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SUBSTRATE ASSOCIATION AND PATTERNS OF MICROHABITAT USE BY FISHES AT FERNANDO DE NORONHA ARCHIPELAGO (BRAZIL)

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ABSTRACT

The present study tested the degree of substrate association of five common species and their patterns of non-random preferences to benthic categories. Benthic estimates were made on four sites at the Fernando de Noronha Archipelago, and using focal observations we determined substrate preferences of each species testing whether the observed patterns were different than randomly expected. Mobile species showed random substrate preferences, whereas site-attached and

territorial species showed somewhat distinguished patterns. Differences in substrate preferences of these two groups are likely to be an effect of contrasting foraging strategies. Nevertheless, even mobile species spent over 80% of their time within up to 30 cm above the substrate, suggesting that substrate plays an important role on their life histories, possibly offering protection sites against predators.

Key Words: Benthic cover, Oceanic island, Reef fishes.

RESUMO

O presente estudo avaliou o grau de associação ao substrato de cinco espécies comuns e seus padrões não-aleatórios de preferência por categorias bênticas. Estimativas foram realizadas em quatro áreas no Arquipélago Fernando de Noronha, e utilizando observações focais nós determinamos a preferência por substrato de cada espécie testando se os padrões observados foram diferentes do esperado aleatoriamente. Espécies móveis apresentaram preferências aleatórias, enquanto espécies de fundo e

territoriais mostraram padrões distintos. Diferenças na preferência por substrato desses dois grupos são provavelmente um efeito de estratégias de forrageio contrastantes. No entanto, até mesmo espécies móveis passaram mais que 80% do tempo próxima ao substrato (até 30 cm), sugerindo que o substrato desempenha um importante papel na história de vida desses peixes, possivelmente oferecendo proteção contra predadores.

Palavras chave: Cobertura bêntica, Ilha oceânica, Peixes recifais.

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INTRODUÇÃO

Fishes rely on the reef substrate for two main purposes: shelter and food (FRIEDLANDER and PARRISH, 1998). Shelter, whether permanent or temporary, is important as protection and reproduction sites, whereas food, albeit seemingly important only to herbivores, bottom-feeders and invertebrate pickers, which feed directly on the bottom, is also important to piscivores, since fish prey are abundant near the substrate. Given that associations to the substrate are supposedly stronger at sites with high structural complexity (CARPENTER et al., 1981; ALMANY, 2004) and high benthic diversity (BELL and GALZIN, 1984; CHABANET et al., 1997), a scarcity of fishes is expected at sites with low complexity and low benthic diversity. Although this pattern seems to be generally accepted, it seems not to be universal for all species. For example, invertebrate pickers, such as haemulids, are most common in non-complex sandy bottoms (MEDEIROS et al., 2011).

Due to the importance of substrate to fishes, competition for space and resources is usually high, and variations in substrate topography and benthic composition have also been correlated to differences in fish density (see GRATWICKE and SPEIGHT, 2005). Furthermore, given that higher competition is expected amongst ecologically similar species (EAGLE et al., 2001), sites with high species richness tend to show higher degrees of niche specialization.

Given that sedentary and site-attached species have limited movement during adult stages, it is expected that these species be located in close association to their preferred food items. On the other hand, mobile species are expected to dislocate to areas with their preferred food items only during foraging periods. Further, specialized feeders (e.g. herbivores or invertebrate pickers) are most likely to be affected by food limitation within a particular area, and for these species, being located nearby their preferred food may be vital, whereas the plasticity of omnivores allows them to associate to several types of substrates.

Since the majority of studies evaluating patterns of microhabitat use have been conducted at high-diversity sites, mostly in the Caribbean and Indo-Pacific regions (e.g. HIXON, 1991; LETOURNEUR, 1992; GROSSMAN et al., 1997; BELLWOOD et al., 2002), it is not certain whether the above mentioned patterns remain at sites with relative lower diversity, such as those in the South Atlantic. In fact, it is theoretically expected that associations to particular substrates and niche specialization are weaker at these sites, even for site-attached species. Nevertheless, algae-dominated sites with low coral diversity and low fish species richness remain poorly studied. Despite their importance to reef fish ecology, given that microhabitat preferences and differences in food requirements are amongst the most significant factors sustaining diversity among reef fishes (ORMOND et al., 1996), these processes remain poorly known at these sites.

In the present study we tested the degree of substrate association of five common species with different swimming habits and food preferences, and whether associations to particular substrate types were driven by random factors or if they revealed particular food preferences. Thus, we initially addressed the question: does the preferred substrate of each species correspond to their feeding preferences? Specifically, we hypothesized that herbivores with sedentary habits would associate to algae-rich substrates more than expected, whereas mobile omnivores were most likely to show weak associations and random substrate use. Also, we investigated the relationships among these species and tested whether they were grouped by habitat preferences (i.e. site-attached species joined regardless of

MATERIAL AND METHODS

Study sites

The study was conducted at four sites at Fernando de Noronha archipelago, a tropical oceanic island in the Southwestern Atlantic region, 360 km off the Brazilian coast (Fig.1). The archipelago is a marine protected area (MPA) under the Brazilian jurisdiction where fishing is strictly prohibited. The study was conducted at four rocky reefs (depths between 0.6 and 2 m): Sueste bay, Raquel, Atalaia and Porto beach.

