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Space partitioning among damselfishes in the Caribbean coast of Panama: the role of habitat preferences

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This study aimed to assess abundance and habitat use by juvenile and adult damselfishes, as much as the benthic cover of different reefs on Isla Colon, Bocas del Toro, Panama. Reefs were selected considering different levels of wave exposure and depths. Damselfish and benthic communities were distinct between reefs. The most abundant species in the sheltered deeper reef was *Stegastes planifrons* followed by *S. leucostictus*, and they were also recorded in the sheltered shallower reef. Low densities of *S. partitus* and *S. variabilis* were also observed in the sheltered deeper reef, as these species are apparently restricted to higher depths. Additionally, these reefs presented patches with high cover of live and dead massive coral. Shallow depths presented high abundances of *S. adustus*, indicating a preference of this species for shallow habitats and exhibiting a two-fold increase in abundance at higher wave surge. Also, *Microspathodon chrysurus* reached higher numbers in shallow depths. Furthermore, the exposed reef presented a high cover (%) of algae groups and the fire-coral *Millepora alcicornis*, acknowledged as a preferred habitat for *M. chrysurus* and other reef fish. In this study, distinct habitat uses were observed, with patterns regulated by depth and/or wave exposure levels and/or availability of specific benthic cover. For site-attached species as damselfish, habitat specialization, competition and/or non-random recruitment patterns have been found to rule distributional patterns. Similar results for damselfish relative abundances were found compared to studies conducted within Panama and other reefs throughout the Caribbean region over three decades ago, indicating strong habitat affinity for the most abundant species. However, severe reductions of habitat availability following coral mass-mortality events may have disrupted their distributional patterns.

Este estudo teve como objetivo avaliar a abundância e uso do habitat por juvenis e adultos de peixes-donzela, assim como as comunidades bentônicas em distintos recifes de Isla Colon, Bocas del Toro, Panamá. Os recifes foram escolhidos considerando diferentes níveis de exposição a ondas e profundidade. As comunidades de peixes e bentos estudadas se mostraram distintas. A espécie mais abundante em recifes com maior profundidade e abrigados foi *Stegastes planifrons*, seguida por *S. leucostictus*, que também foram observadas em recifes rasos abrigados. As baixas abundâncias de *S. partitus* e *S. variabilis* também foram observadas no primeiro recife citado e estas espécies foram aparentemente restritas à profundidade maiores. Adicionalmente, estes mesmos recifes apresentaram uma vasta cobertura de corais massivos, vivos ou mortos. *Stegastes adustus* apresentou sua maior abundância em baixas profundidades, indicando uma preferência por habitats rasos, aumentando em duas vezes com a exposição a ondas. Os recifes rasos também tiveram maior abundância de *Microspathodon chrysurus*. Além disso, o recife com maior exposição apresentou extenso percentual de cobertura por algas e o coral-de-fogo *Millepora alcicornis*, reconhecido habitat preferencial de *M. chrysurus* e outras espécies de peixes. Neste trabalho, diferentes padrões de uso do habitat foram encontrados, sendo regulados pela profundidade e/ou exposição e ainda a disponibilidade de determinada cobertura bentônica. Para espécies fortemente associadas ao substrato, a especialização, a competição e padrões não aleatórios do recrutamento são conhecidos determinantes dos padrões distribucionais. Este estudo apresentou resultados similares a outros conduzidos há 30 anos no Panamá e outros recifes do Caribe, indicando que as espécies mais abundantes mantêm forte afinidade com o habitat. Entretanto, severas reduções na disponibilidade de habitat, seguidas de eventos de mortalidade em massa, podem ter possivelmente afetado seus padrões de distribuição.

Key words: Bocas del Toro, Coral reefs, Pomacentrid, Reef fish, Territorial herbivores.

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Introduction

Coral reefs are among the most productive systems in the marine environment (Spalding *et al*., 2001). These systems are changing worldwide in the last decades, due to climate changes, hurricanes, diseases, overfishing, and eutrophication (Hughes *et al*., 2003; Pandolfi *et al*., 2005). Such disturbances have often resulted in ecological phase shifts, from coral- to macroalgal-dominated reefs (McCook, 1999; Scheffer *et al*., 2001), which may be observed on many Caribbean reefs (Hughes, 1994; McClanahan *et al*., 2002) and other regions worldwide (Hughes *et al*., 2007).

Coral cover declined by nearly 80% in the Caribbean in the late 1970s and 1980s (Gardner *et al*., 2003), with decreases as high as 50-70% recorded in several areas along the coast of Panama (Guzman, 2003). Massive coral loss, in turn, has caused declines in structural complexity, leading to negative consequences to the entire reef community (Alvarez-Filip *et al*., 2009). Especially when species strongly dependent upon the cover, diversity and complexity of their respective habitat are usually more jeopardized by these natural and/or anthropogenic disturbances (Jones & Syms, 1998; Jones *et al*., 2004; Graham *et al*., 2006).

