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ORIGINAL PAPER

How wave exposure, group size and habitat complexity influence foraging and population densities in fishes of the genus *Halichoeres* (Perciformes: Labridae) on tropical rocky shores

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Abstract Wave exposure and habitat complexity have been used to explain variations in the distribution patterns and behavior of many reef fishes. This study analyzed the influence of both factors on density and foraging activity, and the influence of group size on foraging in three species of the genus *Halichoeres* (Labridae) on tropical rocky shores. It was shown that initial phases (IP) and terminal phases (TP) *Halichoeres*, were influenced by wave exposure, although foraging in *Halichoeres brasiliensis* TP was not influenced by wave exposure. The IP in all three species were positively associated with rugosity and algal cover while the TP was positively associated with depth. Habitat complexity also influences foraging in these species. Group size influenced foraging activity, except in *H. brasiliensis* TP. We also found variations in microhabitat patches used for foraging between species and differences in the stomach contents between species and phases, showing that functional roles change in response to ontogenetic shifts.

Introduction

One of the most relevant questions regarding reef ecology is how the environmental variables interfere in fish communities structure (Jones and Syms 1998; Bellwood and Wainwright 2002). In fact, several studies have examined the effect of both biotic and abiotic variables on the structure of fish communities (Gladfelter and Gladfelter 1978, Luckhurst and Luckhurst 1978; Chabanet et al. 1997; Ornellas and Coutinho 1998; Arbuto-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. Habitat complexity can therefore be an important factor explaining the 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 fish on tropical rocky shores have received relatively little attention (Ferreira et al. 2001), probably because in this region most studies are focused on coral reefs, but despite their lower complexity, rocky shores and adjacent environments can also support a rich fauna and flora (Ferreira et al. 1998; Guimaraens and Coutinho 1996; Ornellas and Coutinho 1998; Floeter et al. 2007).

Understanding the effects of habitat structure on the population density of fish is essential to assessing which variables are important (e.g., the influence of algae and corals on fish densities) and whether current predictions can also be applied to different reef environments, such as

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rocky shores. Habitat complexity, as well as the composition of the substratum, can influence the 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 is considered to be one of the key factors in shaping coral reef fish assemblages, since hydrodynamics affects fish according to their various swimming abilities. Field and laboratory studies have investigated the effects of water flow on the behavior and energy processes of reef fish (Bellwood and Wainwright 2001; Fulton et al. 2001; Fulton and Belwood 2002). In general, they showed that when water flow increases, fish spend more time in refuges (Bellwood and Wainwright 2001; Fulton and Belwood 2002; Fulton et al. 2005; Floeter et al. 2007; Johansen et al. 2007a, b).

Foraging behavior is a key aspect of habitat use by animals, and fish are no exception (Fulton and Belwood 2002). The optimal foraging theory considers the distribution of prey within patches of microhabitat together with excursions between or within those patches to be important factors affecting foraging (MacArthur and Pianka 1966; Schoener 1971; Norberg 1977). Some studies have suggested that foraging depends on the distribution and size of the patches of preferred habitat (Covich 1976; Fulton and Belwood 2002).

Aggregation with other foragers is a common risk-reduction strategy, allowing more time to be spent foraging without incurring a higher probability of becoming prey (White and Warner 2007). Therefore, foraging in a group has been suggested as a way to reduce risk and to increase the amount of information acquired regarding where to find food and how long to stay on a patch of a certain quality (Stenberg and Persson 2005). Surgeonfish (Acanthuridae) and parrotfish (Labridae) forage more efficiently in large groups (Wolf 1987; Clifton 1991), but fish in high-density aggregations may forage less effectively or simply 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, which is important in structuring reef communities (Randall 1967; Hobson 1974; Deloach and Humann 1999). Although these fish have been the focus of studies in the Pacific Ocean and in the Caribbean (Thresher 1979; Bellwood and Wainwright 2001; Jones 2002, 2005, 2006), few such studies have been conducted in the South Atlantic (Sazima et al. 1998, 2005; Francini-Filho et al. 2000; Coni et al. 2007, 2010).

Wrasses exhibit a variety of behavioral characteristics and have a variety of preferred microhabitats for foraging, but generally, there needs to be a positive relationship between swimming ability and home range used for foraging (Fulton and Belwood 2002; Jones 2002). The *Halichoeres* genus is considered to be highly diverse and widely distributed in the Atlantic Ocean (Rocha et al. 2010). These wrasse species are diurnal, exhibit opportunistic behavior and feed on invertebrates (Randall 1967; Sazima et al. 1998, 2005; Carvalho-Filho 1999). In Brazil, there are eight species of this genus, five of which are endemic (Rocha et al. 2010; Froese and Pauly 2010).

