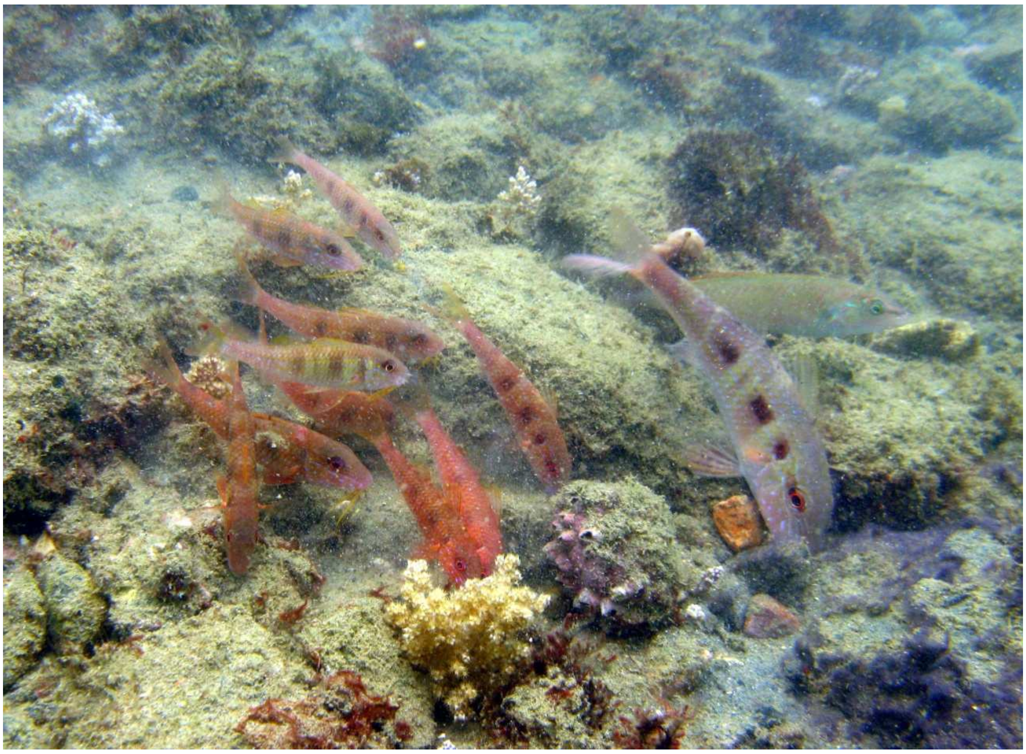
Figure 6. Results of Ivlev's index showing the preference of forage substratum by *Halichoeres* species. Black bars= initial phases; Gray bars= terminal phases. Note that each histogram has a different scale.

