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Microhabitat characteristics of *Stegastes planifrons* and *S. adustus* territories

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ABSTRACT

Stegastes adustus and *Stegastes planifrons* are two species of damselfishes commonly found in the Caribbean. These territorial fishes have been widely studied due to their major ecological role on coral reef in controlling the growth of macroalgae that compete with corals for space and, inversely, on their deleterious role in destroying coral tissues to impulse the development of algae. However, few studies were conducted on the biotic and abiotic components of their territories. In the present study, territory size and surfaces of benthic components (macroalgae, algal turf, massive corals, branching corals, Milleporidae, sponges, sand and rubbles) were estimated for the two species at two contrasted sites.

At Ilet Pigeon site (IP), the two damselfishes were found at different depth and exhibited different territory sizes. *S. adustus* defended a larger territory characterized by massive corals, sand and Milleporidae, while *S. planifrons* territories were smaller, deeper and characterized by branching corals, sponges and rubble. At Passe-à-Colas site (PC), the two fish species coexisted in the same depth range and defended territories of similar size. Their territories presented higher proportions of macroalgae, but smaller surfaces of Milleporidae than at IP. At PC, the main difference between the two species was a higher surface of massive corals inside *S. planifrons* territories than *S. adustus* territories. Differences in microhabitat characteristics between the two *Stegastes* seemed mostly site related. This resulted from the high plasticity of two species, allowing them to persist on Caribbean coral reefs after the decline of most branching acroporids, their former favorite habitats.

Keywords: damselfish, benthic habitat, biotic and abiotic components, territory size

INTRODUCTION

The dusky damselfish *Stegastes adustus* (Troschel, 1865) and the threespot damselfish *S. planifrons* (Cuvier, 1830) are two species of damselfishes (Pomacentridae) commonly found in the Caribbean. Several studies focused on their ecology and biology, as well as diet (Emery 1973; Lobel 1980; Dromard *et al.* 2013), reproduction, recruitment and settlement (Tolimieri 1995; Gutiérrez 1998; Booth and Beretta 1994), agonistic behavior (Thresher 1976; Mahoney 1981) or habitat (Emery 1973; Waldner and Robertson 1980).

These small herbivorous fishes are territorial and maintain a surface of algal lawns or “turf” and young palatable macroalgae inside the boundaries of their territory (Brawley and Adey 1977; Ceccarelli *et al.* 2001). They aggressively defend this area against larger herbivorous fishes, such as parrotfishes and surgeonfishes (Myrberg and Thresher 1974; Thresher 1976) to maintain their food resources. Their diet is principally focused on algal turf, macroalgae but also detritus and invertebrates living inside the lawn (Dromard *et al.* 2013).

Stegastes sp. have been widely studied due to their major ecological role in controlling the algal biomass on reef, preventing the algal coral phase shift or in enhancing the diversity of macroalgae (Hinds and Balantines 1987; Ferreira *et al.* 1998; Ceccarelli *et al.* 2001, 2005; Hoey and Bellwood 2010), algal turf (Gobler *et al.* 2006; Dromard *et al.* 2013), benthic invertebrates (Lobel 1980; Wilson and Bellwood 1997) or corals (Glynn and Colgan 1988; Gochfeld 2009). In parallel, some studies highlighted the negative effects of *Stegastes* on their environment (Wellington 1982; Ceccarelli *et al.* 2001). Damselfishes are able to remove polyps from coral colonies to increase the surface of substratum available for their farming activity, leading to the death of corals by consequence.