Herbivorous reef fish play major roles in reef resilience, as they control abundance and distribution of macroalgae (Szmant, 2001; Hughes *et al*., 2007). Territorial herbivores such damselfishes (family Pomacentridae) are capable of modifying algal communities in different ways (Hata & Kato, 2003, 2004; Ceccarelli *et al*., 2005; Jones *et al*., 2006), such as enhancing the net primary production (Klumpp *et al*., 1987; Ferreira *et al*., 1998). Indirectly, territorial herbivores exert significant effects on the foraging activity of roving herbivores through their aggressive territorial defense (Hixon & Beets, 1993), and through "weeding" behavior distress coral recruitment, survival, and diversity (Gleason, 1996; Gochfeld, 2010). Overall, these species are considered keystone species in reef systems (Hixon & Brostoff, 1983).

As widely distributed and abundant on reef systems worldwide (Doherty, 1983; Meekan *et al*., 1995; Ceccarelli *et al*., 2001), damselfishes occupy up to 90% of some reef areas (Ceccarelli, 2005; Ilarri *et al*., 2008; Medeiros *et al*., 2007, 2010). Thus, by their abundance, behavior and directly use of turf algae, the main bulk of primary production on coral reef systems, they can be relevant actors on phase shifts from coral- to algae-dominated reefs (Ceccarelli *et al*., 2011). Distribution patterns found for this particular group of species, however, are highly variable at several spatial scales (*e.g.* microhabitats, depth, exposure, reef zones, systems) (Williams, 1982; Meekan *et al*., 1995; Holbrook *et al*., 2000; Medeiros *et al*., 2010). Although pre-recruitment processes are important driving forces in adult abundance and distribution (Doherty, 1983), post-settlement processes such as presence of preferred microhabitats (Holbrook *et al*., 2000), predator abundance (Hixon & Beets, 1993), intra- and interspecific competition (Sweatman, 1985; Tolimieri, 1998; Bay *et al*., 2001) are as much as important. Nevertheless, different key mechanisms can be acting synergistically for each species.

This group has been studied throughout the Caribbean, with data available for habitat use, recruitment, behavior, diet and, age and growth of some species (Robertson, 1984, 1996; Gutierrez, 1998; Holbrook *et al*., 2000; Wilson & Meekan, 2002). However, most of these studies to date focused separately on a single or few species, thus not providing more comprehensive data on damselfish community and their association with environmental descriptors. This study aimed to determine abundance and space use of damselfishes across a coastal island of Panama, as well as their relationship with environmental factors such as depth, wave exposure and benthic cover using a more quantitative approach.

Material and Methods

Study area

The present research was conducted in Bocas del Toro archipelago, Isla Colón, Panama. The whole archipelago comprises an area of *ca.* 3,500 km², formed by six large forested islands and hundreds of small mangrove cays (Guzmán, 2003). Surrounding all these islands and along a large part of the mainland coast, there are fringing coral reefs up to 20 m deep and dozens of shallow reef patches. The whole area represents the second most important contributor on reef formations in the Caribbean coast of Panama with approximately 87 km² of fringing reefs (Guszmán, 2003). The reefs of the archipelago have been evaluated in the past decade and live coral cover up to 50% has been reported, depending on the depth, reaching up to 90% in shallow areas (Guzmán & Guevara, 1998a, 1998b, 1999, 2001). Nevertheless, declines on coral cover throughout this area have also been observed in the last decade (Guzmán, 2003).

Three distinct reefs were chosen for this study (Fig.1). Pete's Reef (PT) is a shallow lagoon with patch reefs near mangrove mud flats (~1m). Water motion is low and benthic communities are dominated by numerous species of sponges and the fingercoral *Porites porites* (Pallas, 1766). Conch Point (CO) is a wave-protected near-shore fringing reef lined with mangroves (*Rhizophora mangle* L.). Depths range from 0.5 to 1 m at the mangrove edge and increase to approximately seven m at a 20 m distance from shore. The substratum immediately adjacent to the mangrove edge is covered with turtle grass *Thalassia testudinum* Koenig and green algae, while deeper areas are characterized by the presence of patch reefs and sponges. Shallower (~0.50 m) and relatively more exposed, Lime Point (LM) has a much longer fetch reaching the open waters of the Caribbean; lacking mangroves and characterized by patches of *T. testudinum* and *Syringodium filiforme* Kuetzing (manatee grass), as well as sand alongside its extension. Within this reef, sites closer to the reef edge, and deeper (~1 m) ones showed higher coverage of live coral. On PT and LM observations were done through snorkeling, whereas SCUBA was used in CO.

Surveys

The abundance and distribution of territorial damselfishes and benthic community were assessed in December 2010 and January 2011. Abundance of juveniles and adult damselfishes, as well as habitat use, were assessed using visual census for fish density and percent benthic cover over transects of 10 x 2 m (PT=20; CO=20, and LM=16; N=56). The studied damselfish species are easily distinguishable underwater based on their coloration, both as juveniles and adults. To minimize edge effect, records included damselfishes with at least 50% of its territory inside the transect boundaries.

