

Local variations in microhabitat use by *Stegastes fuscus* (Cuvier, 1830) (Teleostei: Pomacentridae) in a tropical reef of Brazil

Paulo Roberto de Medeiros¹, Ana Luisa Pires Moreira² and Ana Maria Alves de Medeiros³

¹Universidade Federal de Campina Grande. Centro de Formação de Professores. Unidade Acadêmica de Ciências Exatas e da Natureza. Rua Sérgio Moreira de Figueiredo, S/Nº. Cajazeiras-PB. Brazil (CEP 58900-000). Email: medeirospr@gmail.com.

²Instituto de Desenvolvimento Sustentável e Meio Ambiente do Rio Grande do Norte (IDEMA). Núcleo de Unidades de Conservação (NUC/IDEMA). Área de Proteção Ambiental dos Recifes de Corais (APARC). Av. Alm. Alexandrino de Alencar, S/Nº. Tirol. Natal/RN (CEP: 59015-350).

³Laboratório de Ecologia. Departamento de Sistemática e Ecologia. Centro de Ciências Exatas e da Natureza. Universidade Federal da Paraíba. João Pessoa-PB. Brazil. (CEP 58050-900).

Abstract. Due to their widespread abundance and territorial habits, damselfishes play central roles in reefs worldwide, but the extent to which they modify the reef's substrate varies both amongst and within species. The present study evaluated microhabitat preferences and the role of the common damselfish *Stegastes fuscus* (Cuvier, 1830) (Teleostei: Pomacentridae) as a benthic community modifier in a tropical algal-dominated reef. We employed video survey techniques to assess fish density and microhabitat use and, additionally, the biomass of sessile components were compared inside and immediately outside algal farms of *S. fuscus*. Individuals showed pronounced microhabitat preference, but with prominent local (i.e. small-scale) variations in benthic cover. These local variations are reported for the first time and were due to individuals defending one of two contrasting microhabitats (i.e. turf-dominated or *Palythoa caribaeorum*-dominated). Further, significant differences in the biomass of sessile organisms were observed within algal farms suggesting that *S. fuscus* plays a keystone role in the benthic community of the reef. The implications of the prominent local variation in microhabitat use are discussed and strongly illustrate the behavioral plasticity of this damselfish.

Keywords: Damselfish; Habitat Complexity; Benthic Biomass; Southwestern Atlantic.

Received
November 17, 2016

Accepted
December 22, 2016

Released
December 31, 2016



Open Access
Full Text Article



ORCID

0000-0002-8534-7331

Paulo Roberto de
Medeiros

0000-0001-7748-6131

Ana Luisa Pires
Moreira

0000-0002-8119-0197

Ana Maria Alves de
Medeiros

Introduction

Territorial pomacentrids such as the damselfishes play central roles as benthic modifiers in reefs worldwide (Hixon, 1996; Ceccarelli, 2007). These ecologically significant tasks are largely the result of their ability to specifically remove undesired and surplus components, therefore maintaining selected species (Ceccarelli et al., 2001; Ceccarelli et al., 2005) and, often, monoculture algal farms (Hata and Kato, 2002; Hata and Kato 2003). Additionally, effects on the benthic community come about from the territorial exclusion of herbivores (e.g. fishes and sea urchins) via aggressive behaviors (Kamura and Choonhabandit, 1986). Therefore, damselfishes' territories are often regarded as zones of high productivity (Klumpp et al., 1987). Hixon and Brostoff (1983) were amongst the first to demonstrate how damselfishes maintain benthic diversity via intermediate-disturbance, but several other studies also investigated the role of damselfishes as keystone species in reefs worldwide (e.g. Brawley and Adey, 1977; Branch et al., 1992; Ceccarelli et al., 2001; Barneche et al., 2009).

Nonetheless, although territoriality seems to be a behavioral synapomorphy shared by all damselfishes and regarded as somewhat conservative and stereotyped across species, the extent to which damselfishes are able to defend territories is highly variable (Hata and Kato, 2002). For example, the two most common damselfishes in tropical reefs of Brazil (*Stegastes fuscus* and *S. variabilis*) show distinct territorial defense patterns, the former being more aggressive towards intruders than the latter (Medeiros et al., 2010a). The extent to which algae are deliberately removed from the territories (i.e. weeding) also differs among species (Ferreira et al., 1998; Ceccarelli et al., 2001; Hata and Kato, 2002). Therefore, variations in algal composition are mostly due to differences in algal biomass and richness within territories of different species (Ceccarelli et al., 2001; Gobler et al., 2006). In fact, variations may also show

an intraspecific component, with fish of different size (Foster, 1985) and from different stages (Medeiros et al., 2010a) defending territories with different algal composition.