Stegastes usually settle on a high quality habitat *i.e.* with a complex spatial refuge (Itzkowitz 1977; Ebersole 1985; Tolimieri 1998). Initially, *Acropora cervicornis* has been cited as a preferred habitat for *Stegastes planifrons* and *Acropora palmata* for *Stegastes adustus* (Itzkowitch 1977; Waldner and Robertson 1980). After the decline of the two *Acropora* species in the Caribbean, some authors observed that *Stegastes* shifted to other coral species complexes or other type of substrate (Tolimieri 1995; Pretch *et al.* 2010). *Stegastes planifrons* was recorded in habitats associated with live corals (Gutiérrez 1998) as *Orbicella annularis* (Emery 1973) or *Agaricia* sp. (Waldner and Robertson 1980, Booth and Beretta 1994, Lirman 1994, Meadows 1995), while *Stegastes adustus* was recorded on rocky substrate (Waldner and Robertson 1980; Gutiérrez 1998) in association with corals of the genus *Orbicella* (Rivera-Betancourt 2009) or large coral rubble (Itzkowitz 1977). The microhabitat characteristics of *Stegastes* territories were studied in Barbados (*S. diencaeus*: Cheney and Côté 2003), in Puerto Rico (*S. adustus*: Rivera-Betancourt 2009) and in Panama (*S. planifrons*: Meadows 1995). To our knowledge, no study was devoted to comparing the microhabitat composition of territories between *S. adustus* and *S. planifrons* in similar sites.

The principal objective of the present study was to determine the microhabitat characteristics of *Stegastes planifrons* and *S. adustus* territories in measuring territory size and evaluating their occupation by biotic and abiotic benthic components. These characteristics were then compared to investigate if they vary according to sites or fish species.

METHODS

This study was carried out in Guadeloupe, Lesser Antilles (16°15'N; 61°30'W, Fig. 1a), on two contrasting reef systems (Fig. 1b). One site was located at Ilets Pigeon (IP) on the leeward west coast of the island (Fig. 1c). From the shore of Ilets Pigeon down to 16 m depth, the slope is gentle with its higher part composed of rocky blocks colonized by a coral community. The other site was located at Passe-à-Colas channel (PC) on the barrier reef of

the Grand Cul-de-Sac Marin Bay, located on the northern coast of Guadeloupe (Fig. 1d). This site was located on the top of the steep side of the channel.

Sampling was performed between February and April 2010, in scuba diving. At each site, five territories of each fish species were chosen haphazardly and delimited following a method adapted from Odum and Kuenzler (1955): aggressive fish movements were observed during 15 min. Weighted colored strips were then placed on the bottom where fish stopped chasing intruders and turned back so marking the boundary of its territory. A quadrat of 20 x 20 cm was placed at the middle of the territory in order to give a scale. Then, picture from above of each territory was taken. The surface area of each territory was estimated by a numerical analysis with Adobe™ Photoshop and transformed in square meters. On each photograph of territory, the surfaces occupied by different items (macroalgae, algal turf, live massive coral, live branching corals of the genus *Porites*, Milleporidae, sponges, sand and rubble) were estimated based on the number of pixels of each category (Fig. 2). The presence of other biotic components, such as gorgonians (Gorgoniidae) and sea anemones (Actinaria) was also recorded. Finally, fish were speared and their total length (TL) measured to the nearest millimeter.

As data were normally distributed, territory sizes were compared with one-way analysis of variance (ANOVA), using four categories of factor corresponding to the four situations (two sites and two fish species). ANOVAs were combined with a Tukey's honestly significant difference (HSD) post hoc test to perform multiple comparisons. The correlation between territory size and fish size (TL) was tested with the Spearman's rank correlations coefficient. Microhabitat characteristics (surfaces occupied by each biotic and abiotic components) were analyzed with a principle component analysis (PCA) to identify differences among sites and fish species. For each benthic component, the frequency of occurrence (FO) was calculated as follows: $FO\%_{(i)} = N_i / N_{total} * 100$, where N_i is the number of territories in which a benthic component i was found and N_{total} is the number of territories studied.

All statistical analyzes were performed with the program R.