Fish Preferences and Substrate Composition

Five fish species were subjects in the present study: *Acanthurus chirurgus* (Acanthuridae) (roving herbivore), *Malacoctenus* sp. (Labrisomidae) (site-attached omnivore), *Ophioblennius trinitatis* (Blennidae) (site-attached herbivore), *Stegastes rocasensis* (Pomacentridae) (territorial herbivore) and *Thalassoma noronhanum* (Labridae) (roving omnivore). *Malacoctenus* sp., formerly *M. triangulatus*, is currently under investigation to be described as a new species in the Brazilian province. Albeit it remains being frequently cited as *M. triangulatus* (e.g. GUIMARÃES et al., 2010), the term *Malacoctenus* sp. was adopted in the present study. Focal species of the present study are amongst the most abundant fishes in the study area (SOTO, 2002) and belong to common genera and families of reefs worldwide (HUMANN and DELOACH, 2002). Therefore, observations made for these species may be cautiously extrapolated to, and/or serve as comparative background of counterpart species from other reefs.

We used focal animal observations (LEHNER, 1996) to determine the degree of association of each species to the substrate and to quantify the percentage use of each substrate category at each site. Five minutes was spent observing each focal individual ($n = 10$ per species and site), totaling 200 minutes of observation per species. During focal observations, a randomly chosen individual was selected and the diver spent one minute observing the individual before initiating the counts, for the fish to get accustomed to his presence. After the 1-minute adaptation period the diver recorded the nature of the substrate located below the head of the focal fish, swimming or immobile, within 30 cm above the substrate (KRAJEWSKI et al., 2010) at 10-seconds intervals (i.e. 30 counts per focal individual). Substrate use by focal individuals was recorded at one of six categories: 1) turf algae, 2) macroalgae, 3) coralline algae, 4) live coral, 5) sand, and 6) uncolonized pavement. Also, the instances in which the focal individual was located 30 cm or more above the substrate were categorized as non-associated to the substrate. During the observation, an individual lost at any point was discarded and a new event initiated.

Investigations were carried out during daytime between 08:00 and 16:30 from October 14 2009 to October 28 2009. To account for possible time of day and tidal biases, focal individuals were investigated following a determined sequence, that is, a second focal observation on a given species was only conducted when the first focal individuals of all other species had been conducted.

Benthic composition at each site was evaluated using photoquadrat estimations (PRESKITT et al., 2004). At each site, ten photographs, each encompassing a $1 \times 1 \text{ m}^2$ area, were taken within the limits of the area where focal individuals were observed. Posteriorly, each photograph was analyzed using the coral point count with Excel extension software (CPCe 3.6) (KOHLENER and GILL, 2006), where the proportion of the same substrate categories described above was evaluated.

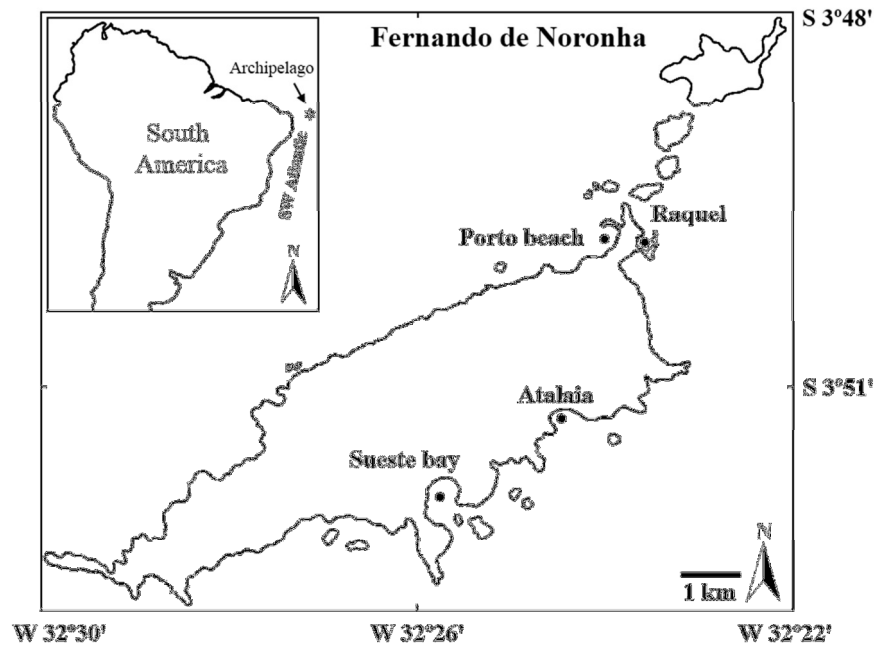


Figure 1 – Location and map of study areas in Fernando de Noronha archipelago, Southwestern Atlantic ocean.

Data Analysis

The degree of substrate association of each species was determined. To calculate this, the proportion of associated events (i.e. those in which the individual was recorded within up to 30 cm above the substrate) was determined relative to the total number of events, (i.e. associated plus non-associated events). Non-associated events were those in which the individual was recorded, swimming or immobile, at a >30 cm vertical distance from the substrate. Subsequently, fishes were classified according to the following arbitrary scale of substrate association: 1) <25%: very low association; 2) 25 to 50%: low association; 3) 50 to 80%: intermediate association; 4) 80 to 95%: high association and 5) >95%: very high association.

Spatial variability in the degree of substrate association was tested for each species individually using one-way ANOVAS with Tukey's HSD as the post hoc test. To determine whether substrate preferences were different than randomly expected, χ^2 tests were used to compare the observed proportions of habitat association of each species to the expected based on estimates of benthic composition done at each site. Therefore, since fishes are most likely to associate to substrate categories with higher proportions, the χ^2 tests the significance of these relationships assuming their different proportions.