The relationships between habitat characteristics, foraging activity and densities of *Halichoeres* species on tropical rocky shores are poorly understood. Moreover, trophic ecology and social behavior can change with development in these species (Lukoschek and McCormick 2001; Jones 2002; Bonaldo et al. 2006), but there has been no study on ontogenetic shifts in the behavior of the *Halichoeres* species endemic to Brazil.

This study examined the relationship between wave exposure, group size (i.e., number of fish in a school), habitat complexity (rugosity, benthic cover) and depth on the foraging and densities of the wrasse species *Halichoeres poeyi* (Steindachneir 1867), *H. penrosei* (Starks 1913) and *H. brasiliensis* (Bloch 1791) on tropical rocky shores in Brazil. The hypotheses were (1) that there would be a negative relationship between wave exposure and foraging in these species in different ontogenetic phases, (2) that there would be a positive relationship between habitat complexity and foraging in these species and (3) that there would be a positive relationship between foraging activity and group size. The variables which correlate with population densities, preference to form schools, the preference for foraging patches and the diets of these species were also investigated.

Materials and methods

Study area

The study was carried out on nine rocky shores located in the city of Salvador, Bahia, Brazil (Fig. 1), which were assessed by means of snorkeling between September 2011 and February 2012. The maximum depth was 6 m and the hard substrata was composed predominantly of 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. were also found. During our study, horizontal visibility ranged from 5 to 12 m, and water temperature was around 27 °C.

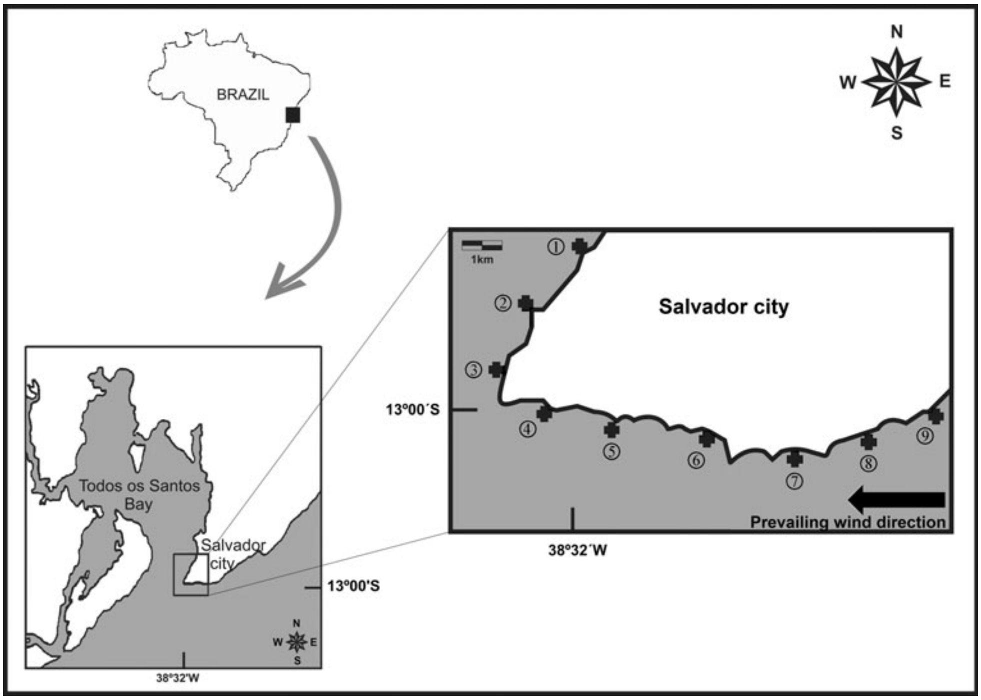

Fig. 1 Map with samplings sites, rocky shores along Salvador city: *1* Solar, *2* Vitória, *3* Barra, *4* Cristo, *5* Ondina, *6* Sereia, *7* Buracão, *8* Amaralina and *9* Pituba

Foraging activity

Foraging activity, i.e., feeding frequency (bites/min), and selection of the substrate were obtained using the ‘focal animal’ method in which we counted the number of bites invested on each type of substratum (Lehner 1979). We observed a total of 540 focal animals. For each of the nine sampling sites, 60 focal observations were conducted (each one with 3 min duration), 20 for each species (10 TP and 10 IP), during which all occurrences were recorded on plastic clipboards. Observations were made between 09:00 a.m. and 16:00 p.m., which appeared to be the peak activity period for labrids (Jones 2002).

When a fish was found, we waited 1 min before starting an observation. In each observation, the species and number of fish in the school (max. 1 m distance) were recorded. To avoid recording fish from the same school, we moved at least 5 m away at the end of each observation.