RESULTS

Territory depth and size

At Ilets Pigeon (IP), *Stegastes adustus* was found from 5 to 8 m depth, while *S. planifrons* lived deeper between 12 and 15 m. At Passe-à-Colas (PC), the two fish species were found in the same depth range (10 - 12 m). Significant difference in territory size was observed according to species or site (ANOVA, $F_{(3,38)}=13.6$, $p=0.0001$). *S. adustus* defended larger territories at IP than at PC, while *S. planifrons* defended a similar territory size at both sites (Table 1). In contrast, no significant difference of territory size between species was observed at PC, where the two species coexisted and colonized on average (\pm 95% confidence interval) 1.26 (\pm 0.24) m² of reef. However, at IP, where depth partitioning between species was observed, the mean size of territories defended by *S. adustus* was 2.6 times larger than those defended by *S. planifrons* (Table 1). Total length of fishes ranged between 8 and 12 cm, which corresponded to their adult size. No significant correlation was found between the length of fishes and the size of their territory (Spearman's rank correlations, $p = 0.62$).

Benthic components of Stegastes territories

The surfaces occupied by the different items (macroalgae, algal turf, live massive corals, live branching corals, Milleporidae, sponges, sand and rubble) were recorded in each territory (Table 2). Algal turf was found in all territories and was the dominant component in terms of

surface (mean > 68%). Macroalgae, massive corals and sponges were also found in all territories (FO = 100%, Table 2), but occupied smaller surfaces than algal turf (mean < 16%). At IP branching corals (*Porites*) were frequent (FO = 80%) in *S. planifrons* but absent of *S. adustus* ones. Milleporidae were particularly common in *S. adustus* territories at IP (FO = 100%), but rare in other territories. Sand was relatively common in both *Stegastes* territories and the surface occupied greatly varied according to fish species and site, while rubbles occupied very small areas in both fish territories (mean < 5%). Other biotic components of territories were three sea anemones recorded in a *S. adustus* territory at PC and two Plexauridae gorgonians (one in a *S. adustus* territory and one in a *S. planifrons* territory, both at PC).

Variations in microhabitat characteristics

Principle component analysis showed a difference in benthic occupation according to site and fish species (Fig. 3). The two first axes of the PCA explained 57.8% of the variance of the data. The first axis separated the two fish species at IP according to the characteristics of their territories. *S. planifrons* territories were associated with large surfaces of branching *Porites*, sponges and rubbles, while *S. adustus* territories were characterized by large surfaces of massive corals and sand. The patterns of microhabitat of *S. adustus* were correlated with a larger territory size than *S. planifrons* as indicated by previously analysis.

The second axis divided fish territories according to site. At IP, fish territories were occupied by higher surfaces of Milleporidae. At PC, extensive areas of macroalgae characterized the composition of fish territories. At PC, the two fish species slightly differed by the coverage of macroalgae (larger in *S. adustus* territory) and the surface of massive corals and sand (higher in *S. planifrons* territory). The surface of algal turf was very abundant in each territories (70% of fish territories in average) and was not determinant in the distinction of microhabitat differences between fish species or sites.

DISCUSSION

Gutiérrez (1998) and Waldner and Robertson (1980) previously described space partitioning between the two species and found *S. planifrons* deeper along the reef slope while *S. adustus* was recorded on the top of the reef. Emery (1973) also indicated that *S. planifrons* occupied deeper waters than other species of damselfishes in the Caribbean. A similar pattern was observed at Ilet Pigeon. At Passe-à-Colas, the two species were found in the same depth range (10 - 12 m), on the top of the side of a channel. The cohabitation of the two species at PC can be explained by the topography on this site where they share a flat terrace cutting the steep side of the channel and the absence of suitable habitats deeper.

A significant difference of territory size was observed between sites. When the two species were found at the same depth, their territory size was similar, while when they were segregated by depth, *S. adustus* defended a larger area. This observation reveals the existence of an interspecific competition for space between the two species when the site offers a restricted area for settlement (PC site), as suggested in Dromard *et al.* (2013). The existence of competitive interactions between *S. planifrons* and *S. adustus* was described by Williams (1978). In Guadeloupe, territory sizes ranged between 1 and 2 m², which corresponded to the previous measures of *S. fuscus* territories (Ferreira *et al.* 1998; Osorio *et al.* 2006). To our knowledge, no previous studies measured and compared the territory sizes of *S. adustus* and *S. planifrons*.