Depth measures were taken for each transect. Benthic cover was estimated using the linear point-intercept method adapted from Liddell *et al*. (1984). At each 50 cm interval, substratum was recorded according to the following categories: (1) articulated calcareous algae (algae that project <5 cm above the substratum, mainly branched calcareous forms), (2) macroalgae (algae that project >5 cm above the substratum, mainly fleshy algae), (3) encrusting coralline algae, (4) filamentous algae, (5) branching corals (mainly *Millepora* spp. and *Porites* spp.), (6) massive corals (*Siderastraea* spp., *Montastraea* spp., *Diploria* spp., *Porites* spp.), (7) massive dead corals (overgrown by algae), (8) zoanthids, (9) sea urchins, (10) sponges, (11) sand, (12) rubble (pieces of broken corals), and (13) mud.

Statistical analysis

One-way Analysis of Variance (ANOVA) was used to test differences between species abundance at both life stages (juvenile and adult) and benthic percent cover among reefs. When necessary, data was log10 ($x + 1$) transformed, and the Student-Newman-Keuls *a posteriori* test was used. The structure of damselfish assemblages (*i.e.*, relative abundance of the different species and life stages) was analyzed using non-Metric Multidimensional Scaling Analysis (MDS), which was later tested for significance of groups formed for exposure and depth factors by the Analysis of similarity (one-way ANOSIM). Separate One-way ANOSIM for these factors was also used to test differences between benthic communities (Clarke & Gorley, 2001). Species' life stages and benthic community relationship was obtained, using the canonical correspondence analysis (CCA) ordination. Significant environmental parameters were selected with the Monte Carlo permutation test. Data were log-transformed and the CANOCO for Windows 4.5 software was used (ter Braak, 1995).

Results

Damselfish distribution among reefs

Fifty-six visual censuses yielded sightings of 1,178 damselfishes belonging to six common Caribbean species: the dusky damselfish *Stegastes adustus* (Troschel 1865), the threespot damselfish *S. planifrons* (Cuvier, 1830), the beaugregory *S. leucostictus* (Müller & Troschel, 1848*)*, the bicolor damselfish *S. partitus* (Poey, 1868), the cocoa damselfish *S. variabilis* (Castelnau, 1855), and the yellowtail damselfish *Microspathodon chrysurus* (Cuvier, 1830) (Table 1). The former two species represented the majority of overall abundance, including adults and juveniles (~90%). *Stegastes adustus* was especially abundant in shallow reefs (PT and LM) (Fig. 2). The abundance of both juveniles and adults from this species were very similar in Pete's Reef, but adult abundance was significantly different between this site and Lime Point (ANOVA; $p<0.0001$) - on the latter it was observed a two-fold increase with wave (Fig. 2). *Stegastes planifrons* presented closer affinity to sheltered reefs (PT and CO), with a significant three-fold increase (ANOVA; $p<0.0001$) in shallow waters (PT). On the exposed reef (LM) juveniles presented very low abundances and adults were absent. The beaugregory *S. leucostictus* was not very abundant when compared with other species, but were observed only in sheltered reefs (PT and CO). Adults from this species were restricted to deeper patch reefs (CO), whereas juveniles did not differed in abundance between depths. Juveniles and adults of *S. variabilis* and *S. partitus* presented very low abundances and were restricted to deeper patches (CO). The yellowtail damselfish *M. chrysurus* was recorded both in the shallow and exposed (LM) and the deeper and sheltered reef (CO), showing no constraint concerning depth or exposure. Adults and juveniles, however, significantly increased 3x and 8x, respectively at LM (ANOVA; $p=0.0037$ and $p=0.0002$, respectively) together with the abundance of adult *S. adustus* (Table 1; Fig. 2), indicating preference for exposed reefs.

Non-metric multidimensional scaling analysis presented in Fig. 3 (a-b) showed distinct groups for damselfish communities, which were separated between wave exposure and depth. The low stress value indicated that the observed sample distribution in the two dimensional space provided a reliable interpretation of the differences among damselfish community structure at the study sites. Separated one-way ANOSIM corroborated the formation of these groups, with low degree of overlap between exposure (global R= 0.654, $p=0.001$) and depth (global R=0.589, $p=0.001$).

Benthic communities

Benthic communities also contributed for differences found among reefs. However, one-way ANOSIM tests detected significant differences among reefs regarding exposure (R=0.655; $p=0.001$), but not for benthic cover (R=0.092; $p=0.055$).

Pete's Reef (PT) and Conch Point (CO), both being sheltered reefs, presented higher cover of live or dead corals, including massive corals (mainly brain corals) and the branching finger coral *Porites* spp. (Table 1). Coral cover was always higher on the shallower reef (PT). Particularly, the deeper reef (CO) presented higher cover of sponges and sand, the latter being a consequence of more dispersed patch reefs. The exposed reef (LM) was an algae-dominated reef, comprising crustose, articulated and macroalgae. Also, colonies of the firecoral *Millepora alcicornis* Linnaeus, 1758, zoanthids and rubble were commonly observed.

Table 1. Species abundance by life stage and percent composition of substrata (Mean ± SE), plus ANOVA results and Student-Newman-Keuls (SNK) comparison between reefs. ns = non-significant; *p<0.05; **p<0.01; ***p<0.001.