Density estimates

We used stationary visual censuses adapted from Bonsack and Bannerot (1986), with a 4 m radius and a duration of 5 min to measure fish densities. The censuses were taken from the surface. We used color to determine the life phase of each individual as there are considerable differences in color among these labrids as well as between the life intervals within each species (Jones 2002). Terminal phases (TP) were easily distinguished from initial phases (IP) by their bolder color patterns (except *H. poeyi*) and changes in morphology. A total of 10 visual censuses were performed randomly on each rocky shore with data recorded on plastic clip boards. Identifications of all species, including species belonging to other genera, were made using specialized literature (Humann and Deloach 2002; Sampaio and Nottingham 2008).

Habitat complexity and depth

For each visual census ($n = 10$), two measurements of rugosity and benthic cover were taken, for a total of 40 measurements of habitat complexity for each site. Rugosity was measured using the chain-link method proposed by Luckhurst and Luckhurst (1978). A 1-m chain was draped over the substrate, conforming as closely as possible to all of its contours and crevices, and a measure of the actual surface distance relative to the linear distance was thus obtained. Benthic cover ($n = 20$ per site) was obtained using replicates of a 25 × 25 cm quadrant (100 % cover), each quadrant had 20 intercept points, and the organism below each intercept point was recorded. Only higher taxonomic levels of benthic organisms were discriminated, including macroalgae, turf algae (epilithic algae and macro algae recruits under 5 mm), coralline algae and corals.

Benthic cover (algae and corals) and rugosity were chosen as habitat complexity variables in this study because (1) *Halichoeres* species are found in habitats with corals (Jones 2002), (2) algal habitat provides opportunities to feed (Morton et al. 2008) and (3) high rugosity provides protection against large-sized predators and a high diversity of microhabitats for feeding (Tuya et al. 2009).

For each visual census, two depth measurements were taken using a dive computer. Although one of the rocky shores studied was 6 m deep, the majority (6 of 9 rocky shores) were less than 4 m deep. Our data were collected at depths between 1 and 2.5 m. Water depth may have an influence on the association of wrasse species with different habitats (Morton and Gladstone 2011).

Wave exposure

We used a similar scale of wave exposure to that proposed by Krajewski and Floeter (2011), in which wave exposure was classified on an arbitrary scale from 1 to 9, the score 9 being the highest exposure recorded among the sites. In this classification, Krajewski and Floeter (2011) used the authors' previous dive experience to classify wave exposure. We also used the plaster dissolution method (Jokiel and Morrissey 1993; Angradi and Hood 1998) to check the exposure gradient. Sites with high exposure were expected to suffer greater weight loss of plaster objects. Three plaster balls of known size and weight were placed on each rocky shore and removed after 24 h. We found a strong relationship ($r^2 = 0.81$) between the arbitrary scale of exposure gradient and the data obtained with the plaster dissolution method (see supplementary material), thus validating the values of the arbitrary scale.

Diet

A total of 102 fish were collected: 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 09:00 am and 16:00 pm (the active time for the species) using a hand spear or hand nets while snorkeling. Fish were preserved in formaldehyde (10 % concentration) for a maximum of 1 week, 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

The influence of wave exposure and group size on fish foraging were also investigated with linear regressions. To achieve statistical test requirements, foraging data were log $(x + 1)$ transformed. Fish densities and habitat relationships were analyzed using Canonical Correspondence Analysis (CCA). The Monte Carlo permutation test was used to check whether the axes were significant. This analysis was performed on CANOCO for Windows 4.0 (ter Braak and Verdonschot 1995). Principal component analysis (PCA) was utilized for dimension reduction of the environmental variables (rugosity, depth, coralline algae, macro algae, turf and coral cover) with the data log $(x + 1)$ transformed and normalized; Primer 5.0 software was used for this analysis (Clarke and Warwick 2001). Linear regressions were conducted to investigate the influence of habitat complexity and depth (using PCA scores) on fish foraging. All regressions were conducted using Software R version 2.12.1 for Windows (R 40 Development Core Team 2010).

An electivity index was used to identify the preferred substrate for foraging. This was calculated using the 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 on the substrate i and n_i is the percentage of substrate i in the studied location. 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). Group formation preferences were also investigated using an 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 the diets of the species and ontogenetic phases; Primer 5.0 software was used for this analysis (Clarke and Warwick 2001).

