

Negative effects of gardening damselfish *Stegastes planifrons* on coral health depend on predator abundance

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ABSTRACT: On Bonaire, we studied the effects of predator abundance and habitat availability on the abundance of the threespot damselfish *Stegastes planifrons*, a species that creates algal gardens at the expense of live coral cover. Across 21 sites, predator biomass ranged from 12 to 193 g m⁻² (mean = 55.1; SD = 49.1) and benthic cover of *S. planifrons*' preferred habitat (corals of the *Orbicella* species complex) ranged from 2.2 to 38.0% (mean = 14.3; SD = 9.6). Across these gradients, the local abundance of *S. planifrons* was significantly and negatively related to predator biomass, but not to habitat availability. Increased local abundance of *S. planifrons* corresponded to an increasingly larger proportion of coral colonies affected by its 'farming behavior', resulting in an increased prevalence of coral disease. Thus, predators indirectly affected the composition of reef communities around Bonaire by controlling damselfish abundance. Furthermore, the abundance of *S. planifrons* could not be correlated with its preferred habitat, despite such correlations having been observed elsewhere in the Caribbean.

KEY WORDS: *Stegastes planifrons* · Bonaire · MPA · Prey release · Damselfish · *Orbicella* spp.

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INTRODUCTION

The reduction in fish stocks is one of the most notable changes on Caribbean reefs over the last decades (Jackson et al. 2001, Pandolfi et al. 2003), and marine fishes that otherwise influence community structure over vast areas, such as herbivorous fish and large predatory fish, are no longer abundant

enough to fulfill such ecological functions. After predatory fish have declined in abundance through overfishing, their prey, such as fish species untargeted by fishermen, often increase in number as these prey species become relieved of historically experienced predator-induced mortality rates of 90% or more (e.g. Shulman & Ogden 1987, Hixon & Carr 1997). The decline in abundance of predators can

affect the integrity of the wider reef community when their prey species can modify their habitat in a detrimental way (Sandin et al. 2010).

The best known examples of reef organisms that increase numerically after their predators are fished out are echinoderm species capable of modifying their surrounding habitat. Examples include corallivorous starfish (Dulvy et al. 2004) and substrate-eroding sea urchins (Vermeij et al. 2010). One fish species that has increased in abundance relative to historic baselines is the Caribbean threespot damselfish *Stegastes planifrons* Cuvier 1830 (Bruckner & Bruckner 2003, Steneck & McClanahan 2005). This fish historically (>50 yr ago) occurred in extremely low abundances (0.2 to 1.2 g m⁻²) on Bonaire and Curaçao in the southern Caribbean (Collins 1956, Nagelkerken 1974), where it was considered a 'cryptic species' since it hid underneath and between branches of coral (Luckhurst & Luckhurst 1978). Like echinoderms, *S. planifrons* has the ability to modify its benthic surroundings by building, maintaining and defending permanent individual territories consisting of erect algal mats. These 'gardens' are created at the expense of corals that previously occupied the same area (Hinds & Ballantine 1987). *S. planifrons* aggressively defends its territory against herbivores (e.g. Williams 1980) and selectively prunes specific algal species to grow in the mat, serving as a continuous food source (Ceccarelli et al. 2001).

After overfishing drives a population of predatory fish to 'ecological extinction' (i.e. a species is reduced to such low abundance that it no longer interacts significantly with other species), local prey abundance can become dependent on other structuring processes, such as the availability of food and shelter (Dulvy et al. 2004). In Caribbean reef communities that are characterized by a low abundance of predators (between 2.3 and 22.5 g m⁻²), species-specific microhabitat preferences and the availability of topographically complex microhabitats determine the local abundance of *S. planifrons* (Precht et al. 2010). Inside well-protected marine parks, the biomass of predators is higher (approx. 10 to 200 g m⁻²; Newman et al. 2006), which raises the question whether the abundance of *S. planifrons* under such 'predator-heavy' conditions can still be predicted from the abundance of their preferred habitat.

Given the effects of *S. planifrons* on Caribbean reef communities (i.e. facilitating the replacement of living corals with turf algae), we aimed to elucidate the environmental factors that best predict *S. planifrons* local abundance in a relatively healthy reef system within the Bonaire National Marine Park (Grimsditch

et al. 2011). On Bonaire, predators are more abundant than on many other Caribbean reefs (Precht et al. 2010). We therefore investigated whether the abundance of *S. planifrons* depended on the availability of its preferred habitat (large *Orbicella* corals), general benthic community characteristics or the abundance of potential predators.