	PETE'S REEF	CONCH POINT	LIME POINT	p	F	SNK
JUVENILES						
S.planifrons	4.05±0.63	4.75±1.01	0.12±0.08	***	10.36	PT=CO>LM
S.adustus	5.75±0.89	0	4.00±0.83	***	19.38	PT=LM>CO
S.leucostictus	0.20±0.11	0.10±0.06	0	***	9.73	PT=CO>LM
S.variabilis	0	0.10±0.07	0	ns	1.89	-
S.partitus	0	0.25±0.16	0	ns	2.18	-
M.chrysurus	0	0.20±0.15	1.62±0.50	***	10.07	LM>CO>PT
ADULTS						
S.planifrons	12.40±1.56	4.55±0.72	0	***	33.59	PT>CO>LM
S.adustus	4.40±0.78	0.05±0.05	17.81±1.11	***	147.69	LM>PT>CO
S.leucostictus	0	1.75±0.48	0	ns	1.89	-
S.variabilis	0	0.05±0.05	0	ns	0.98	-
S.partitus	0	0.45±0.18	0	**	5.32	CO>PT=LM
M.chrysurus	0	0.20±0.15	0.75±0.23	**	6.24	LM>CO>PT
CORAL						
Dead	26.90±2.68	15.48±2.39	0.60±0.41	***	32.98	PT>CO>LM
Massive	43.81±5.46	29.52±2.78	12.80±3.03	***	13.77	PT>CO>LM
Branching	7.86±2.32	0	7.74±2.57	**	5.71	PT=LM>CO
ALGAE						
Turf matrix	0.95±0.56	0.24±0.24	37.80±3.95	**	108.1	LM>PT=CO
Macroalgae	0.24±0.24	0	10.12±2.98	***	14.11	LM>PT=CO
Crustose	0	0.24±0.24	7.74±1.68	***	25.28	LM>PT=CO
Filamentous	8.33±4.09	12.86±1.96	13.10±2.52	ns	0.78	-
OTHER						
Zoantids	0.95±0.56	0.24±0.24	6.25±2.60	**	5.58	LM>PT=CO
Sponges	6.19±1.04	12.62±1.63	0.30±0.30	***	24.98	CO>PT>LM
Urchins	1.90±1.44	0	0	ns	1.56	-
Sand	2.62±0.94	23.57±4.07	0.30±0.30	***	24.99	CO>PT=LM
Rubble	0.24±0.24	1.19±0.59	3.27±1.28	*	4.06	LM>PT=CO
Mud	0	4.05±2.92	0	ns	1.72	-
Depth	1.15±0.02	8.15±0.08	1.34±0.04	**	1.36	CO>PT=LM

Fish-habitat relationships

Habitat relationships for damselfish and benthic descriptors using the canonical correspondence analysis are presented on Fig. 4a-b. The first two axes were significant (p=0.001) and accounted for 61.4% and 21.6%, respectively, of the relationship between species and explanatory variables. The first axis, responsible for most of explained variation, was positively related to habitats that presented high cover of branching corals, macroalgae and articulated calcareous algae (Fig. 4a). Such descriptors represented samples of Lime Point (shallow and exposed), which *S. adustus* and *M. chrysurus* were more associated with (Fig. 4b). A discrete segregation between juvenile and adult conspecifics from these species was observed, where *S. adustus* juveniles were strongly associated to the complex structure of fire-corals. This axis was, in the other hand, negatively represented by deeper patch reefs, contributing to high records of sandy bottoms, together with a high cover of live and dead massive corals. Such descriptors represented mostly Pete's reef and Conch Point samples (Fig. 4b). Axis I drove most of the juveniles of S. *leucostictus*, *S. partitus*, and *S. variabilis* abundance, as they were found associated with depth. *Stegastes planifrons* (juveniles and adults) showed a close relationship with massive and dead coral cover, together with adult *S. partitus* and *S. leucostictus*, showing preference for sparser patch reefs with higher cover of massive corals interspersed with sandy bottoms. Adult *S. variabilis* presented a distinct segregation from juveniles, but also associating with deeper patch reefs, explained by axis II.

Discussion

Habitat use

Although this work used a more quantitative approach than previous studies, damselfish distribution seemed to follow the prevailing patterns of habitat use found for this group of fishes throughout the Caribbean Sea in the last decades (Itzkowitz, 1977; Waldner & Robertson, 1980; Robertson, 1981, 1984, 1996). However, differences were found in respect to benthic cover they associated to. In addition, it was possible to detect the habitat partitioning and segregation among different species.