Results

Influence of habitat complexity and depth on foraging activity

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

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

Influence of habitat complexity, depth and wave exposure on densities

The Monte Carlo Permutation test showed that the axes from CCA analysis were significant ($p = 0.006$) and that the first two axes accounted, respectively, for 40 and 33 %

Table 1 Results of regression analysis between fish forage and habitat complexity

	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

IP = initial phase and *TP* = terminal phase

* Significant results

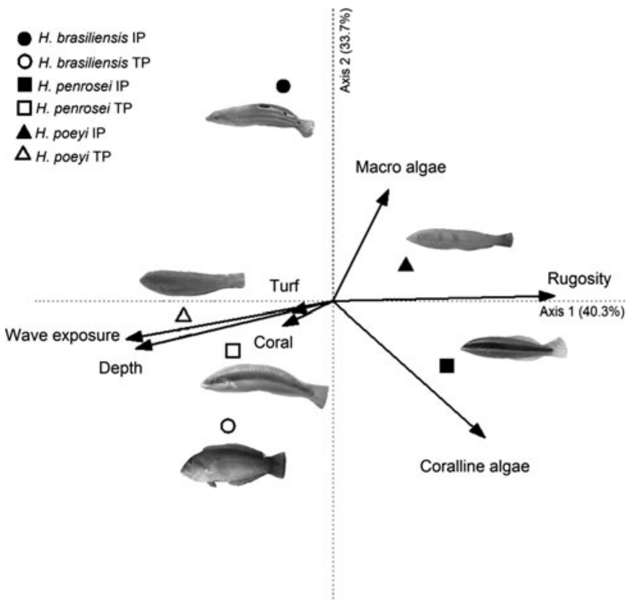

Fig. 2 Correspondence canonical analysis between densities of *Halichoeres* species and variables of habitat complexity and depth. *IP* initial phases and *TP* terminal phases

of the variance between species and variables. The IP densities of *H. poeyi* and *H. penrosei* correlated positively to rugosity and coralline algae, respectively. *Halichoeres* species in the terminal phases correlated positively to depth and wave exposure (Fig. 2).

Influence of wave exposure on foraging activity

There was a change of foraging activity for all species on the exposure gradient, with foraging activity decreasing on rocky shores with a higher degree of wave exposure (Fig. 3). The results of the 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.

Influence of group size on foraging and group formation preferences

Linear regressions showed a positive relationship between foraging activity and group size, except for *H. brasiliensis* TP (Fig. 4). 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), whereas *H. brasiliensis* was found to be more solitary (31.1 % IP and 17.7 % TP).

The majority of the schools observed included other *Halichoeres* species (74 %). *H. poeyi* and *H. penrosei* were found foraging together (less than one meter apart, searching for food and eating in the same school) in 53 % of the observations involving these two species. IP and TP of *H. penrosei* and *H. poeyi* had a preference for foraging with *Acanthurus bahianus* (Acanthuridae) and *Pseudupeneus maculatus* (Mullidae) (Fig. 5a, b). IP of *H. penrosei* also selected *Thalassoma noronhanum*. IP of all species preferred *Sparisoma axillare* (Labridae). IP of *H. brasiliensis* also preferred *A. coeruleus* (Acanthuridae) and *A. bahianus* (Fig. 5c).

Microhabitat preference for foraging and diet

The results of Ivlev's electivity index showed a foraging preference in *Halichoeres* species for turf and macroalgae for both phases of *H. penrosei* and *H. poeyi* (Fig. 6a, b); however, *H. brasiliensis* had a preference for foraging on turf, coral and coralline algae (Fig. 6 C).

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

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 a significant influence on the foraging activities of at least two of the species investigated. Jones (2006) analyzed the distribution of behaviors within home range contours and found that *Halichoeres maculipinna*, a sister species of *H.*