ANEXOS

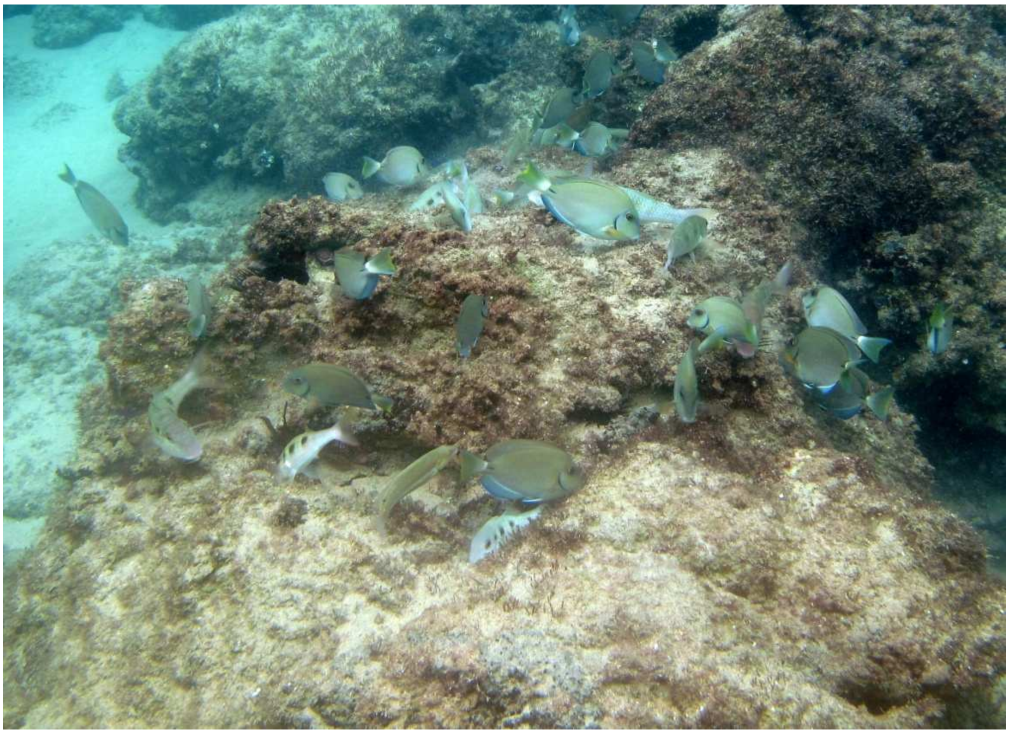


Anexo 1. *Halichoeres penrosei* forrageando com *Acanthurus bahianus*

Anexo 2. *Halichoeres penrosei* forrageando com *Thalassoma noronhanum*



Anexo 3. *Halichoeres poeyi* forrageando com *Pseudupeneus maculatus*

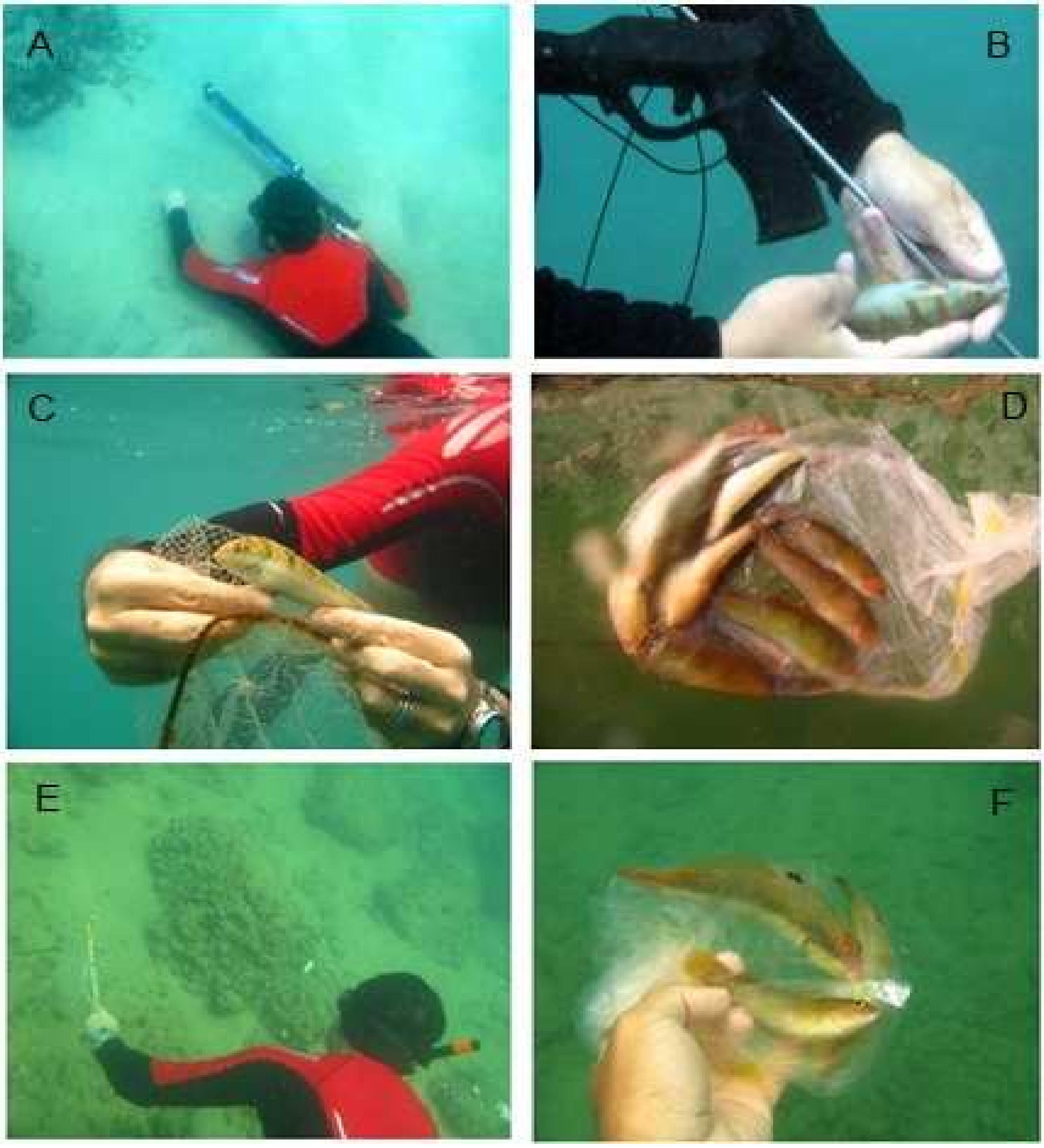


Anexo 4. *Halichoeres poeyi* forrageando com *Acanthurus bahianus* e *P. maculatus*