Also based on observed and expected values, Ivlev's selectivity index (IVLEV, 1961) was used to test the degree of substrate preference, with data from all sites pooled, following the equation: $E = (r_i - p_i)(r_i + p_i)^{-1}$, where E is the selectivity index and r_i and p_i are the relative proportions of the i category of substrate use (r) and in the environment (p), respectively. This index ranges from -1 to 1, where positive values indicate a preference, negative values avoidance or inaccessibility, and values close to zero suggest an expected random substrate use.

A similarity matrix (cluster analysis) using Euclidian-distance was computed from data of all species pooled across all sites to test the relationships among species as a means to determine whether species grouped based on habitat or feeding preferences.

RESULTS

A significant difference in the degree of substrate association among sites was only detected for *Acanthurus chirurgus* (ANOVA; $F_{2,20} = 8.07$; $p < 0.001$) (Fig.2). This species showed a somewhat high degree of spatial fluctuation and was classified as having an intermediate/high substrate association. *Thalassoma noronhanum* also showed some spatial fluctuation, albeit not significant, with the lowest values of substrate association and being classified as intermediate. *Malacoctenus* sp. and *Ophioblennius trinitatis* were classified as having very high degrees of substrate association, whereas *Stegastes rocasensis* showed high values (Fig.2).

The four sites evaluated were characterized by high percentages of turf and macroalgae and, with the exception of Raquel, low proportions of live coral (Fig.3). In general, small spatial variation was observed for most benthic categories among sites, but Atalaia showed somewhat unique quantities of macroalgae.

Substrate use was significantly different than expected at random at three of the evaluated sites for *A. chirurgus* (Fig.4). At Atalaia, association to turf algae was higher than randomly expected, whereas macroalgae was used less than randomly expected. The opposite pattern was observed at Raquel, turf algae being used less than randomly expected and macroalgae being used more than randomly expected. Also at this site, live coral was used less than randomly expected. At Porto the only significant difference was for sand, which was used slightly more than randomly expected, albeit this was only marginally significant. In general, this species showed a somewhat common substrate use at all sites, with slight differences regarding turf algae and macroalgae (i.e. similar at Atalaia and Sueste, and similar at Raquel and Porto).

For *Malacoctenus* sp., substrate use was also significantly different than expected at random at three of the evaluated sites (Fig.5). At Atalaia, macroalgae was used less than randomly expected and sand was used more than randomly expected. At Raquel, coralline algae, sand and uncolonized pavement were used more than randomly expected, whereas macroalgae and live coral were used less than randomly expected. At Sueste, uncolonized pavement was used more than randomly expected and turf algae and sand were used less than randomly expected. At Porto, the apparent differences in turf algae use were not statistically significant.

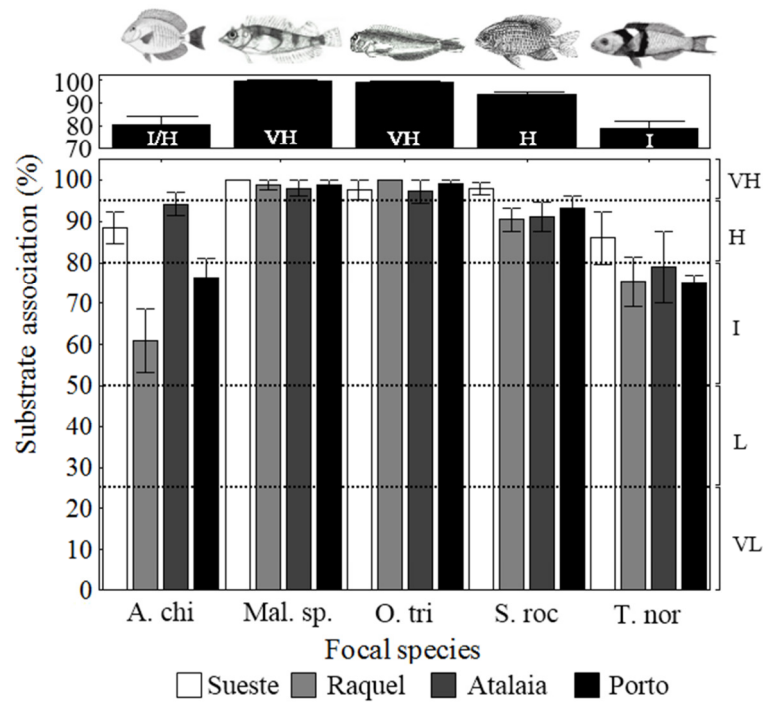


Figure 2 – Degree of substrate association of five reef fish species. Top panel shows the index with data from all sites pooled. Bottom panel shows index separated by site. Associations are interpreted as: very low (VL), low (L), intermediate (I), high (H) and very high (VH). A. chi: *Acanthurus chirurgus*, Mal sp.: *Malacoctenus* sp., O. tri: *Ophioblennius trinitatis*, S. roc.: *Stegastes rocasensis* and T. nor.: *Thalassoma noronhanum*.

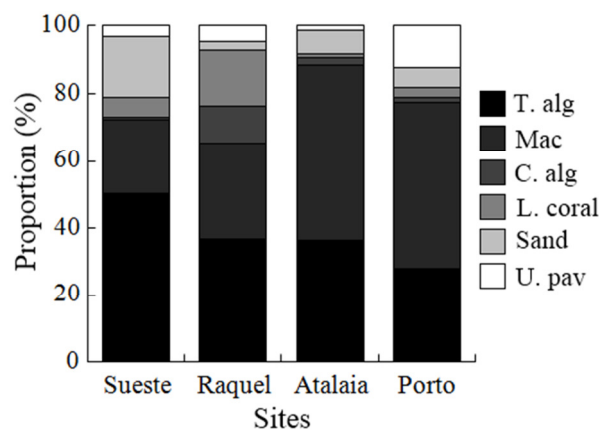


Figure 3 – Relative proportions of six benthic categories at the four study sites. T. alg: turf algae, Mac: macroalgae, C. alg: coralline algae, L. coral: live coral, Sand: sand and U. pav: uncolonized pavement.