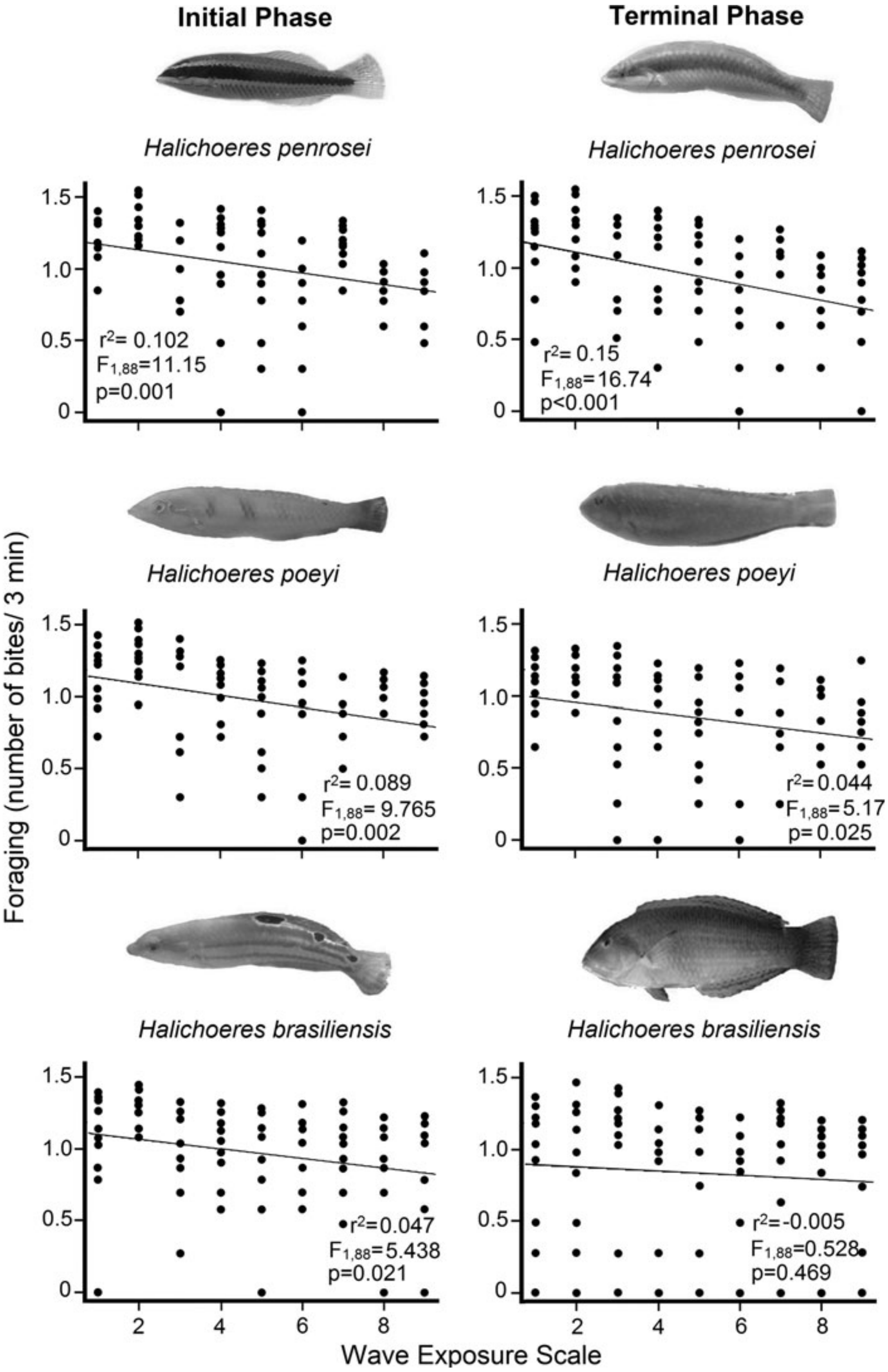

Fig. 3 Relation between wave exposure and foraging activity. Data were transformed in log $(x + 1)$

penrosei (Rocha 2004), and *H. poeyi*, displayed a random distribution of feeding throughout their home range areas at St. Croix, Virgin Islands. Our results do not corroborate Jones (2006), since the *Halichoeres* species in that study selected only certain substrates (see the topic: Microhabitat preference to forage and diet).

According to Krajewski et al. (2010), we might expect that substratum foraging preferences mediate behavioral responses to substratum composition; however, they did not find relationships between general behavioral responses and the abundance of certain substrata. Although we investigated the relationship between habitat complexity (including benthic cover and rugosity) and depth on foraging activities of *Halichoeres* using a different method, we found that foraging activities increase in places with high rugosity and algae cover. Algal habitat provides opportunities to feed (Morton et al. 2008), and rugosity indicates a high diversity of microhabitats for feeding (Tuya et al. 2009).