Anexo 5. *Halichoeres brasiliensis* forrageando solitariamente

Anexo 7. *Halichoeres penrosei* seguindo *Pseudupeneus maculatus*

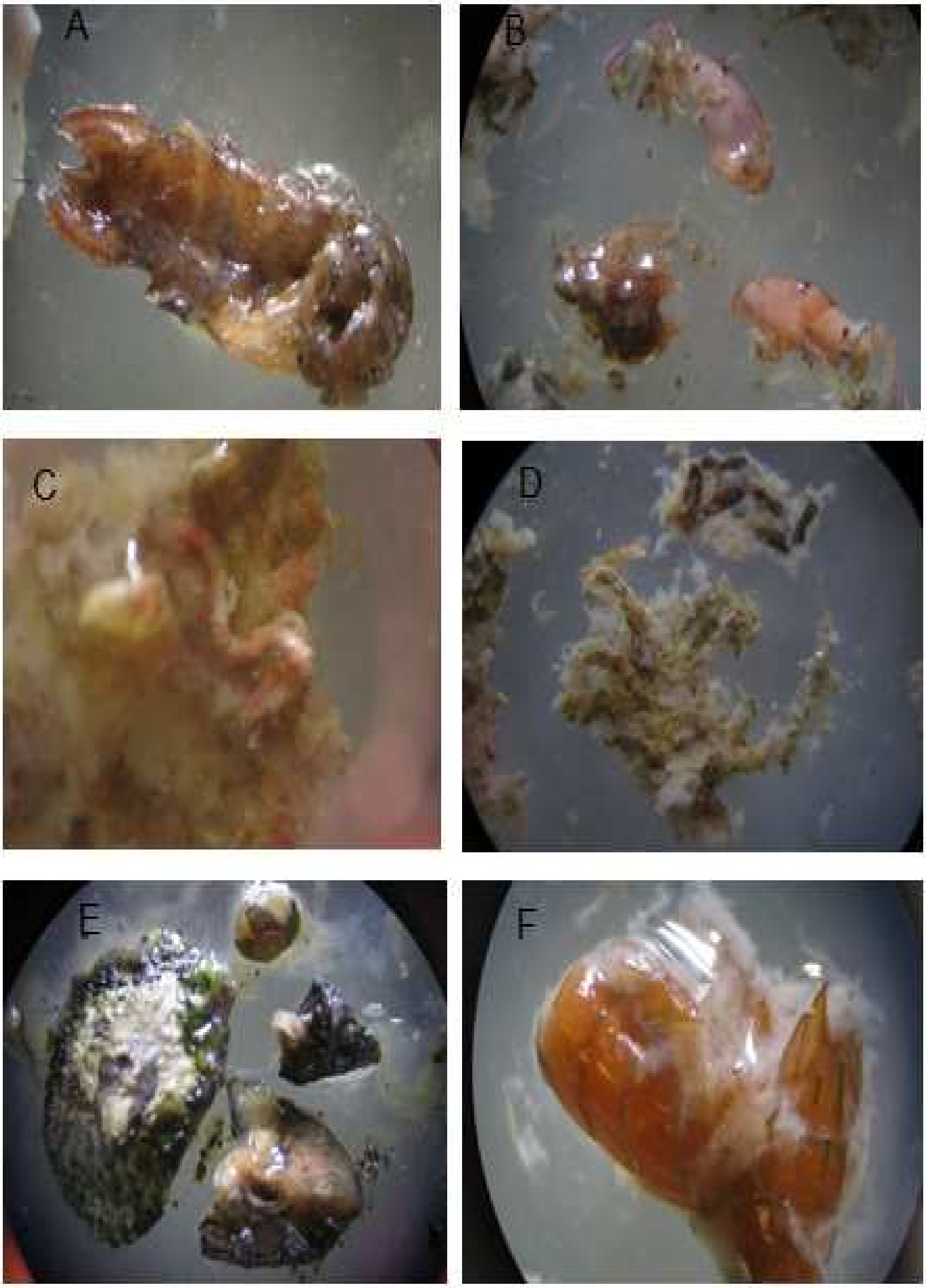
Anexo 8. *Halichoeres poeyi* seguindo *Pseudupeneus maculatus*



Anexo 9. Coletas dos peixes para análise de conteúdo estomacal: A) Mirando com arbalete, B) *Halichoeres poeyi* capturado com arpão, C) *H. poeyi* capturado com puçá, D) *Halichoeres* spp coletados em um mergulho, E) Coletando com puçás e F) Peixes recém capturados.