For *O. trinitatis*, substrate use was significantly different than expected at random at two sites (Fig.6). At Atalaia, differences were due to a higher than randomly expected use of coralline algae and a lower than randomly expected use of turf algae and sand. At Raquel, turf algae and coralline algae were used more than randomly expected, whereas macroalgae and live coral were used less than randomly expected.

Substrate use of *S. rocasensis* was significantly different than randomly expected at all sites (Fig.7). In general, a similar substrate use was observed at all sites with turf algae being the predominant benthic item. Thus, turf algae was used more than randomly expected and macroalgae was used less than randomly expected at all sites. Also, sand was used less than expected randomly at Sueste, sand was used more than

randomly expected at Porto and uncolonized pavement was used more than randomly expected at Porto.

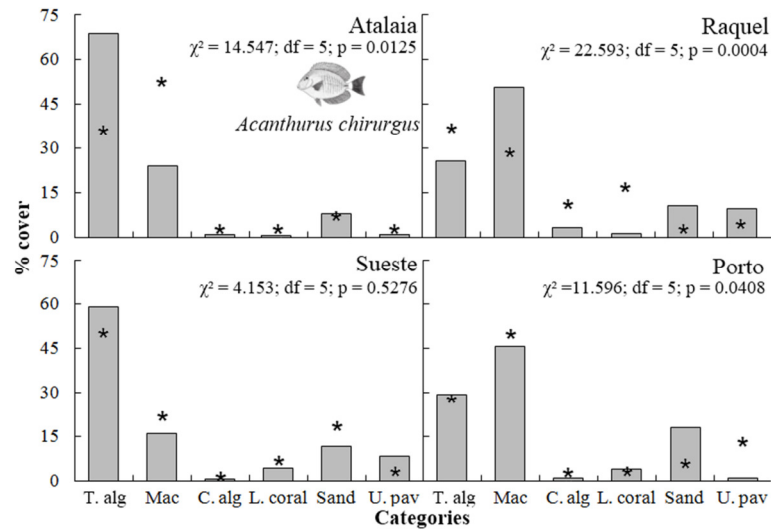


Figure 4 – Substrate use by *Acanthurus chirurgus* (columns) and expected values (*) based on benthic cover estimates at the four study sites. Chi-square results are given for each site. Benthic categories are the same as in Figure 3.

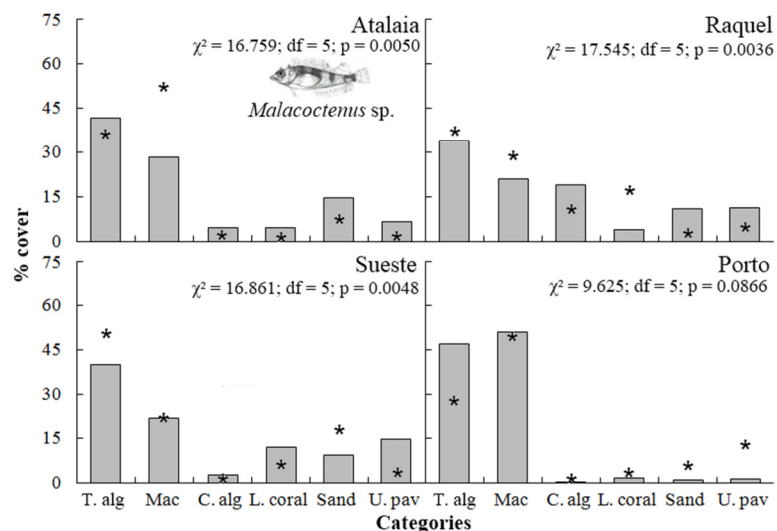


Figure 5 – Substrate use by *Malacoctenus sp.* (columns) and expected values (*) based on benthic cover estimates at the four study sites. Chi-square results are given for each site. Benthic categories are the same as in Figure 3.

T. noronhanum was the only species in which substrate use was not significantly different than expected at random at any of the evaluated sites (Fig.8).

With data from all sites pooled, *Malacoctenus sp.*, *O. trinitatis* and *S. rocasensis* associated to particular substrates more than *A. chirurgus* and *T. noronhanum*, but these relationships were somewhat weak even for these former species. Coralline algae (*Malacoctenus sp.* and *O. trinitatis*), uncolonized pavement (*Malacoctenus sp.*), turf algae (*O. trinitatis* and *S. rocasensis*) and live coral (*S. rocasensis*) were the preferred

substrates of the three former species, whereas *A. chirurgus* and *O. trinitatis* neglected the majority of substrates (Fig.9).

Cluster analysis grouped species based on substrate preferences, with two groups being formed (Fig.10). The first group comprised the mobile species *A. chirurgus* and *T. noronhanum*, whereas the second grouped the site-attached *Malacoctenus* sp., *O. trinitatis* and *S. rocasensis*.