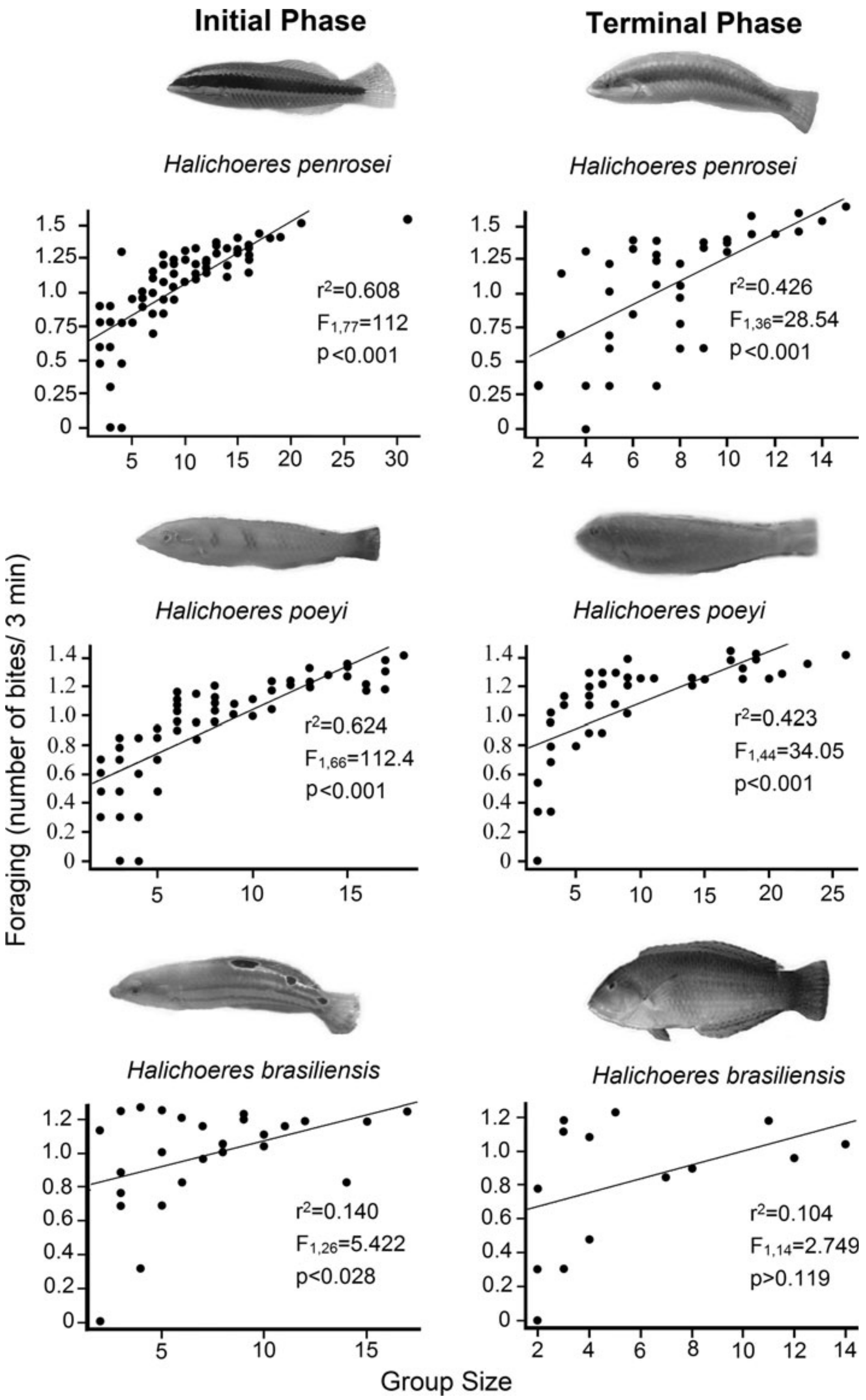

Fig. 4 Relation between group size (number of fish/sample) and foraging activity. Note that each graphic has a different scale. Groups that varied in size during the 3 min

Influence of habitat complexity, depth and wave exposure on densities

Our results showed that TP densities of all species studied correlated to depth and exposure, while IP densities correlated to rugosity and algae cover. According to Morton and Gladstone (2011), depth may have an influence on the association of wrasse species with different habitats. It is likely that other habitat characteristics also contribute to these associations, and as an example, Morton and Gladstone (2011) cited the fact that cobbles and sediment are removed from habitat fringes and barren grounds by high wave energy, whereas smaller substrates accumulate in deeper sponge gardens. Recently, Krajewski and Floeter