Hata and Kato (2002; 2004) referred to damselfishes that strongly defend small, monospecific farms and selectively remove unpalatable algae as intensive farmers. On the other hand, territories of less aggressive damselfishes tend to be larger and include indigestible algae, characterizing an extensive farmer. Intensive farmers gain an increased food supply per unit area at the expense of a higher energy prompted during territory defense and weeding, whereas extensive farmers dispend less energy in territory maintenance, but territories are larger due to the low crop yield per unit area.

The overall aim of the present study was to determine microhabitat preference by the dusky damselfish in a tropical shallow reef, and to compare benthic composition inside and outside their territories as a means of understanding the role played by these fishes as benthic community modifiers.

Materials and Methods

Study area

The study was conducted at Seixas reefs, João Pessoa, PB, Northeastern, Brazil (Figure 1). It is a shallow (< 6 m) sandstone reef made up by scattered consolidated substrata surrounded by a contiguous limestone bottom. Common algae include *Gelidium* spp., *Caulerpa racemosa*, *Halimeda opuntia*, *Dictyopteris delicatula* and *Lithothamnium* spp. and algal diversity is high throughout the reef. Common sessile animals in the area include the hydrocoral *Millepora alcicornis*, the zoanths *Palythoa caribaeorum* and *Protopalyythoa variabilis*, and the corals *Agarices agaricites* and *Siderastrea stellata*. These zoanths and corals show a somewhat patchy distribution, but with peak abundances in particular microhabitats.



Figure 1. Location and map of the study area.

Microhabitat preferences

Density of juvenile and adult *Stegastes fuscus*, and benthic composition were evaluated by means of video surveys on ten randomly assigned 10 m x 2 m transects (length x width). Data were recorded during daytime by the same diver in January 2013 at depths below 2 m and during low tides. Video was recorded using high definition configuration using a Canon digital camera equipped with appropriate water housing. In each transect, one diver swam at constant speed, resulting in transects lasting (mean \pm SD) 2 min 19 sec \pm 9 sec (average diver speed: 4.32 m.min⁻¹).

To determine the density of *S. fuscus*, each video was cautiously examined three times and individuals (settled juveniles and adults) were quantified. Repeated counts were conducted as a means of minimizing observer error during video quantification. Nonetheless, divergences among counts within each video transect were not observed whatsoever.

Given that the video transects included all microhabitats of the reef (some of which were not occupied by *S. fuscus*), we evaluated the degree of microhabitat fidelity by comparing benthic composition

of still frames where one or more *S. fuscus* individuals appeared in the center frame (total of 33 frames) with 50, randomly chosen frames (with or without *S. fuscus*). This was done to test the degree of randomness in microhabitat use and to specifically determine composition of algal farms in relation to the overall benthic composition. Therefore, benthic estimates were treated in a twofold manner: observed (benthic cover estimated in still frames exclusively associated to *S. fuscus*; i.e. the actual microhabitat use) versus randomly expected (benthic cover estimated in all microhabitats, associated or not to *S. fuscus*). Twenty points were randomly plotted on each still frame and assigned to one of ten categories, as follows: fleshy macroalgae (e.g. *Dictyopterys*, *Caulerpa* and *Sargassum*), turf algae (e.g. *Gelidium*, *Griffithsia*), *Lithothamnium*, *Halimeda*, *Protopalyythoa variabilis*, *Palythoa caribaeorum*, *Zoanthus sociatus*, *Siderastrea stellata*, uncolonized pavement and limestone. Percent cover, therefore, is the relative proportion of a category relative to the overall composition. Number of crevices was also estimated on each still frame. These procedures were conducted on

Coral Point Count Software (Kohler and Gill, 2006).