At a broader scale, differences regarding reefs were found not only for damselfish species composition, but also for benthic communities. These differences may be due to the influence of wave energy. It has been demonstrated that wave-stressed habitats are dominated by organisms with life histories adapted to a disturbance regime, presenting high resistance, such as coralline algal communities (Witman, 1992). In this study, reefs with more pronounced wave surge allowed a diverse algal community, including crutose types, as much as the encrusting and heavily calcified firecoral *Millepora alcicornis*, with a major

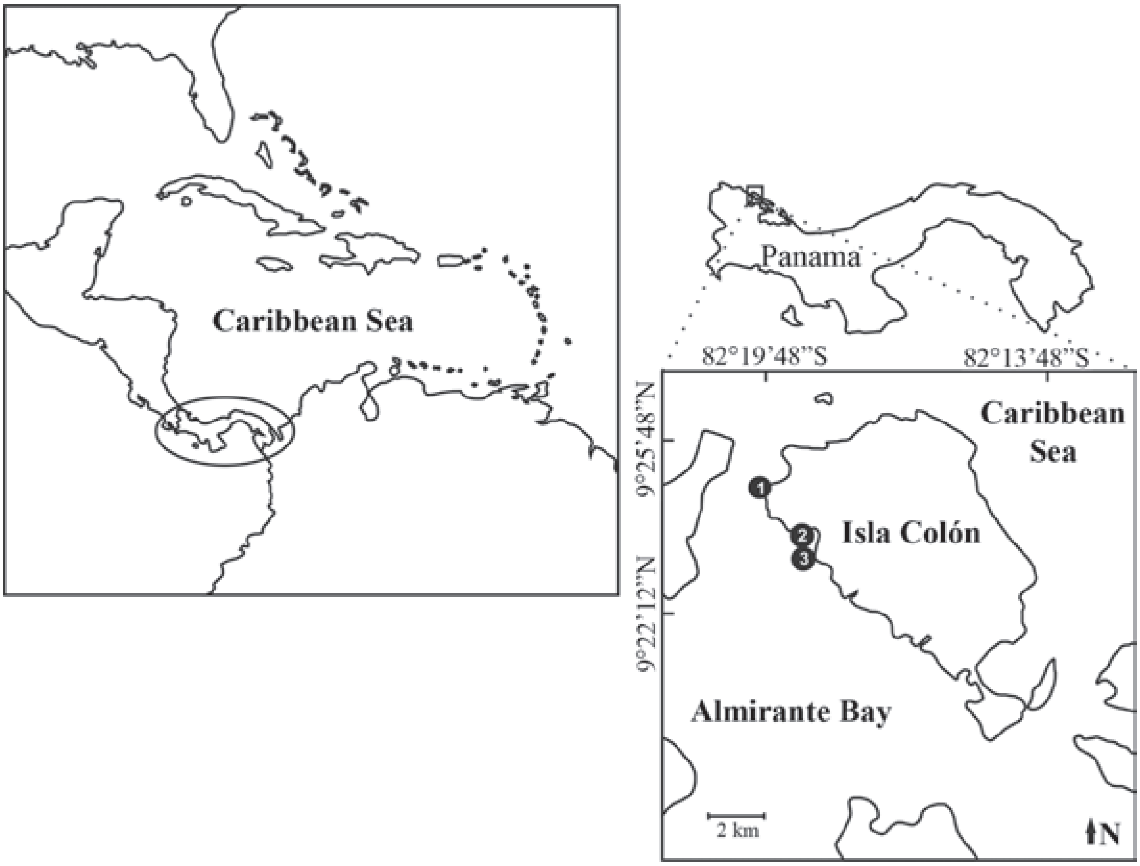

Fig. 1. Map of study area within the Caribbean region. 1-Lime Point; 2-Pete's reef and; 3-Conch Point

contribution to bottom cover. In the other hand, sheltered reefs had a more prominent colonization of massive corals, such *Montastraea* spp. and *Diploria* spp.

Considering damselfish abundance, the dusky damselfish *S. adustus* presented higher abundances on Pete's reef and Lime Point, indicating a preference of this species for shallow habitats, but it exhibited a two-fold increase in abundance at higher wave surge. This species is not particularly abundant in other Panamanian reefs (Robertson, 1996), but has been already recognized to prefer shallow and high wave energy habitats (Waldner & Robertson, 1980; Gutierrez, 1998; Dominici-Arosemena & Wolff, 2005). It also refuges on structural complex colonies of the elkhorn coral *Acropora cervicornis* (Waldner & Robertson, 1980). However, in this study, this species associated with colonies of the firecoral *Millepora alcicornis*, very resistant to water motion. As this hydrocoral presents a ramified hard structure, it apparently sustained the high abundance of *S. adustus*, as in many other reef fish species (Pereira *et al*., 2012; Coni *et al*., 2012). Moreover, wave exposure and any branching coral seem to be habitat requirements to the dusky damselfish, which should increase their vulnerability to habitat loss considering the massive mortality of Acroporid species throughout the Caribbean (Precht *et al*., 2002; 2010). Colonies of *M. alcicornis* seem to be also a preferred substrate for *M. chrysurus*, such as on Jamaica, Florida, Bahamas and Panama (see Waldner & Robertson, 1980; Robertson, 1984), and also on Brazilian tropical reefs (Ferreira *et al*., 2005). This study found that highest abundance of juvenile *M. chrysurus* followed this association and fish may use *Millepora* spp. not only for shelter, but perhaps also for feeding on the soft tissues, mucus or small epibionts (Ciardelli, 1967; Pereira *et al*., 2012).