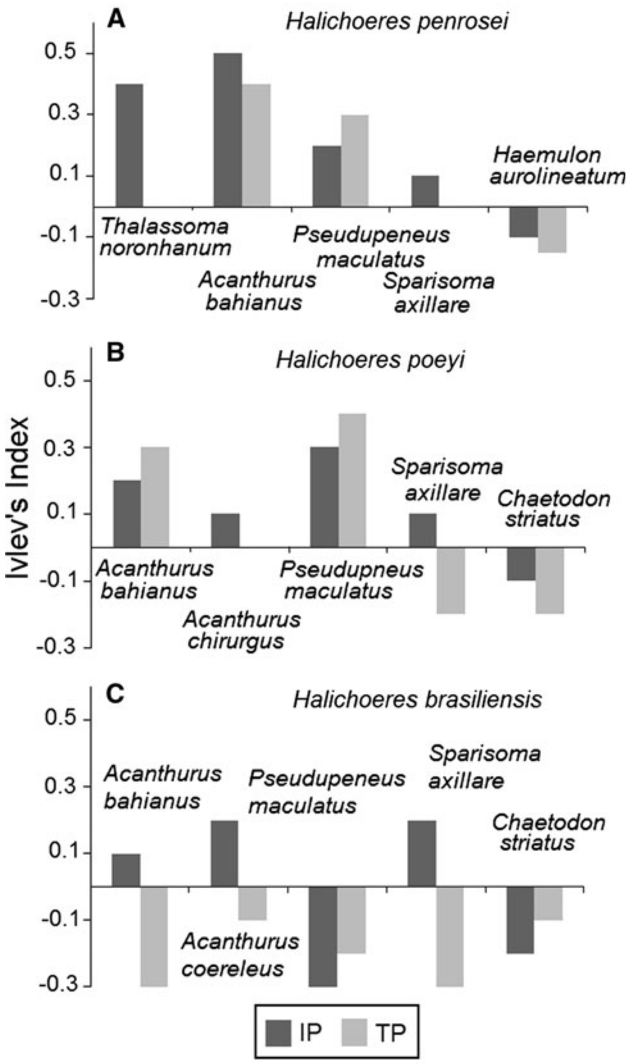

Fig. 5 Results of Ivlev's index showing the species preference to forming of groups by *Halichoeres* species. *Black bars* = initial phases; *Gray bars* = terminal phases

(2011) found that *H. radiatus*, a 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 that the densities of the species studied clearly changed with the distribution of depth strata associated with ontogenetic shifts, even on shallow rocky shores.

The preferential use of shallow habitat rich in algae by IP of wrasse species has also been observed on 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 smaller individuals with 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

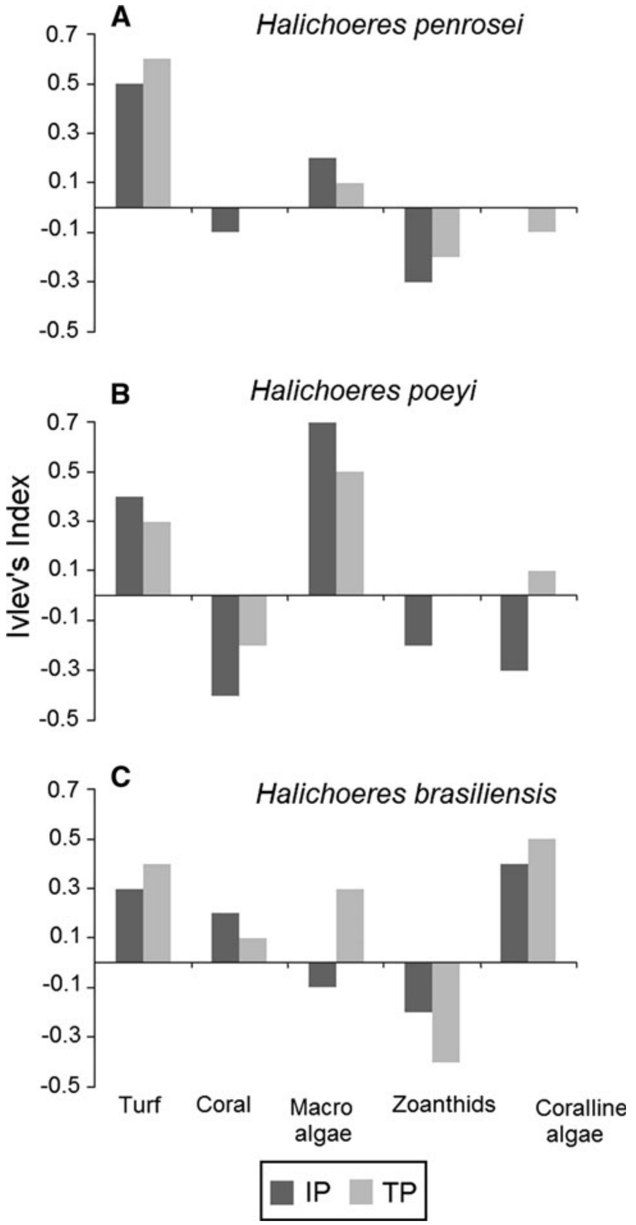

Fig. 6 Results of Ivlev's index showing the preference of forage substratum by *Halichoeres* species. *Black bars* = initial phases; *Gray bars* = terminal phases

wrasse species are susceptible to the influence of wave surge on their swimming performance and their ability to undertake daily activities.

Rocha et al. (2005) studying the abundance of *Halichoeres* in different habitats found that *H. brasiliensis* was more abundant on spur/groove, rock and patch reefs than non-reef habitats. *H. maculipinna* was more abundant on linear reefs and *H. poeyi* on 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 shore habitats, which are shallow and narrow, and this probably explains why our findings

Table 2 Diet of the *Halichoeres* species studied

	Crustaceans	Bivalves	Gastropods	Echinoids	Polychaetes
H. penrosei IP	19 ± 33.9	23.8 ± 37.8	–	–	57 ± 50.9
H. penrosei 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

Numbers correspond to mean of percentage ± SD

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

	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*

* Significant differences

indicate 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, such as the species in this study seem to avoid extra energy expenditure by avoiding foraging under high wave exposure (Johansen et al. 2007a). Our results support most findings for the behavioral responses of fish to water flow (Fulton et al. 2001; Fulton and Bellwood 2005; Johansen et al. 2007a, 2008; Krajewski et al. 2010), where fish decrease their foraging activity at sites with high wave exposure. The exception was *H. brasiliensis* TP. This is the largest species of the genus *Halichoeres* on the Brazilian coast, it can reach 39 cm (Froese and Pauly 2010) and probably has better swimming ability than smaller species. Feeding performance is affected by the locomotion abilities which are used during the search and capture of prey (Colar et al. 2008). Larger size also improves locomotion abilities, allowing movements over large reef areas and into various microhabitats, including those that are exposed to wave action (Fulton and Bellwood 2004).