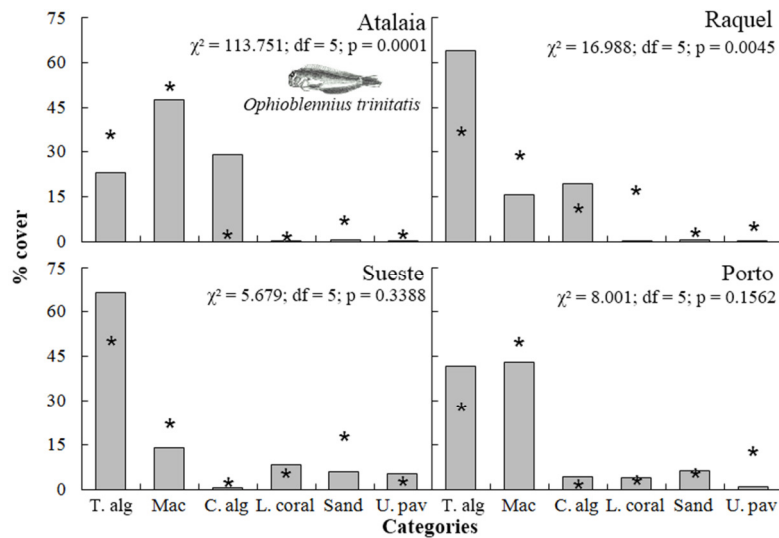


Figure 6 – Substrate use by *Ophioblennius trinitatis* (columns) and expected values (*) based on benthic cover estimates at the four study sites. Chi-square results are given for each site. Benthic categories are the same as in Figure 3.

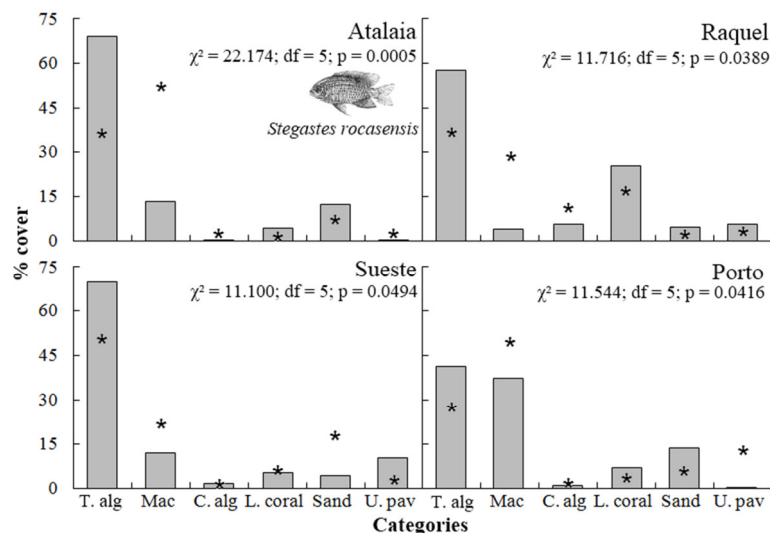


Figure 7 – Substrate use by *Stegastes rocasensis* (columns) and expected values (*) based on benthic cover estimates at the four study sites. Chi-square results are given for each site. Benthic categories are the same as in Figure 3.

DISCUSSION

As expected, the two site-attached species (*Malacoctenus* sp. and *Ophioblennius trinitatis*), and the territorial pomacentrid (*Stegastes rocasensis*) showed stronger associations to the substrate than the mobile species (*Acanthurus chirurgus* and

Thalassoma noronhanum). In fact, these three former species were observed in close association to the substrate (i.e. within up to 30 cm) during over 90% of the observations, considering all sites pooled. Considering their microhabitat preferences and the underlying effects of each particular substrate category investigated, these species also showed stronger patterns of microhabitat preferences, whereas the two latter species associated to these categories randomly. Cluster analysis further confirmed these two groups, which separated by degree of substrate association and microhabitat preferences. Given these observations, we propose that differences in substrate use are a direct effect of two contrasting foraging strategies, discussed below.

Albeit microhabitat preferences were not very strong even for the first group, patterns indicating non-randomness in substrate use were observed. For example, the herbivores (*O. trinitatis* and *S. rocasensis*) showed significantly high associations to algae, whereas the omnivore *Malacotenus* sp. correlated positively to algae, but also to uncolonized pavement and sand, substrates in which mobile invertebrates are commonly found (FERREIRA et al., 2004). Given their sedentary habits, microhabitats used by these fishes should be those which improve accessibility to preferred food. Therefore, these species tend to show stronger substrate preferences than mobile fishes.

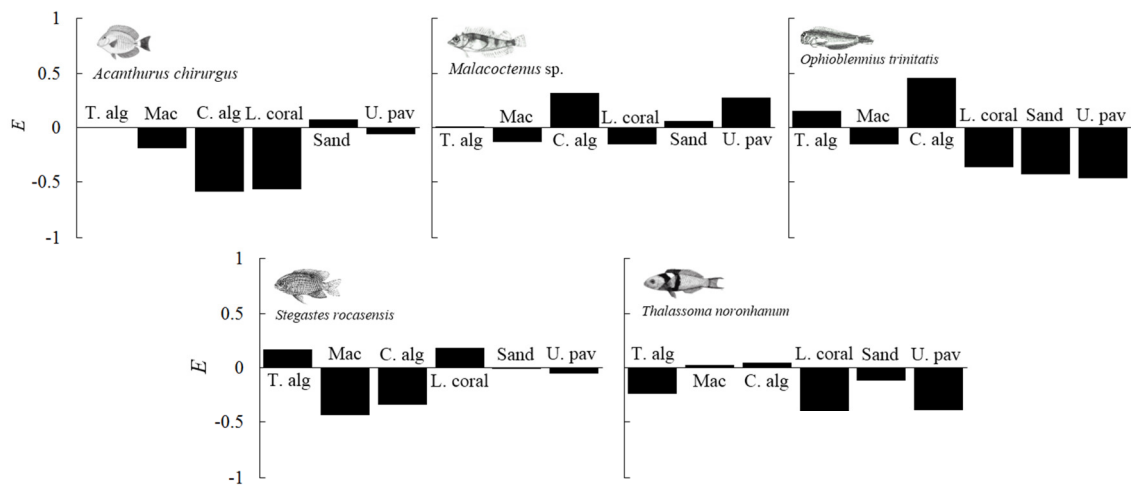


Figure 8 – Substrate use by *Thalassoma noronhanum* (columns) and expected values (*) based on benthic cover estimates at the four study sites. Chi-square results are given for each site. Benthic categories are the same as in Figure 3.