Letourneur (2000) showed the existence of a correlation between fish size and the size of their territory in a pomacentrid, *Stegastes nigricans*, from La Reunion Island. In the present study,

fish size did not influence the size of territories, probably because the range of fish size was small (*i.e.* all fishes were adults).

At the two sites, the major component in terms of surface was algal turf. The mean surface occupied by turf in *Stegastes* territories was 70%. This value is in accordance with the estimation of Cheney and Côté (2003) who found that algal lawn covers 66% of *Stegastes* territories. These results are consistent with the “farming” activity of *Stegastes*. These territorial fishes cultivate preferred algae species, maintain them in the form of an algal lawn and remove the other algae species by a “weeding” process (Ceccarelli et al. 2001).

Clear differences in the coverage rate of other benthic components within their territories appeared. Macroalgae were found in all territories, but were more abundant in fish territories located at PC. Usually, mature and erected macroalgae are removed by *Stegastes* because they are not consumed and are maintained at a small stage in the lawn. The higher surface occupied by macroalgae in PC territories can be explained by 1) a spatial variation of the water quality such as higher input of nutrients at PC, or 2) a reduced “weeding” activity lead by a longer time dedicated to the defense of territories. The second hypothesis is more likely because the two fish species found next to each other at PC were more aggressive and their territory sizes reduced. In this competition, *S. planifrons* seemed to be the dominant species as it defended the same surface in the two situations, while *S. adustus* had its territory reduced by half in presence of *S. planifrons*.

Live massive corals, principally *Orbicella annularis*, were recorded in all territories indicating that this component could be a favorable parameter for *Stegastes* settlement. Several studies indicated that *S. planifrons* settles preferentially where live corals are present (Emery 1973; Gutiérrez 1998), while *S. adustus* was generally associated with rocky reef substratum without a marked preference for live corals (Gutiérrez 1998; Waldner and Roberston 1980). In Guadeloupe, territories of both species were associated with live massive corals, but their higher surfaces were measured in *S. adustus* territories at IP and in *S. planifrons* at PC. Usually, the preferred habitat of *S. planifrons* and *S. adustus* are branching corals, such as *Acropora cervicornis* or *A. palmata* (Emery 1973; Waldner and Roberston 1980). However, branching corals (here mostly *Porites*) were not abundant inside fish territories and only found in *S. planifrons* territories at both sites. This observation is due to the global composition of the sites, where branching *Acropora* are rare. Milleporidae were not very common in PC territories and were only recorded in *S. adustus* territories at IP. This last pattern can be due to the depth partitioning of species at IP, as Milleporidae are preferentially located in shallow waters (Emery 1973) where *S. adustus* was located.

While the presence of sponges has never been identified as a favorable factor for the settlement of *Stegastes*, sponges were found in all territories, whatever the site or the fish species. Meadows (1995) measured the surface occupied by sponges in *S. planifrons* territories located on the edge and on the center of a patch reef in Panama. Sponges covered larger surfaces inside territories located on the edge of the patch reef (28.9%) than in ones located in the center of the patch reef (8.1%) where habitat complexity was high. It is possible that sponges were here positively associated with fish territory because of their three-dimensional structure which enhanced the complexity and quality of the habitat, as *Stegastes* are known to prefer complex spatial refuges (Itzkowitz 1977; Ebersole 1985; Tolimieri 1998). However, sponges cannot provide an interesting substratum for “farming” activities. The toxic compounds present in sponges may perhaps prevent *Stegastes* to remove them. A hypothesis to be tested.