In contrast, *Stegastes planifrons* was highly abundant in sheltered reefs, as previously noticed in other studies (Waldner & Robertson, 1980; McGehee, 1994; Dominici-Arosemena & Wolff, 2005). It was correlated especially with cover of live massive and dead corals, where its abundance increased. As past information on benthic cover is lacking one could not confirm pervasive habitat loss, however it is strong evidence that a habitat shift have occurred already for *S. planifrons*, as recently described by Precht *et al*., 2010. This author provided valuable information on the lethal consequences of habitat shifts of this species, from branching forms (*Acropora* spp.) to massive corals (*Montastraea* complex) and *Porites porites*, which are the main corals found in sheltered reefs of Isla Colón. *Stegastes planifrons* predation on living tissue and consequent extensive coral mortality, benefits the proliferation of algal gardens (Precht *et al*., 2010), and its association also with dead corals could be an indication of this activity by *S. planifrons*. Such relationship should be specifically addressed at this point.

The role of interspecific interactions

Size and aggressiveness differences are among the most important factors driving the outcomes of competition for space in damselfish (Robertson & Lassig, 1980; Robertson, 1984; Danilowicz, 1997). Damselfish of the genus *Stegastes* are relatively small territorial fish and some are considered extremely aggressive (Itzkowitz, 1977; Robertson, 1984; 1996; Menegatti *et al*., 2003; Osório *et al*., 2006; Medeiros *et al*., 2010). An invasion of territory usually results in aggressive responses towards both conspecifics and heterospecifics, including individuals two or three size bigger (Pereira & Ferreira, 2012).

Adults of *S. adustus* and *S. planifrons* are more strongly

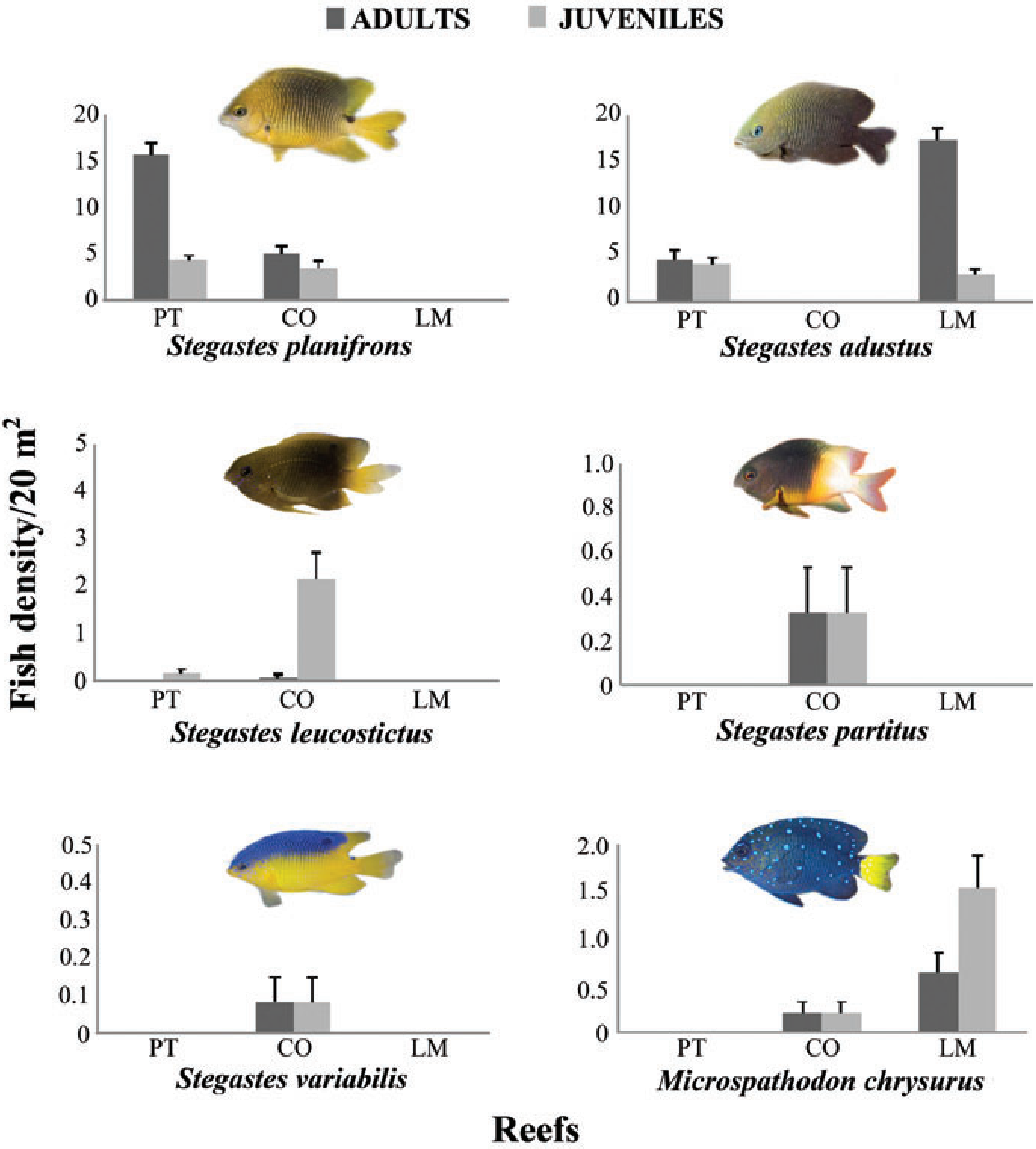

Fig. 2. Mean density per 20 m² (±S.E) of damselfish species observed in Pete's Reef (PT), Conch Point (CO) and Lime Point (LM).