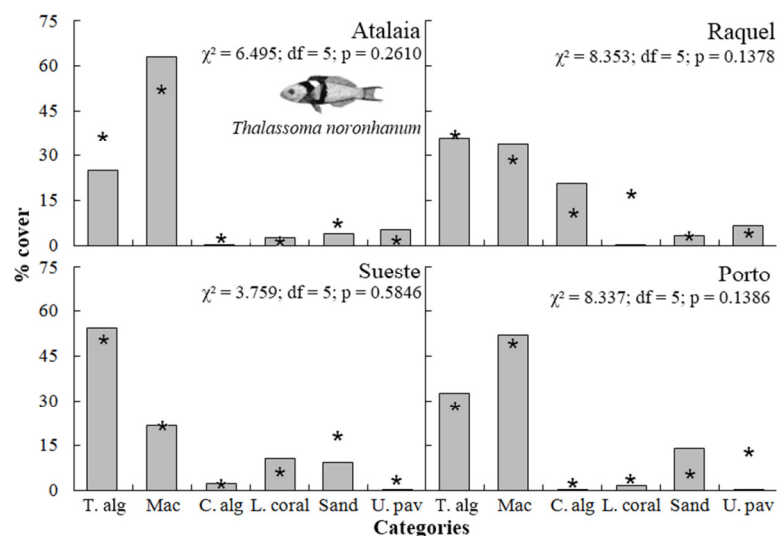


Figure 9 – Ivlev's selectivity index regarding substrate preferences of five reef fish species with data from the four study sites pooled.

The somewhat weak substrate preferences of the acanthurid and the labrid species are likely to be an effect of their mobile habits. While this is an expected finding for the plastic omnivore *T. noronhanum* (FRANCINI-FILHO et al., 2000), for the herbivore *A. chirurgus* it would be expected that a significant budget of its time was to be spent over turf and macroalgae substrates, which make up the greatest proportion of their diet, but these patterns were not very consistent. Although some acanthurids show solitary and even sporadic territorial habits during juvenile stages (ITZKOWITZ, 1974; THRESHER, 1984; FOSTER, 1985), adults form dense foraging schools, tending to show an erratic substrate use (LAWSON et al., 1999). Therefore, the roving and erratic feeding strategies of *A. chirurgus*, in addition to the high availability of algae in the study area, precluded a non-random microhabitat use by this species. Nevertheless, schools of acanthurids were commonly observed over algal mats in the study area feeding on the high-quality food defended by territorial fishes, in a strategy similar to that originally reported by Foster (1985). In sum, the somewhat arbitrary association to algae by this species seems to be a direct effect of their random feeding, where this species does not need to allocate more than the necessary time to feed on their preferred food.

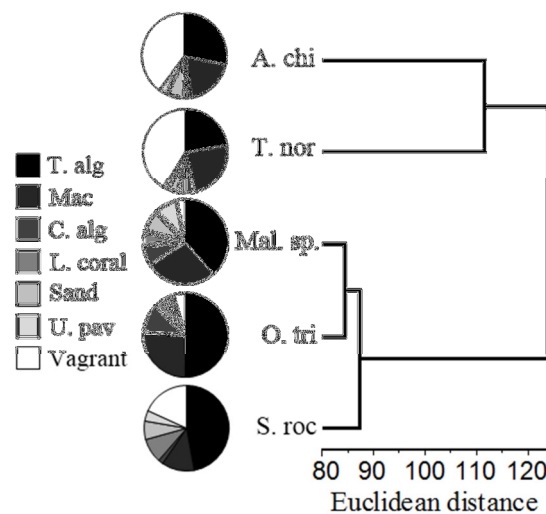


Figure 10 – Similarity matrix using Euclidian distances on the relationship among five reef fishes based on their degree of substrate association and substrate preferences.

Species of the two groups mentioned above were separated due to stronger and weaker associations to the substrate, respectively and, mostly, due to differences in substrate use. This dissociation was clearly a direct effect of their intrinsic ecological foraging strategies. The first group showed species which rely on being permanently associated to their preferred food. An obvious positive effect of this strategy is the low energy cost spent during foraging, given that long dislocations are unnecessary. A trade-off, however, is the underlying energy cost of defending food from nearby intruders (WARNER and HOFFMAN, 1980; MEEKAN et al., 2010), a common feature of several site-attached fishes. Contrasting to this, the second group consisted of species which spent a great deal of time and energy erratically swimming in search of food. Fishes of this group are most likely to be affected at sites or periods with high food limitation, unlikely to be the case in the study area (see below), whereas sedentary fishes which defend high-quality food from other fishes are most likely to overcome these harsh situations. In fact, schools of roving herbivores investing on algae located within substrates defended by territorial herbivores, as reported above, is a strong evidence of the high-quality of their food resources.