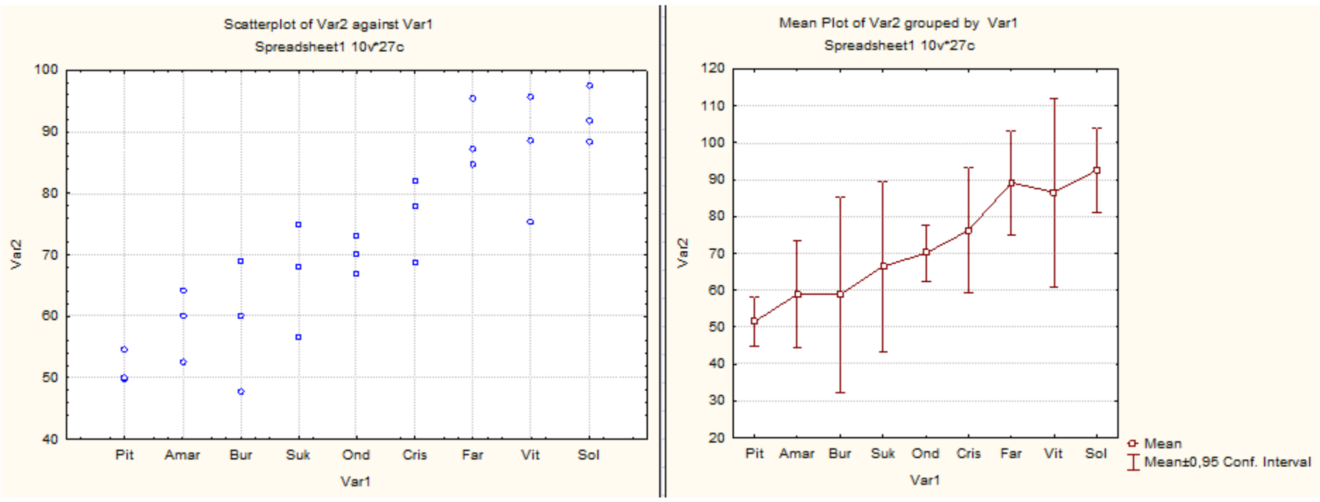
Anexo 10. Retirada de estômago de *Halichoeres brasiliensis.* Foto: Patrícia Costa

Anexo 11. Retirada de estômago de *Halichoeres penrosei.* Foto: Patrícia Costa



Anexo 12. Conteúdos estomacais encontrados: A) Crustáceo Decapoda, provavelmente um Stomatopoda, B) Crustáceos Decapoda, provavelmente Dendobranchiata, C) Poliqueta, D) Crustáceo Decapoda, provavelmente Majidae, E) Moluscos Gastropodas e outro molusco da família Acmaeidae, F) Crustáceo Decapoda, provavelmente um Stomatopoda.

Anexo 13. Bola de gesso colocada para averiguar gradiente de exposição de ondas.



Anexo 14. Gradiente de exposição de ondas obtido através do método de dissolução de gesso.

APÊNDICE

- Marine Biology
- Instructions for Authors

Types of Papers

- Original papers:

  These are the most important components of Marine Biology. They report on original research in all fields of marine biology and conform to the accepted standards of scientific quality. Interim reports and papers with inconclusive results will usually not be published. In the latter case, exceptions can be made if the inconclusiveness is a robust and important result with relation to widely debated theory. Original research articles have a length limit of 12 printed pages.

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  Slifka MK, Whitton JL (2000) Clinical implications of dysregulated cytokine production. J Mol Med. doi:10.1007/s001090000086
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  South J, Blass B (2001) The future of modern genomics. Blackwell, London
- Book chapter

  Brown B, Aaron M (2001) The politics of nature. In: Smith J (ed) The rise of modern genomics, 3rd edn. Wiley, New York, pp 230-257

- Online document

  Cartwright J (2007) Big stars have weather too. IOP Publishing PhysicsWeb. http://physicsweb.org/articles/news/11/6/16/1. Accessed 26 June 2007
- Dissertation

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- ISSN List of Title Word Abbreviations