A large part of territories was composed of sand. This observation is probably unrelated to habitat selection of *Stegastes*, because sand cannot bring a real advantage to these herbivorous fishes. Sediment is not appropriated to the culture of algal turf and is probably not used by fishes. On the contrary, coral rubbles offer a suitable surface for algal growth. However,

rubbles were not very abundant at PC and were mostly recorded in *S. planifrons* at IP. Association between *Stegastes* and rubbles was demonstrated in several studies (Itzkowitz 1977; Wellington 1992; Meadows 1995), but if *Stegastes* could take advantage of the presence of rubbles, this type of substrate did not appear essential for this fish in Guadeloupe. Variations in the surface of some components could be strictly attributed to site differences (macroalgae, Milleporidae), while other components varied more according to fish species (branching corals, massive corals, sponges, rubbles and sand). At IP, the two species were spatially segregated leading to a difference in territory size. *Stegastes adustus* territories were larger, located in shallow waters (between 5 and 8 m), dominated by live massive corals and characterized by the presence of Milleporidae. Rivera-Betancourt (2009) found that *S. adustus* territories were mostly constituted by colonized pavements or turf (40%), dead and live corals (17.8% and 10.4% respectively). At the same site (IP), *S. planifrons* was found deeper (between 12 and 15m) defending smaller territories characterized by the presence of rubble, sponges and branching corals. These differences can be attributed to the difference of depth. At PC, the two species were found at a similar depth (between 10 and 12m) and presented a more similar composition of their territories, with higher proportions of macroalgae. Nevertheless, a higher surface of massive corals like *Orbicella annularis* was found inside *S. planifrons* territories than *S. adustus* territories, an observation in accordance with the idea that *S. planifrons* is more associated with live corals than other *Stegastes* (Emery 1973; Waldner and Robertson 1980; Booth and Beretta 1994; Lirman 1994; Gutiérrez 1998). Thus, the relative proportions of benthic microhabitats in Guadeloupean *Stegastes* territories varied according to both site and fish species. However, the benthic occupation of territories appeared to be more related to differences between sites than to differences in fish requirements.

In a changing marine environment, knowledge on ecological needs of marine organisms is fundamental to predict the adaptability of species. A major threat for coral reefs is the loss of habitat complexity due to the regression of branching corals and faced with this situation, damselfishes show a high plasticity in terms of habitat selection. However, the notion of time has not been introduced in this study and further investigations including a temporal approach are needed.

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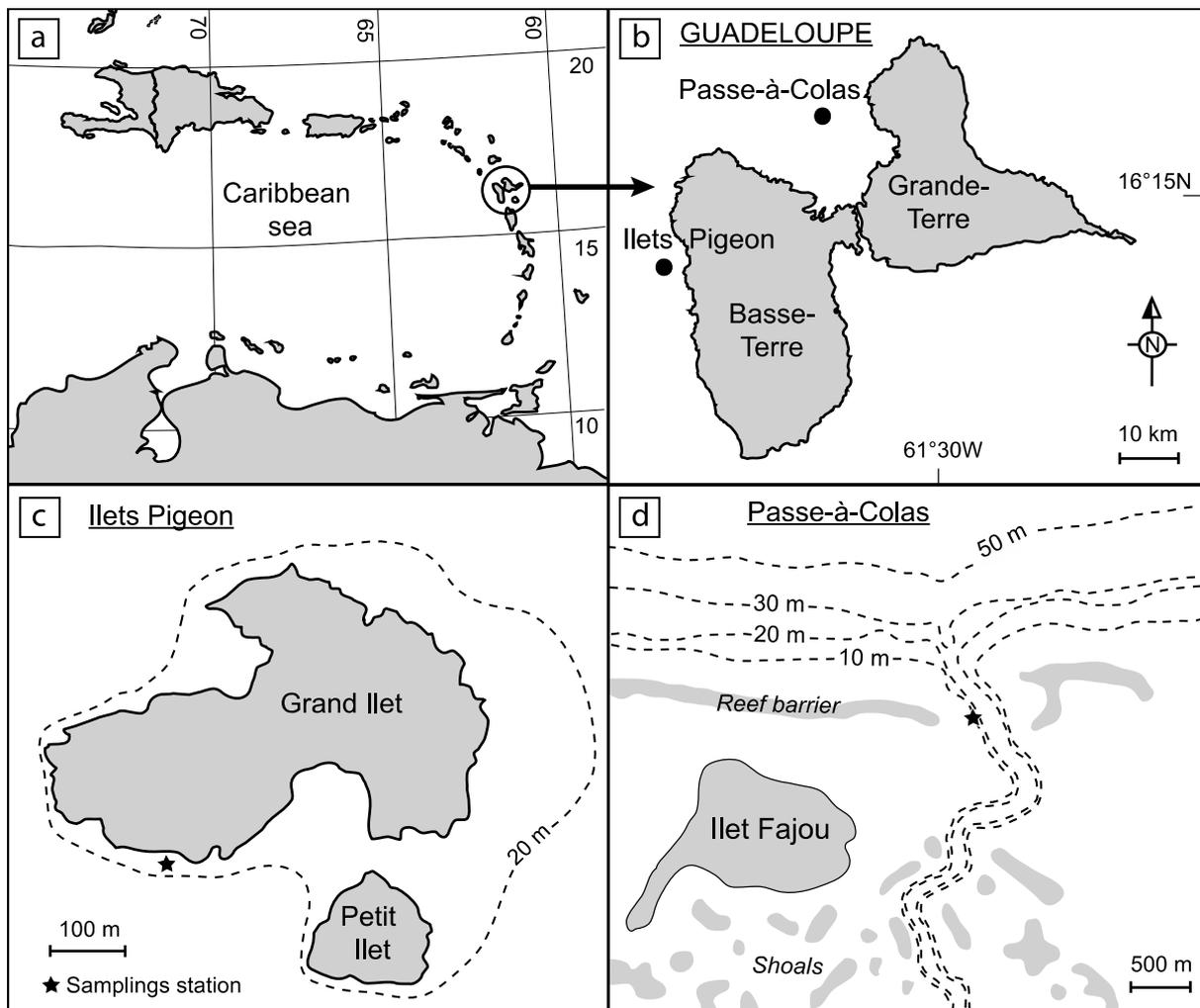
FIGURES CAPTIONS