According to Krajewski et al. (2010), fish may save energy by avoiding swimming in the higher water layers, which have higher water flux (Johansen et al. 2007b), especially at exposed sites. Krajewski and Floeter (2011) also showed a significant positive correlation between wave exposure and proximity to the bottom for *H. radiatus*.

Influence of group size on foraging and school formation preferences

Our data shows that there is an increase in the rate of *Halichoeres* foraging as the group size increases. The schooling behavior of fish is acknowledged to be 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).

Halichoeres poeyi and *H. penrosei* were found more in schools than solitarily, while *H. brasiliensis* was found solitarily several times. Jones (2002) stated that larger individuals of *Halichoeres* spend more time swimming alone, possibly because more effective at escaping predation or they are more efficient at finding food. To confirm the pattern found by Jones (2002) and corroborated in this study, other *Halichoeres* populations should be investigated.

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

In general, our results for group selection showed that parrotfish and surgeonfish were selected to form schools by *Halichoeres* species. Jones (2002) found similar results where parrotfish and surgeonfish were present in the schools of Caribbean *Halichoeres* species; however, goatfish were not registered by Jones (2002) in the *Halichoeres* schools. The characteristics of the tropical rocky shores studied can partly explain the presence of goatfish at the sites, where unconsolidated substratum can be found near the rocky shores, since goatfish are known to use unconsolidated substratum for foraging (Barros et al. 2001; Krajewski et al. 2006).

The schools observed were formed by species of different families and trophic levels. We believe that *Halichoeres* species establish schools with species of fish which do not offer risk from various trophic levels (e.g., invertivores and herbivores), to take advantage of living in groups. According to Welsh and Bellwood (2012), the benefits of schooling behavior may not be restricted to the individual, but may also have significant implications for ecological processes. Although they studied herbivorous species, we believe that school-forming invertivorous species may have an added role on rocky shores by facilitating higher feeding rates in other fishes, thus increasing the functional role of conspecific and heterospecific species which associate with the school.

Microhabitat foraging and diet preferences

The species studied showed a preference for foraging on turf. Azevedo (2009) stated that all the size classes of *H. poeyi on* subtropical rocky shores in Brazil had a preference for foraging on the Epilithic Algal Matrix (EAM). The EAM is widely known as a substrate rich in sediment and debris with quantities of invertebrates of high nutritional value (Crossman et al. 2005; Wilson et al. 2003; Azevedo 2009).

In our study, as expected, the diets of endemic species (*H. penrosei* and *H. brasiliensis*) were similar to their sister species from the 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 have a tendency to feed on soft-bodied prey. Although *H. brasiliensis* and *H. penrosei* followed this pattern, the stomach contents of *H. poeyi* IP were dominated by bivalves. Future studies should test whether preferences in the diets of *Halichoeres* species are correlated with the availability of prey in the foraging habitats.

Morton et al. (2008) showed significant changes in the diet of labrids with increasing body length, mainly reflecting 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 that with increasing body size, fish fed on greater volumes of hard-shelled molluscs. Similar size-related shifts in diet have been observed in other species of labrids in temperate Australia and New Zealand (Jones 1988; Gillanders 1995; Denny and Schiel 2001). Increased mouth size, the greater crushing power of pharyngeal teeth, shifts in foraging microhabitats, and improved locomotion and sensory abilities are the main factors in size-related changes in dietary compositions (Wainwright 1988; Morton et al. 2008).

Our study demonstrates that both densities and the foraging activity of *Halichoeres* species are influenced by wave exposure and habitat complexity on tropical rocky shores. Group size is an important factor in foraging activity, since foraging rates increase with group size and functional roles change according to ontogenetic shifts. Behavioral use of microhabitats may determine large-scale distribution patterns (Fulton et al. 2001). We believe that behavioral use of microhabitats can be a useful tool to investigate the distribution patterns of fish between coral reefs and tropical rocky shores. In times of change in many ecosystems, including alterations due to climate change and overfishing in marine environments such as coral reefs and rocky shores, where many species of fish (especially carnivores and herbivores) are already at risk, efforts at understanding invertivory fish must be encouraged before this trophic level, composed mainly of medium-sized and small fish, is also threatened.

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