One remarkable finding in the present study was that the degree of habitat association was somewhat high even for the mobile species, being strong evidence that reef substrate is very important for all reef fish species. In fact, the two mobile species of the present study, *A. chirurgus* and *T. noronhanum*, were observed within up to 30 cm

above the substrate, respectively, during 80.2% and 78.9% of the observations. This supports our affirmations that association to the substrate is not exclusively a response to food availability, but also to other factors. For example, associations seem to be a direct response to predation pressure, given that the crevices and irregularities of the substrate are the most important temporary and permanent refuge sites for small fishes (ROBERTS and ORMOND, 1987; GRATWICKE and SPEIGHT, 2005). Therefore, protection from predators is a means of potential prey reducing encounter rates with larger, predatory fishes and, thus, even for these randomly-selective fishes, association to the substrate is vital.

Contrary to Caribbean and Indo-Pacific reefs, Southwestern Atlantic reefs are characterized by low coral (CASTRO, 2003) and low fish species richness (FLOETER and GASPARINI, 2000), but of relatively high endemism (FLOETER and GASPARINI, 2001; MOURA, 2002). Therefore, processes determining fish species distribution and abundance are not necessarily shared by these areas (e.g. MEDEIROS et al., 2010), with species-specific responses to particular substrates tending to be weaker in Southwestern Atlantic reefs. Reefs with higher species richness also tend to show higher niche specialization (EAGLE et al., 2001) with abundance of most species being highly dependent on particular habitat features (BROWN, 1984; GASTON et al., 1997). Therefore, one should be able to predict density of fishes at these sites based on particular habitat preferences and the presence of these features at a given environment. These meticulous relationships do not conform entirely to Southwestern Atlantic reefs, where a relatively low number of fish species and niches are observed, and generalized habits prevail over specialized ones (FLOETER and GASPARINI, 2000; 2001; FLOETER et al., 2004), thus, explaining the general substrate preferences observed here. Nevertheless, even for highly site-attached specialists at high-richness sites, associations may be weaker than expected. For example, Eagle et al. (2001) observed that habitat use differed among three *Centropyge* species on a broader scale (10s to 100s of meters), but on a fine-scale (less than few meters), associations were very low.

CONCLUSION

Spatial differences in habitat use, mostly observed for mobile species, albeit also in a smaller extent for site-attached species, is an indication that species which depend less upon particular substrates (i.e. mobile ones) are not affected by local variations in substrate composition, given their random association to the substrate and the consequential higher tolerance to substrate variation. Spatial variations in benthic composition are less likely to affect the density of mobile species, but should play an important role in determining populations of site-attached species with stronger habitat preference. On the other hand, the high abundance of algae in the study area, a common feature of most Southwestern Atlantic reefs (MEDEIROS et al., 2010), strongly suggests that food is not a limiting factor for herbivores and omnivores of the study area, but space and availability of crevices seem more important (MEDEIROS et al., 2011). Future studies determining the extent of local mobility of wanderers should bring up new information.

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REFERENCES

- ALMANY, G. R. Differential effects of habitat complexity, predators and competitors on abundance of juveniles and adult coral reef fishes. **Oecologia**, v. 141, p. 105-113, 2004.
- BELL, J. D.; GALZIN, R. Influence of live coral cover on coral reef fish communities. **Marine Ecology Progress Series**, v. 15. p. 265-274, 1984.

MEDEIROS, P. R. et al. Substrate association and patterns of microhabitat use by fishes at Fernando de Noronha Archipelago (Brazil).

BELLWOOD, D. R.; WAINWRIGHT, P. C.; FULTON, C. J.; HOEY, A. Assembly rules and functional groups at global biogeographical scales. **Functional Ecology**, v. 6, p. 557-562, 2002.

BROWN, J. H. On the relationship between abundance and distribution of species. **American Naturalist**, v. 124, p. 255-279, 1984.

CARPENTER, K. E.; MICLAT, R. I.; ALBALADEJO, V. D.; CORPUZ, V. T. The influence of substrate structure on the local abundance and diversity of Philippine Reef Fishes. **Proceedings of the 4th International Coral Reef Symposium**, v. 4, p. 497-502, 1981.

CASTRO, C. B. **Coral reef in Brazil**. In: PRATES, A. P. L. (Ed.). Atlas of Coral Reef Protected Areas in Brazil. Brasília: MMA/SBF, 2003. p. 25-27.

CHABANET, P.; RALAMBONDRAIN, H.; AMANIEU, M.; FAURE, G.; GALZIN, R. Relationship between coral reef substrata and fish. **Coral Reefs**, v. 16, p. 93-102, 1997.

EAGLE, J. V.; JONES, G. P.; McCORMICK, M. I. A multi-scale study of the relationships between habitat use and the distribution and abundance patterns of three coral reef angelfishes (Pomacanthidae). **Marine Ecology Progress Series**, v. 214, p. 253-265, 2001.

FERREIRA, C. E. L.; FLOETER, S. R.; GASPARINI, J. L.; JOYEUX, J. C.; FERREIRA, B. P. Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. **Journal of Biogeography**, v. 31, p. 1093-1106, 2004.

FLOETER, S. R.; GASPARINI, J. L. The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns. **Journal of Fish Biology**, v. 56, p. 1099-1114, 2000.

FLOETER, S. R.; GASPARINI, J. L. The Brazilian endemic reef fishes. **Coral Reefs**, v. 19, p. 292, 2001.

FLOETER, S. R.; FERREIRA, C. E. L.; DOMINICI-AROSEMENA, A.; ZALMON, I. R. Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. **Journal of Fish Biology**, v. 64, p. 1680-1699, 2004.

FOSTER, S. A. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. **Animal Behaviour**, v. 33, p. 782-792, 1985.