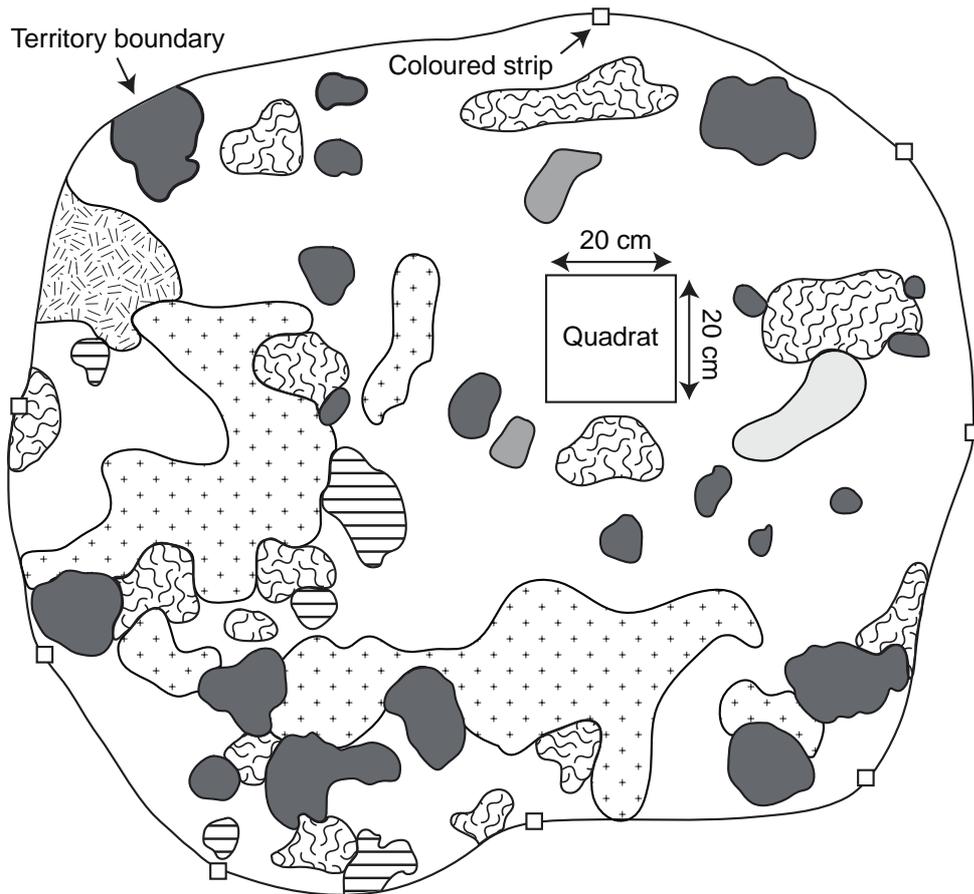
Fig. 1 Location of study sites, a) location of Guadeloupe in the Caribbean, b) location of the two sites in Guadeloupe, c) site of Ilet Pigeon and d) site of Passe-à-Colas