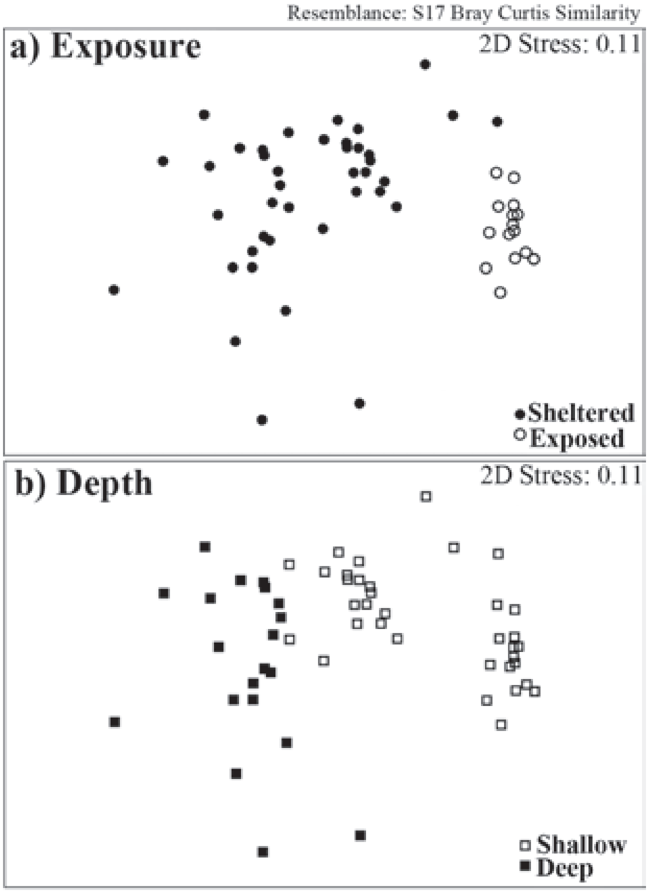

Fig. 3. MDS plots of damselfish community comparison between exposure and depth levels.

dependent on benthic algae for food than *S. partitus*, which commonly feeds on both planktonic and benthic material, or *S. leucostictus* and *S. variabilis*, which are more omnivorous benthic feeders (Emery, 1973; Robertson, 1984), indicating that coinciding food resource use would only be compensated with less territory overlapping. Direct causal relationships between fish abundances are hard to detect and not always clearly evident, as they are highly dependable on the fluctuations in recruitment and adult populations. However, the effects of interspecific competition on demographics and distribution were already detected in damselfish (Robertson, 1996). *Stegastes planifrons*, by its aggressiveness and population numbers, is known to have a negative influence on *S. partitus* and *S. variabilis* abundance, assuming an asymmetric competitive relationship (Robertson, 1996).

Stegastes adustus is also abundant and aggressive (Robertson, 1996), but both species are known to show little overlap in their distribution (Waldner & Robertson, 1980; Robertson, 1984; Gutiérrez, 1998). Herein they clearly followed the same trend in relation to adults of one another. The absence of *S. planifrons* on LM reefs and presence in lower abundance of *S. adustus* in PT indicate that the latter, at some level is a more habitat generalist in shallow depths, whereas *S. planifrons* seems to be more specialized, occurring generally only over live massive coral colonies, as described previously. These distributions indicate that interspecific competition could have strong effects on abundances of species in shared habitats of *S. adustus* and *S. planifrons*. However, habitat preferences would be the primary factor responsible for segregation, and that is observed since very early stages of life (Gutiérrez, 1998).