FRANCINI-FILHO, R. B.; MOURA, R. L.; SAZIMA, I. Cleaning by the wrasse *Thalassoma noronhanum*, with two records of predation by its grouper client *Cephalopholis fulva*. **Journal of Fish Biology**, v. 56, p. 802-809, 2000.

FRIEDLANDER, A. M.; PARRISH, J. D. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. **Journal of Experimental Marine Biology and Ecology**, v. 224, p. 1-30, 1998.

GASTON, K. J.; BLACKBURN, T. M.; LAWTON, J. H. Interspecific abundance-range size relationships: an appraisal of mechanisms. **Journal of Animal Ecology**, v. 66, p. 579-601, 1997.

GRATWICKE, B.; SPEIGHT, M. R. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. **Journal of Fish Biology**, v. 66, p. 650-667, 2005.

GROSSMAN, G. D.; JONES, G. P.; SEAMAN-JR, W. J. Do artificial reefs increase regional fish production? A review of existing data. **Fisheries**, v. 22, p. 17-23, 1997.

GUIMARÃES, R. Z. P.; NUNAN, G. W.; GASPARINI, J. L. *Malacoctenus brunoi* sp. n. (Blennioidei: Labrisomidae), a new scaled-blenny from Trindade Island, off Brazil. **Zootaxa**, v. 2567, p. 50-56, 2010.

MEDEIROS, P. R. et al. Substrate association and patterns of microhabitat use by fishes at Fernando de Noronha Archipelago (Brazil).

HIXON, M. A. **Predation as a process structuring coral reef fish communities**. In: Sale, P. F. (Ed.). The ecology of fishes on coral reefs. San Diego: Academic Press, 1991. p. 475-508.

HUMANN, P.; DeLOACH, N. **Reef fish identification: Florida, Caribbean, Bahamas**. Miami: New World Publications, 2002.

ITZKOWITZ, M. A behavioural reconnaissance of some Jamaican reef fishes. **Zoological Journal of the Linnean Society**, v. 55, p. 87-118, 1974.

IVLEV, V. S. **Experimental ecology of the feeding of fishes**. New Haven: Yale University Press, 1961.

KOHLER, K. E.; GILL, S. M. Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. **Computers and Geosciences**, v. 32, p. 1259-1269, 2006.

KRAJEWSKI, J. P.; FLOETER, S. R.; JONES, G. P.; LEITE, F. P. P. Patterns of variation in behaviour within and among reef fish species on an isolated tropical island: influence of exposure and substratum. **Journal of the Marine Biological Association of the United Kingdom**, v. 91, p. 1359-1368, 2011.

LAWSON, G. L.; KRAMER, D. L.; HUNTE, W. Size-related habitat use and schooling behavior in two species of surgeonfish (*Acanthurus bahianus* and *A. coeruleus*) on a fringing reef in Barbados, West Indies. **Environmental Biology of Fishes**, v. 54, p. 19-33, 1999.

LEHNER, P. N. **Handbook of Ethological Methods**. Cambridge: University Press, 1996.

LETOURNEUR, Y. Spatial and temporal variability in territoriality of a tropical benthic damselfish on a coral reef (Réunion Island). **Environmental Biology of Fishes**, v. 57, p. 377-391, 1992.

MEDEIROS, P. R.; GREMPEL, R. G.; SOUZA, A. T.; ILARRI, M. I.; ROSA, R. S. Non-random reef use by fishes on two dominant zones in a tropical, algal-dominated coastal reef. **Environmental Biology of Fishes**, v. 87, p. 237-246, 2010.

MEDEIROS, P. R.; ROSA, R. S.; FRANCINI-FILHO, R. B. Dynamics of fish assemblages on a continuous rocky reef and adjacent unconsolidated habitats at Fernando de Noronha Archipelago, tropical western Atlantic. **Neotropical Ichthyology**, v. 9, p. 869-879, 2011.

MEEKAN, M. G.; KUERTHY, C.; McCORMICK, M. I.; RADFORD, B. Behavioural mediation of the costs and benefits of fast growth in a marine fish. **Animal Behaviour**, v. 79, p. 803-809, 2010.

MOURA, R. L. Brazilian reefs as priority areas for biodiversity conservation in the Atlantic Ocean. **Proceeding of the 9th International Coral Reef Symposium**. v. 9, p. 917-920, 2002.

ORMOND, R. F. G.; ROBERTS, J. M.; JAN, R. Q. Behavioural differences in microhabitat use by damselfishes (Pomacentridae): implications for reef fish biodiversity. **Journal of Experimental Marine Biology and Ecology**, v. 202, p. 85-95, 1996.

PRESKITT, L. B.; VROOM, P. S.; SMITH, C. M. A rapid ecological assessment (REA) quantitative survey method for benthic algae using photoquadrats with scuba. **Pacific Science**, v. 58, 201-209, 2004.

ROBERTS, C. M.; ORMOND, R. F. G. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. **Marine Ecology Progress Series**, v. 41, p. 1-8, 1987.

MEDEIROS, P. R. et al. Substrate association and patterns of microhabitat use by fishes at Fernando de Noronha Archipelago (Brazil).

SOTO, J. M. R. Peixes do Arquipélago Fernando de Noronha. **Mare Magnum**. v. 1, p. 147-169, 2002.

THRESHER, R. E. **Reproduction in reef fishes**. Neptune City: TFH Publication, 1984.

WARNER, R. R.; HOFFMAN, S. G. Population density and the economics of territorial defense in a coral reef fish. **Ecology**. v. 61, p. 772-780, 1980.