Benthic composition and biomass were also evaluated inside and outside the territories of 10 *S. fuscus* individuals. First, we used focal observations (Lehner, 1996) to determine territory boundaries and, subsequently, benthic samples were collected from inside and outside the territories. Each of 10 focal individuals was observed during 10 minutes, and territory boundaries were marked with natural weights (i.e. rocks). Benthic samples were scraped from a 5 cm² quadrat inside and immediately outside defended areas and stored in plastic containers. Samples were preserved in 4% formalin immediately after collection and, in the laboratory, contents were emptied into a Petri dish and identified to the smallest possible taxonomic category. Following identification, contents were dried in a greenhouse and weighted on a digital scale (0.001 g precision).

Data analysis

Variables were tested for normality (Kolmogorov-Smirnov test) and, when necessary, square root (continuous variables) or arcsine square root (proportions) transformations were conducted (Underwood, 1997).

A one-way MANOVA (Pillai's trace test statistic) was employed to determine whether microhabitat preference (i.e. the observed microhabitat use by *S. fuscus*) was different than randomly expected based on general benthic cover estimates. This was followed by Tukey's HSD post-hoc tests. One way ANOVAs were employed to determine whether benthic diversity (Shannon's index) and number of crevices were different than randomly expected on this microhabitat-scale comparison. Furthermore, we employed simple linear regressions to evaluate relationships between fish density

and single benthic categories, benthic diversity, and number of crevices.

To compare biomass values from inside and outside the territories, a MANOVA procedure, similar to the one described above, was conducted. To minimize the effects of rare benthic components, this analysis excluded taxonomic units or functional groups with frequency distribution lower than 20% considering all samples. Finally, a one way ANOVA was used to test inside/outside territories differences regarding total biomass (i.e. pooled data from the above mentioned categories). This was done separately as a means to avoid autocorrelation of the data.

Results

Mean density (\pm SE) of *Stegastes fuscus* in the study area was 0.29 ± 0.09 individuals per m² (settled juveniles = 0.03 ± 0.01 ; adults = 0.27 ± 0.09). Differences between observed and expected benthic cover estimates were detected (Pillai's trace = 0.74; $F_{10, 31} = 8.66$; $P < 0.001$), suggesting that microhabitat use was different than randomly expected. Benthic categories which significantly contributed to the variation were fleshy macroalgae and *Protopalmytha variabilis*, due to lower observed percent cover values, and turf algae and *Palythoa caribaeorum*, due to higher observed values (Table 1). Also, favored sites of *S. fuscus* showed lower benthic diversity (ANOVA; $F = 17.71$, $df = 1$; $p < 0.001$) and higher number of crevices (ANOVA; $F = 9.87$, $df = 1$; $p < 0.01$) than randomly expected (Table 1).

Three categories (turf algae, *P. caribaeorum* and number of crevices) were positively related to fish density and three categories (fleshy macroalgae, *P. variabilis* and benthic diversity) were negatively correlated (Figure 2).

Table 1 Mean (\pm SE) observed values of microhabitat use by *S. fuscus* versus expected values from benthic cover estimates, benthic diversity and number of crevices based on video frame surveys. ns: non-significant.

Category	Observed	Expected	Post hoc results
Fleshy macroalgae	23.59 \pm 3.74	60.90 \pm 5.14	P < 0.001
Turf algae	56.44 \pm 5.12	22.93 \pm 6.46	P < 0.001
<i>Halimeda</i>	4.13 \pm 2.23	4.31 \pm 1.10	ns
<i>Lithothamnium</i>	0.56 \pm 0.43	0.62 \pm 0.19	ns
<i>Protospalythoa variabilis</i>	1.23 \pm 0.82	5.77 \pm 2.29	P < 0.001
<i>Zoanthus sociatus</i>	0.79 \pm 0.29	0.83 \pm 0.43	ns
<i>Palythoa caribaeorum</i>	10.40 \pm 3.78	0.32 \pm 0.21	P < 0.001
<i>Siderastrea stellata</i>	0.52 \pm 0.31	0.43 \pm 0.28	ns
Uncolonized pavement	0.33 \pm 0.23	0.37 \pm 0.27	ns
Limestone	1.26 \pm 0.99	3.44 \pm 1.07	ns
Benthic diversity	0.15 \pm 0.04	0.44 \pm 0.08	P < 0.001
Number of crevices	6.75 \pm 1.66	1.56 \pm 0.50	P < 0.01