MATERIALS AND METHODS

Study site

Fieldwork was conducted on the fringing reefs of Bonaire (12°N, 68°W), in the southern Caribbean Sea from May to June 2009. The entire reef system has been protected as part of the Bonaire National Marine Park (BNMP) since 1979 and has been under consistent management since 1991. Despite a variety of local threats (Steneck & McClanahan 2005, Grimsditch et al. 2011), Bonaire's coral reefs are considered to be among the healthiest in the Caribbean (Jackson et al. 2013). Fish and benthic community composition were quantified at 21 sites along the southwestern (leeward) shore of Bonaire and around the nearby island of Klein Bonaire, which is located 0.8 km off Bonaire's leeward shore (Fig. 1).

Study organism

The threespot damselfish *Stegastes planifrons* is a small territorial herbivorous damselfish that 'farms' benthic algae in a territory that it defends against roving herbivores. The species has been a part of Caribbean reef systems for at least 125 000 yr (Kaufman 1981) and while coral is a small part of its diet (<1%; Randall 1967), *S. planifrons* destroys living coral surfaces to establish algal gardens (Kaufman 1977, Hinds & Ballantine 1987). Now that the species' preferred habitat (branching Acroporids) has largely disappeared from the Caribbean, *S. planifrons* prefers the scleractinian corals *Orbicella annularis* and *O. faveolata* as its primary microhabitat on shallow reefs throughout the Caribbean (Eakin 1989, Precht et al. 2010).

Benthic surveys

Cover of all major benthic groups and species-specific cover of stony corals (Scleractinia) and of the calcifying hydroid *Millepora complanata* was quanti-

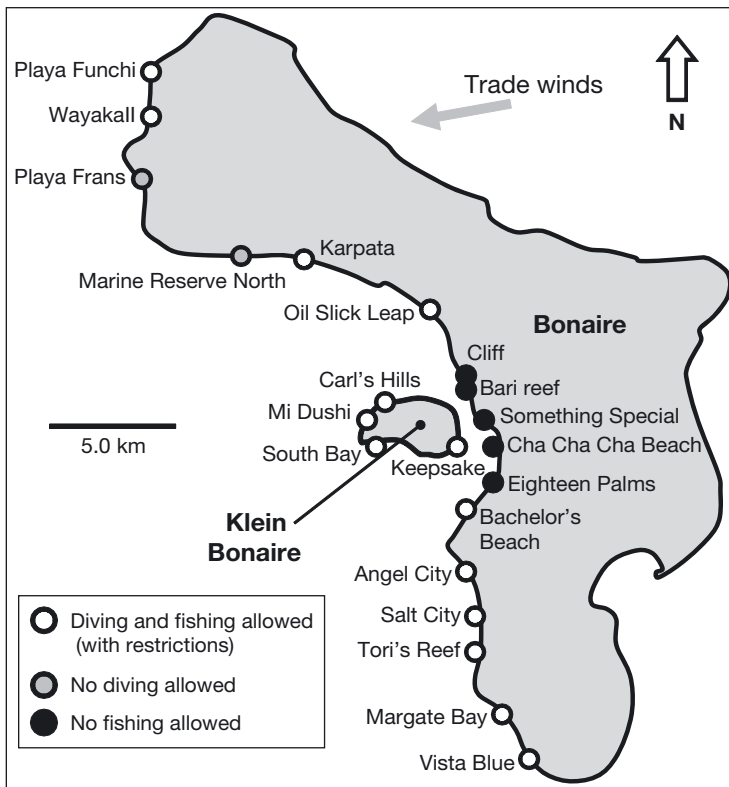


Fig. 1. Study locations on Bonaire. All study sites are on the leeward sides of the island. All sites are within the Bonaire National Marine Park (BNMP) and certain sites are additionally protected from fishing (since 2007) and diving. The area spanned by the filled black circles also correspond to the urbanized area of the island

fied at each site in three 25×1 m belt transects that were laid out parallel to the shore between depths of 8 and 10 m, whereby subsequent transects were separated by at least 10 m. In each belt transect, the size and species of all corals larger than 10 cm in diameter were noted to generate site-specific estimates of local coral community composition. Colonies smaller than 10 cm were not included because of their small relative contribution to overall coral cover. When present, the presence and type of coral disease and *S. planifrons* territories were noted for each coral colony (for more details, see Obura & Grimsditch 2009). All cover data were expressed as the percentage of habitable substrate occupied by each benthic group; sand and/or rubble were considered uninhabitable substrate types.