Furthermore, habitat partitioning by territorial herbivores

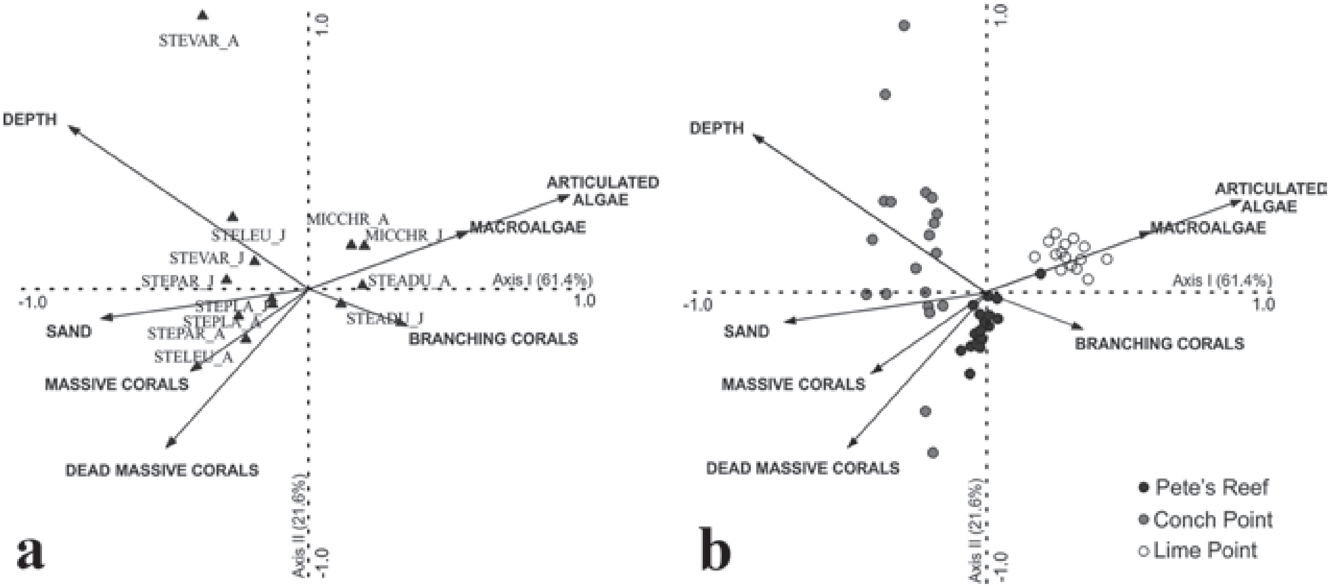

Fig. 4. Canonical correspondence analysis plot showing the correlations of the most significant variables (arrows) with fish species (**a**) and samples (**b**). Species codes: STEPLA = *Stegastes planifrons*; STEADU = *Stegastes adustus*; STELEU = *Stegastes leucostictus*; STEVAR = *Stegastes variabilis*; STEPAR = *Stegastes partitus*; MICCHR = *Microspathodon chrysurus*. The letters (J and A) following the species code names denote juvenile and adult, respectively.

brings also light to other interactions than competition. *Stegastes adustus* and *M. chrysurus* reached higher abundances when sharing habitats at Lime Point reefs. In fact, this association was reported over three decades ago by other authors (Clarke, 1977; Itzkowitz, 1977; Waldner & Robertson, 1980; Robertson, 1984), indicating an interesting pattern of behavior. The exclusion of *M. chrysurus* by adult *S. planifrons* is usually expected, due to the high aggression of the latter (Robertson, 1984). It has been argued that *M. chrysurus* may benefit from the smaller-sized *S. adustus* for its higher ability of territory defense, which may allow then to take long distance movements for reproduction (Sikkel & Kramer, 2006) or feeding activities.

Adults of *M. chrysurus*, although also associated with *Millepora* colonies on this study, are less dependent of shelter, attaining larger shared territories with *S. adustus*, and taking advantages of co-defense of their boundaries. Regardless of the fitness costs for the "host" *Stegastes*, this relationship indicates high stability of damselfish behavioral traits.

Further considerations

In spite of small-scale variability, similar trends were found for damselfish habitat use compared to previous studies. Although pre-recruitment processes are likely to play an important role, the high longevity of this group known to be over a decade long (Kohda, 1996; Schwamborn & Ferreira, 2002), probably confers some population stability and contributes for the maintenance of their distributional patterns over a large time span. This stability, however, may be disrupted by major environmental changes such as the mass mortality of important structuring corals during disturbances (*e. g.* El-Niño events, hurricanes, diseases).

At a local spatial scale the presence of preferred habitats, such as live corals, is of major importance and a massive coral cover loss (almost 80%) throughout the Caribbean in the last decades (Aronson & Precht, 2001; Gardner *et al*., 2003; Guzman, 2003; Edmunds & Elahi, 2007; Alvarez-Filip *et al*., 2009) may have resulted in lower recruitment and associated reduction in damselfish population size. For instance, *S. planifrons* faced decreased adult abundance after declines of *Acropora* spp. throughout Caribbean reefs, which represented negative consequences for secondary preferred habitats, such algae overgrowing massive corals (Precht *et al*., 2010).

Although the reefs studied are not yet considered algae dominated systems and past data are lacking, they have probably suffered modifications in the last decades due to natural and land based impacts. Bocas del Toro has been subjected to several anthropogenic disturbances due to the increasing tourism activity. This came together with other human impacts such as artisanal fisheries, sport fishing and the environmental stresses resulting from diving activities (Dominici-Arosemena & Wolff, 2005). Yet, we have no knowledge on how damselfishes responded in a pervasive manner to these changes.

Damselfish patterns of local distribution may be good indicators of health on coral reef systems. As well adapted species to present conditions and in a scenario of community homogenization due to overfishing, hurricanes and other stressors along the Caribbean, the abundance patterns of *S. planifrons* and *S. adustus* in Isla Colón may be an important reference point. Moreover, understanding how these fish are facing changes and how good indicators they are would be a useful tool to become aware of such environment modifications.

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