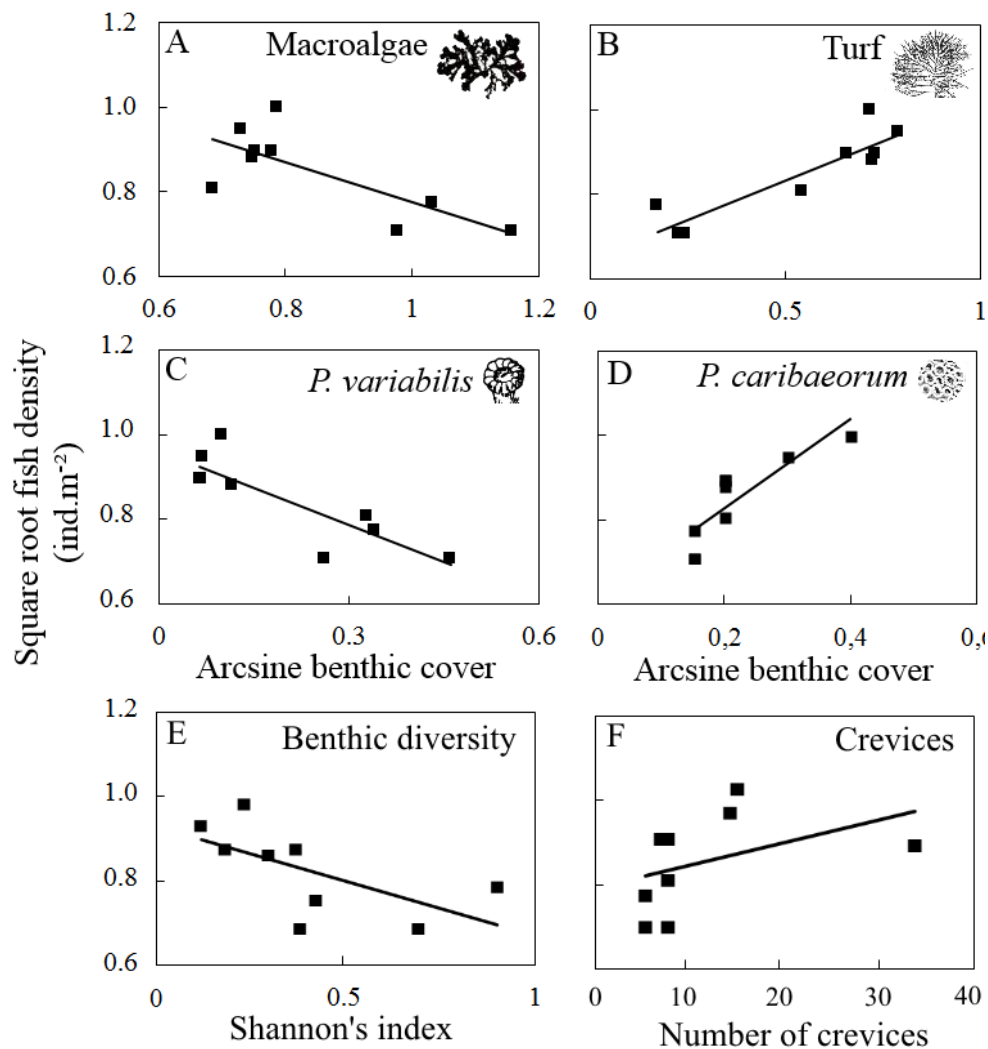


Figure 2. Effect of benthic cover, benthic diversity and number of crevices on the density of *S. fuscus*. Only significant relationships are shown. a) fleshy macroalgae ($r^2 = 0.55$; $P < 0.05$); b) turf algae ($r^2 = 0.80$; $P < 0.05$); c) *Protospalythoa variabilis* ($r^2 = 0.72$; $P < 0.05$); d) *Palythoa caribaeorum* ($r^2 = 0.73$; $P < 0.01$), e) benthic diversity ($r^2 = 0.79$; $P < 0.01$) and f) number of crevices ($r^2 = 0.69$; $P < 0.01$).

Video transects revealed six common general microhabitat types: *Halimeda*-dominated, *P. caribaeorum*-dominated, macroalgae-dominated, *P. variabilis*-dominated, turf-dominated and limestone-dominated (Figure 3). Based on frequency of observations, *S. fuscus* individuals were very common on turf- and *P. caribaeorum*-dominated microhabitats (> 90% of observations), customary on macroalgae-dominated (~40%), rare on *Halimeda*- and *P. variabilis*-dominated (< 10%), and not observed whatsoever on limestone-dominated microhabitats (0%).