Fish surveys

Fish surveys focused on herbivore functional groups and predatory fish following the methods of

Green et al. (2009). The total length (TL) and species identity of all herbivorous and predatory fish near the benthos and in the overlying water column (<2 m) were recorded in up to three 30×4 m belt transects per site. Transects were positioned near to, but not overlapping, the benthic transects, thereby allowing for concurrent sampling of the benthos without disturbance of fish behavior. Transects were laid out similarly to those used for the benthic surveys following a depth contour between 8 and 12 m. After a new transect was laid out, fish surveys were started 5 min later to allow fish that might have hidden when the transect was laid to resume their normal behaviors. Surveys were completed in 5 min per transect to standardize sampling effort among transects. The fish surveys focused on 3 functional groups of fishes: (1) *S. planifrons* and 3 other damselfish species (*S. leucostictus*, *S. diencaeus* and *Microspathodon chrysurus*), (2) herbivorous fish capable of removing epilithic turf and macroalgae from the reef substratum (members of the families Scaridae, Acanthuridae, Kyphosinae), and (3) piscivorous fish (members of the families Lutjanidae, Haemulidae, Aulostomidae, Serranidae, Carangidae, Synodontidae) (Randall 1967, Froese & Pauly 2011). Fish length was estimated to the nearest cm by sight and

calibrated by exact measurement of nearby landmarks when needed. Accuracy of length estimates was maintained with periodic tests for the divers *in situ*, and observer bias was minimal as all census data was collected by the same divers. Total lengths of fish were converted into biomass estimates (in g m^{-2}) based on the product of species- and size-specific density estimates and species-specific weight-length relationships (available at www.fishbase.org; (Froese & Pauly 2011). For details see Obura & Grimsditch (2009).

Statistical analyses

Relationships among the local abundances of functional groups on Bonaire's reefs were investigated using Kendall's rank correlation making no *a priori* assumptions regarding the distributions of X or Y or the distribution of (X,Y). The same approach was used to determine whether predictable relationships existed between abundance of *S. planifrons* and

number of diseased coral colonies at a site. Because the abundance of *S. planifrons* is hypothesized to be dependent on predator abundance and/or habitat availability (i.e. the abundance of *Orbicella* spp.; sensu Precht et al. 2010), we explicitly tested the prediction that *S. planifrons* abundance is dependent on both factors using multiple correlation. To test whether *S. planifrons* individuals preferred certain coral species to establish their territories, the relative abundances of all coral species were pooled at an island level across Bonaire and compared to the distribution of *S. planifrons* across the same coral species. We then assumed a random distribution of *S. planifrons* across all coral species and tested for deviations to this expected distribution using a chi-squared goodness-of-fit analysis.

RESULTS

Damselfish distribution

Of all benthic and fish groups considered in this study, only the abundance of predatory fishes could be related to the local abundance of *S. planifrons* (Fig. 2a). The local biomass of predatory fish correlated significantly and negatively with the local abundance of *S. planifrons* ($r = -0.46$, $p < 0.05$). In contrast, the local abundance of *S. planifrons* did not vary in response to its preferred habitat (*Orbicella* spp.) (Fig. 2b, $r = 0.35$) even when the stronger effect of predators was removed (multiple correlation; $r_{\text{orbicella}} = -0.06$, $p = 0.81$). All possible relationships between the abundance of benthic groups and *S. planifrons* abundance were tested; apart from the above relationships, the abundance of no other benthic group (overall coral, turf and macroalgal cover) was related to the local abundance of *S. planifrons* (Table 1). The abundance of *S. planifrons* was, however, significantly and positively correlated with the proportion of local coral colonies affected by disease (Fig. 2c, $r = 0.62$, $p < 0.01$). Across Bonaire, most coral colonies with signs of disease ($n = 69$) belonged to the *Orbicella* species complex and suffered from yellow blotch disease (sensu Bruckner 2003). The abundance of other territorial damselfishes (*Stegastes leucostictus*, *S. diencaeus* and *Microspathodon chrysurus*) did not affect the abundance of *S. planifrons* ($-0.38 < r < -0.08$, $p > 0.09$), suggesting a low degree of interspecific competition (sensu Robertson 1996). None of the other 3 damselfish species were affected by the abundance of predators or habitat availability like *S. planifrons* (multiple correlation; $r_{\text{orbicella}} > -0.30$;