Fig. 2 Cartography of a *Stegastes* territory and surfaces occupied by macroalgae, algal turf, massive corals, branching corals, Milleporidae, sponges, sand and rubble

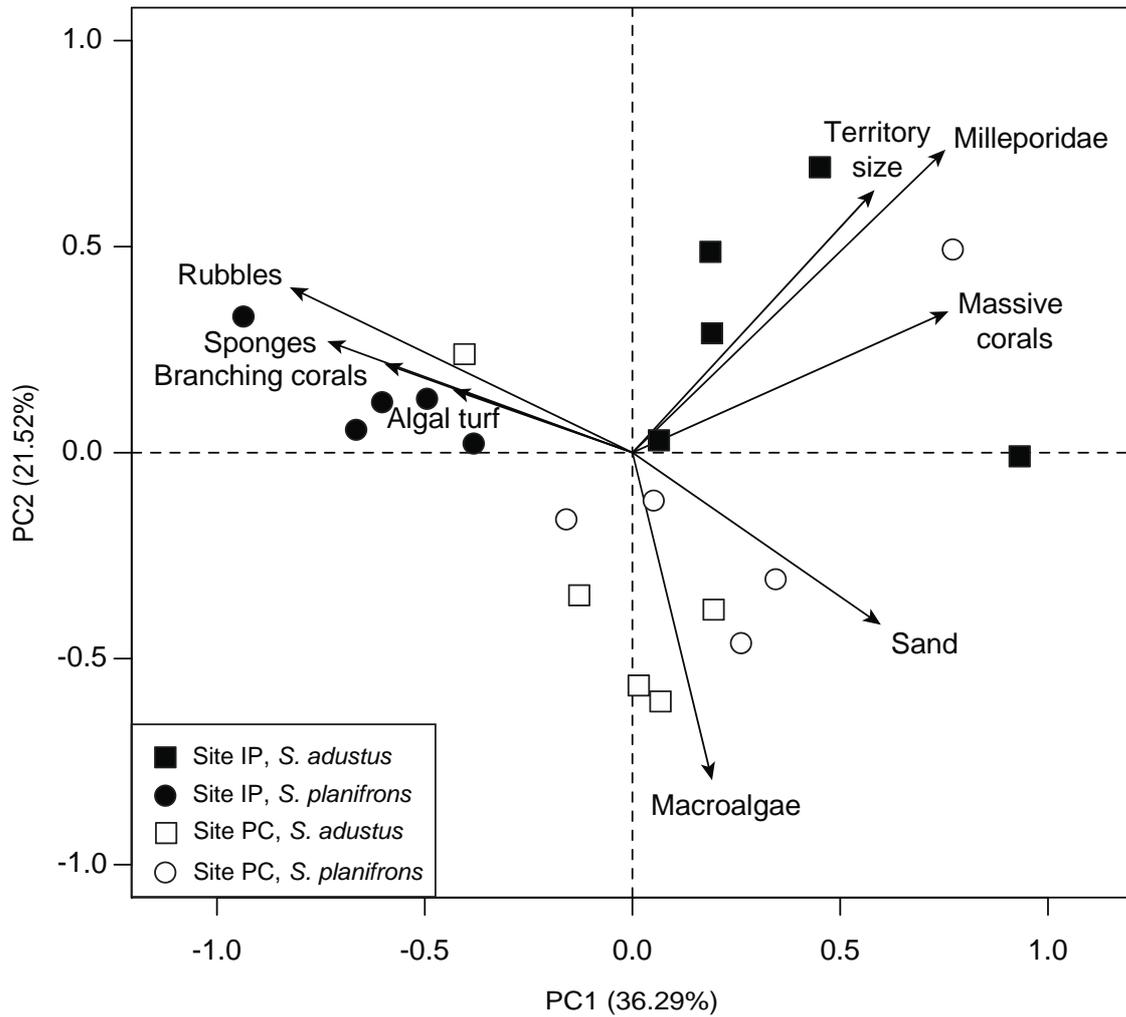
Fig. 3 Principle component analysis (PCA) performed on size of territories and the surfaces of benthic components recorded in territories of *Stegastes adustus* (squares) and *S. adustus* (circles) at Ilet Pigeon (close symbols) and Passe-à-Colas (open symbols)