Multivariate comparison of taxonomic groups and/or benthic categories biomass revealed differences between the inside and outside of damselfishes territories (Pillai's trace = 0.99; $F_{7,2} = 30.85$; $P < 0.001$). Higher biomass values were observed inside territories for *Gelidium* sp., *Ceramium* sp. and *P. caribaeorum*, whereas lower biomass values were observed for *Halimeda* sp., *Lithothamnion* sp., *Protopalythoa variabilis*, sediment and total biomass (Table 2).

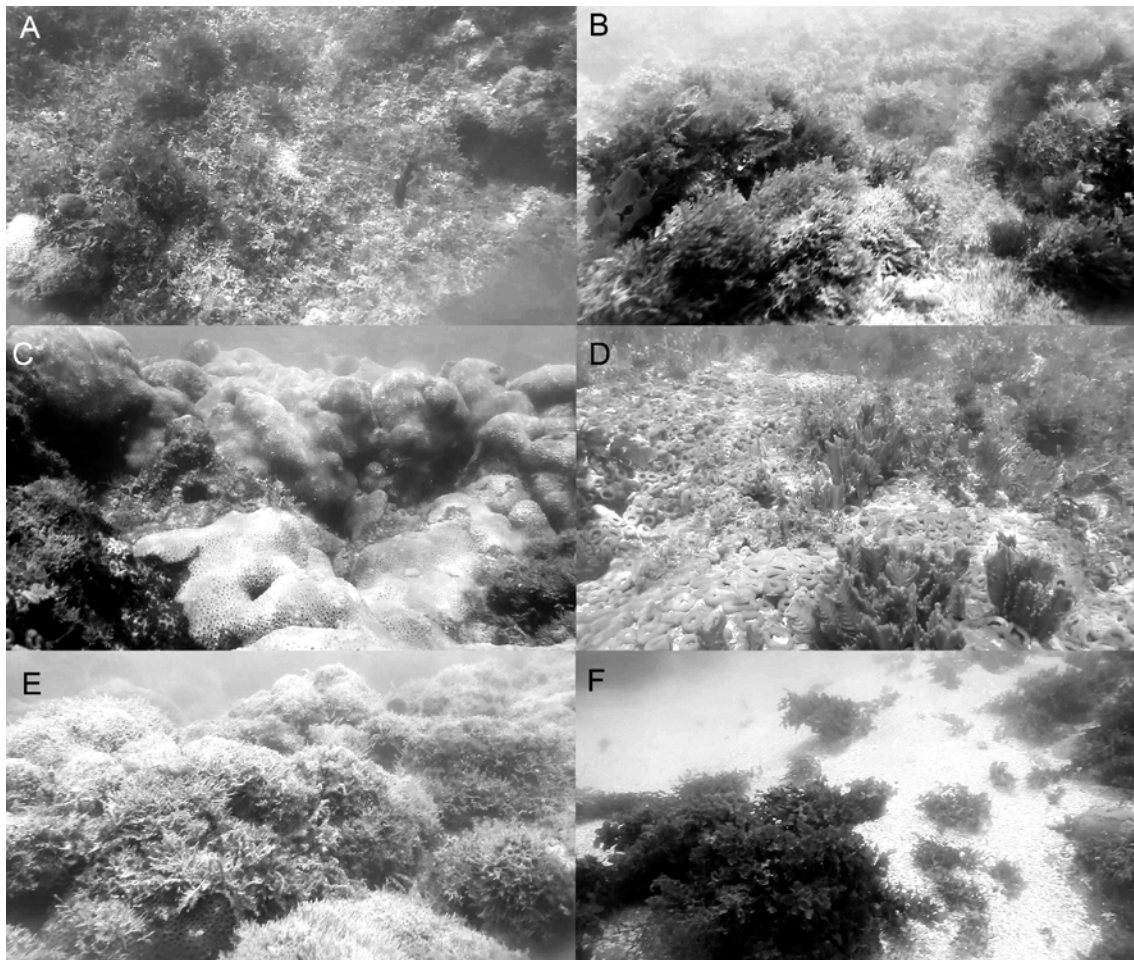


Figure 3. The most common general microhabitat types assessed by means of video surveys in the study area. a) *Halimeda*-dominated; b) macroalgae-dominated; c) *Palythoa caribaeorum*-dominated; d) *P. variabilis*-dominated; e) turf-dominated; and f) limestone-dominated.