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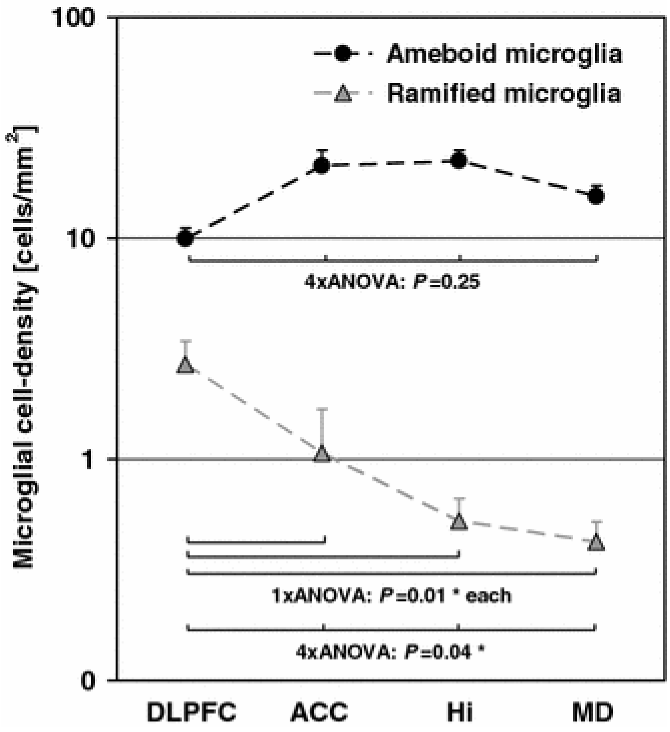

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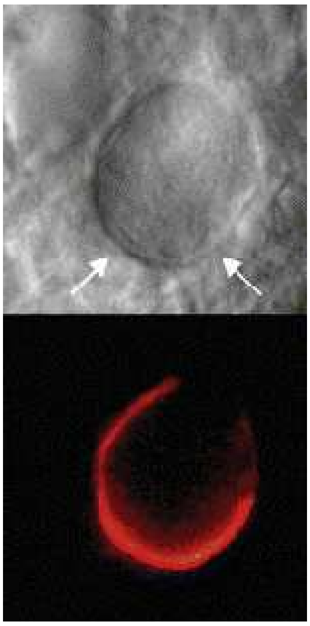

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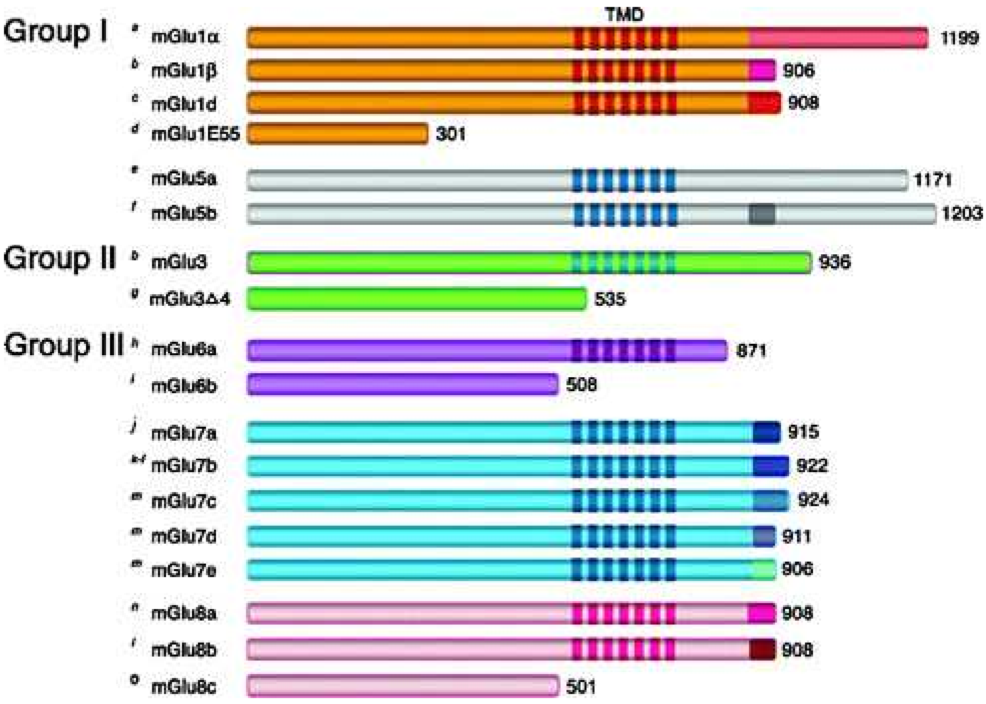

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