FIGURES





- | | | | | | | | |
|---|------------|---|---------------------------------|---|--------------|--|--------|
|  | Macroalgae |  | Massive corals (Scleractinia) |  | Milleporidae |  | Sand |
|  | Algal turf |  | Branching corals (Scleractinia) |  | Sponges |  | Rubble |



TABLES

Table 1 Mean territory size ($m^2 \pm 95\%$ CI) of *Stegastes adustus* and *Stegastes planifrons* at Ilets Pigeon (IP) and Passe-à-Colas (PC). Territory size was compared between fish species and sites. p Values indicate the results of Tukey's HSD post hoc test. Results in bold show significant differences of territory sizes.

Species/Sites	Ilets Pigeon	Passe-à-Colas	p Values
<i>S. planifrons</i>	1.08 ± 0.17	1.33 ± 0.24	0.94
<i>S. adustus</i>	2.83 ± 0.57	1.18 ± 0.26	0.0001
p Values	0.0001	0.97	-

Table 2 Mean percentages of surface (ranges) occupied by biotic and abiotic components inside fish territories and frequencies of occurrence (%) of each component according to fish species and site.

	Ilet Pigeon		Passe-à-Colas	
	<i>S. adustus</i>	<i>S. planifrons</i>	<i>S. adustus</i>	<i>S. planifrons</i>
A. Mean percentages (%)				
Macroalgae	2.6 (2.1 - 3.8)	1.8 (0.6 - 3.5)	15.5 (0.5 - 22.7)	5.4 (1.7 - 10.2)
Algal turf	69.6 (47.1 - 79.4)	72.2 (57.1 - 79.3)	68.9 (63.1 - 74.9)	68.0 (56.7 - 81.3)
Massive corals	13.4 (8.4 - 23.7)	3.7 (1.3 - 5.7)	3.6 (2.1 - 5.9)	14.6 (4.8 - 37.5)
Branching corals	0.0	7.5 (0.0 - 24.1)	0.0	0.2 (0.0 - 0.9)
Milleporidae	2.0 (0.8 - 3.8)	0.0	0.6 (0.0 - 1.7)	0.6 (0.0 - 2.8)
Sponges	4.0 (1.4 - 7.1)	8.6 (1.3 - 11.9)	5.2 (2.2 - 12.5)	2.3 (0.3 - 4.6)
Sand	7.9 (3.0 - 21.6)	1.5 (0 - 3.7)	5.3 (3.3 - 8.4)	8.9 (1.0 - 14.8)
Rubble	0.4 (0.0 - 2.2)	4.7 (0.0 - 8.2)	0.8 (0.0 - 3.1)	0.0
B. Frequency of occurrence (%)				
Macroalgae	100	100	100	100
Algal turf	100	100	100	100
Massive corals	100	100	100	100
Branching corals	0	80	20	40
Milleporidae	100	0	40	20
Sponges	100	100	100	100
Sand	100	60	100	100
Rubble	20	80	40	0