Table 2 Mean (\pm SE) biomass values (g/5 cm²) of taxonomic groups and categories inside and outside territories of *Stegastes fuscus*. Groups and categories which contributed to less than 30% of total observations were excluded from the analyses. ns: non-significant.

Taxonomic group	Category	Inside	Outside	Post hoc results
<i>Gelidium</i> sp.	Turf algae	1.43 \pm 0.17	0.01 \pm 0.01	P < 0.001
<i>Halimeda</i> sp.	Calcareous algae	1.58 \pm 0.44	3.01 \pm 0.14	P < 0.01
<i>Dictyopteris</i> sp.	Fleshy macroalgae	0.05 \pm 0.01	0.07 \pm 0.02	Ns
<i>Ceramium</i> sp.	Turf algae	0.06 \pm 0.01	0.01 \pm 0.01	P < 0.01
<i>Lithothamnion</i> sp.	Coralline algae	0.07 \pm 0.04	1.66 \pm 0.42	P < 0.001
<i>Amphiroa</i> sp.	Calcified macroalgae	0.06 \pm 0.04	0.01 \pm 0.01	Ns
<i>Sargassum</i> sp.	Fleshy macroalgae	0.01 \pm 0.01	0.03 \pm 0.02	Ns
<i>Palythoa caribaeorum</i>	Zoanthid	0.56 \pm 0.06	0.01 \pm 0.01	P < 0.001
<i>Protospalythoa variabilis</i>	Zoanthid	0.01 \pm 0.01	0.35 \pm 0.05	P < 0.001
-	Sediment	0.16 \pm 0.04	1.94 \pm 0.62	P < 0.001
-	Total biomass	3.96 \pm 0.33	7.23 \pm 1.10	P < 0.001

Discussion

The damselfish *Stegastes fuscus* is a frequent and abundant component on reefs of Brazil (Ferreira et al., 1998; Osório et al., 2006; Medeiros et al., 2010a), covering up to 90% of the reef's hard surfaces (Medeiros et al., 2010b). In our study, adults showed a 9-fold higher abundance compared to settled juveniles. Similarly to what has been previously reported for other pomacentrids (Hata and Kato, 2002; Ceccarelli et al., 2001), individuals showed pronounced microhabitat fidelity, but local variations in microhabitat use was observed (i.e. small-scale differences within the study area).

Both microhabitat use and biomass analyses revealed somewhat consistent patterns indicating a strong microhabitat preference. The two general microhabitat types in which *S. fuscus* (both juveniles and adults) was most abundant were dominated by turf algae or *Palythoa caribaeorum*. Turf-dominated microhabitats were mostly colonized by *Gelidium* spp. and *Ceramium* spp., which were positively selected, but other filamentous algae were also abundant (albeit not different from sites immediately outside territories). The unpalatable *Dictyopteris* (Hay et al., 1988), for example, was tolerated within algal farms. On the other hand, territories located within *P. caribaeorum*-dominated microhabitats were composed exclusively by this zoanthid.

The two most prominent microhabitats used by *S. fuscus* (turf-dominated and *P. caribaeorum*-dominated) are ecologically distinct and should, therefore, play correspondingly different roles in the ecology of *S. fuscus*. For example, given that turf algae make up a great proportion of *S. fuscus* diet (Ferreira et al., 1998), it is expected that these algae be abundant inside their territories. In contrast, although *P. caribaeorum* is not reported as an important diet item for *S. fuscus* (Ferreira et al., 1998; Menegatti et al., 2003; Barneche et al., 2009; Feitosa et al., 2012), extensive areas exclusively colonized by this zoanthid are common in the study area (from several meters to a couple tens of meters long), and *S. fuscus* density and territory defense remain high even at these sites.

P. caribaeorum produces a specific toxin (palytoxin) which is potentially lethal for several species, therefore precluding its utilization by most predators (Moore and Scheuer, 1971; Wiles et al., 1974). Nonetheless, *Stegastes* species are amongst the few reef fishes which have been reported to feed on *P. caribaeorum* (Francini-Filho and Moura, 2010), and it is possible that their importance in the diet of *S. fuscus* may be underestimated. In fact, although regarded as herbivores, the morphology and histology of the stomach and intestine of *S. fuscus* seem to be adapted for both herbivory and omnivory (see Canan et al., 2012).

Alternatively, epiphytic microalgae make up a substantial amount of the diet in many pomacentrids (Lassuy, 1984; Ceccarelli et al., 2001) and the extensive *P. caribaeorum* mats may provide large surface areas for epiphytic microalgae colonization. In fact, Ceccarelli et al., (2005) demonstrated that unpalatable algae were maintained within territories of three damselfishes as a means to increase surface area available for epiphytic palatable microalgae growth. Epiphytic associations were not evaluated during our field surveys, but it is possible that territories within *P. caribaeorum*-dominated microhabitats were defended for epiphytic algal access. Studying the diet of two damselfishes (one of which *S. fuscus*) in a reef of northeastern Brazil with similar geological and biological characteristics as that of the present study, Feitosa et al. (2012) showed that epiphytic diatoms (e.g. *Isthmia*) were the most abundant item in their diet. Due to their microscopic sizes, microalgae may be obscure in typical diet procedures, and their contribution to the overall diet may be underestimated unless appropriate magnification is employed during stomach content analyses. In addition, microalgae are frequently not assessed in benthic surveys and their availability and importance to reef fish energetic and nutrition may be somewhat neglected (but see John et al., 2001).

Despite their contrasting differences one common aspect between turf-dominated and *P. caribaeorum*-dominated zones was the high availability of crevices, which is somewhat low at the other microhabitat sites. This highlights the importance of crevices and overall structural complexity on the biology of damselfishes. Crevices and substrate heterogeneity are important as temporary or permanent refuge sites and provide shelter for nests and eggs (e.g. Connell and Jones, 1991; Komyakova et al., 2013). As previously proposed, since turf algae and overall algal abundance are high on northeastern Brazilian reefs, it seems that refuge sites are more limiting than food availability (Medeiros et al., 2010; Medeiros et al., 2014).

Our results suggest that the role of *S. fuscus* as a microhabitat modifier is highly dynamic, with a somewhat high intraspecific territorial plasticity. Benthic diversity showed a nearly 3-fold lower value inside territories, suggesting their potential to modify the substrate.

Calcareous and coralline algae, *Protopalalythoa variabilis* and sediment showed significant lower abundance inside territories, and this seems to be the coupled result of microhabitat selection and deliberate removal of unpalatable components. The hard calcareous skeleton of *Halimeda* and *Lithothamnium*, and the presence of unpalatable chemical metabolites render these algae inaccessible and physiologically restricted as a food resource to most fishes (Targett and Targett, 1990). The negative selection towards the zoanthid *P. variabilis* was probably due to the fact that these zoanthids are exclusively found on low complexity zones dominated by fleshy macroalgae which were substantially avoided (i.e. macroalgae-dominated microhabitats; see Figure 3). Sediment makes up a small fraction of the diet of *S. fuscus* (usually less than 2%) (Feitosa et al., 2012), and is clearly ingested accidentally. The alkaline components of sediments and the hard calcareous skeletons of *Halimeda* and *Lithothamnium*, may interfere with the chemical digestion reducing energy assimilation.

Hata and Kato (2004) categorized *S. fuscus* as an extensive farmer based on surveys conducted by Ferreira et al. (1998) at a high latitude tropical rocky shore. Our study suggests, however, that the intensive-extensive categories are opposite ends of a continuum, and that *S. fuscus* lies within these two categories, showing typical characteristics of intensive farmers (i.e. territories with low benthic diversity), but with intermediate-sized territories and tolerance to at least some unpalatable components (see Table 1, in Hata and Kato, 2004).

The present study highlights the role of *S. fuscus* as a keystone benthic modifier in a tropical algal-dominated reef. Furthermore, *S. fuscus* individuals are

highly dynamic and defended one of two highly contrasting microhabitats (turf- or *P. caribaeorum*-dominated). Finally, microhabitats described in the present study are uninterrupted and far from representing discrete components. Nonetheless, they are easily distinguishable in the study area and served as a central functional basis for understanding microhabitat preferences by *S. fuscus*. Future studies comparing diet from individuals defending territories within turf-dominated and *P. caribaeorum*-dominated microhabitats are highly encouraged. Furthermore, our observations suggest that *S. fuscus* individuals are unaffected by the presence of *P. caribaeorum* and benefit from its aggressive and competitive inhibition against the growth of potential competitors. These relationships are obscure and deserve further attention.

Conflict of interest statement

Authors declare that they have no conflict of interests.

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