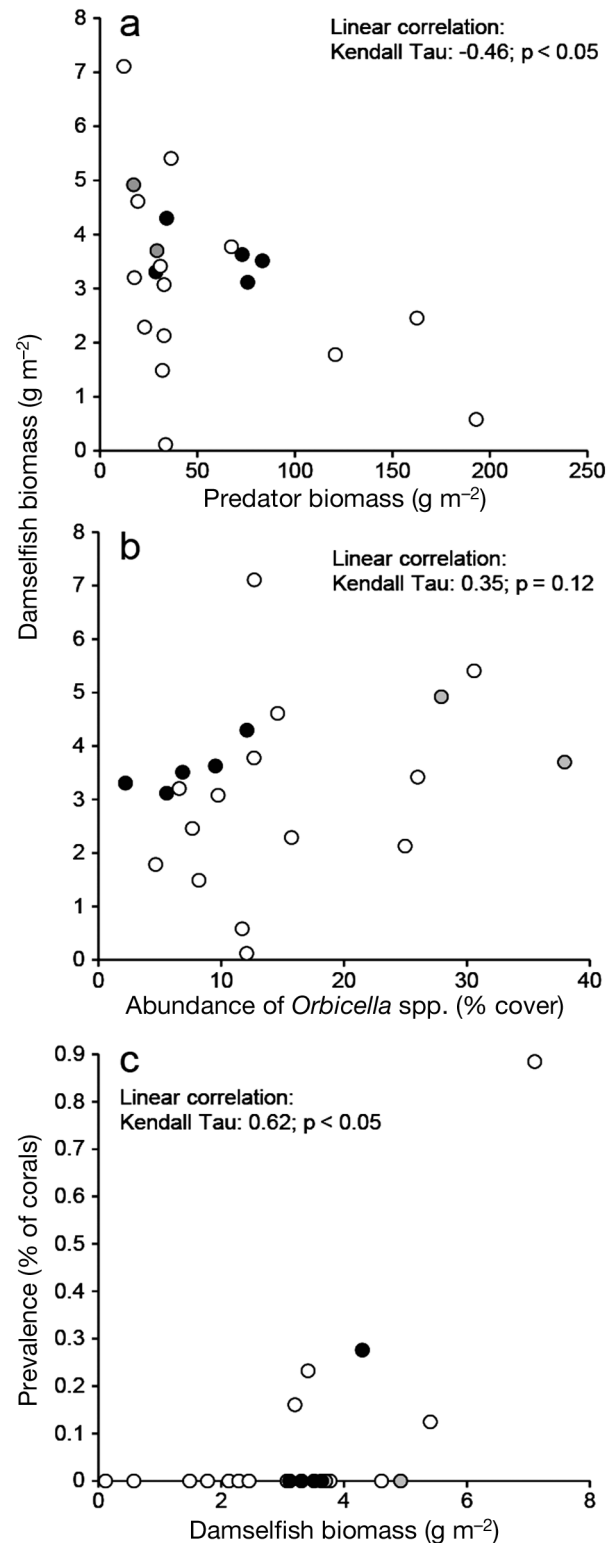


Fig. 2. Relationships between the local abundance of territorial damselfish *Stegastes planifrons* and (a) predatory fishes, (b) availability of preferred habitat and (c) disease prevalence at 21 sites on Bonaire. Circle color corresponds to protection status: white, diving and fishing allowed (with restrictions); grey, no diving; black, no fishing (see also Fig. 1)

Table 1. Matrix of potential correlations (Kendall's rank) among the average abundance of benthic and fish groups considered in this study for 21 sites on Bonaire. Significant correlations ($p < 0.05$) in **bold**

	Macroalgae (% cover)	Turf algae (% cover)	Diseased coral (%)	Predatory fish (g m^{-2})	Damselfish (g m^{-2})
Coral (% cover)	-0.49	0.26	0.04	-0.39	0.35
Macroalgae		-0.06	-0.15	0.22	-0.23
Turf algae			0.65	-0.30	0.50
Diseased coral				-0.29	0.62
Predatory fish					-0.46

$p > 0.20$; $r_{\text{predators}} > -0.44$; $p > 0.06$), except for the yellowtail damselfish, whose abundance was positively correlated with the local abundance of *Orbicella* colonies ($r_{\text{orbicella}} = 0.586$; $p = 0.01$).

Damselfish habitat preference

Territories of the damselfish were observed on colonies of 12 different coral species (Fig. 3a). *S. planifrons* did occur in greater densities than expected from a random distribution on 4 massive coral species: *Orbicella annularis* (2.6 \times higher), *O. faveolata* (3.9 \times higher), *O. franksi* (3.6 \times higher) and *Colpophylia natans* (1.2 \times higher) (chi-square = 176.24, $df = 16$, $p < 0.01$). *S. planifrons* apparently prefers large, massive coral species over small, branching and structurally more complex species such as *Eusmilia fastigiata*, *Millepora complanata*, *Madracis decactis* and *M. mirabilis* (Fig. 3b).

DISCUSSION

Abundance of *Stegastes planifrons* correlated negatively with the abundance of predators on Bonaire's reefs (Fig. 2a), suggesting that within the context of the Bonaire National Marine Park, predatory fish represented a stronger controlling factor on *S. planifrons* abundance (through direct consumption, sensu Paine 1980) than the abundance of its preferred habitat, namely corals of the *Orbicella* species complex (Figs. 2b & 3b; Precht et al. 2010). Precht et al. (2010) found the opposite pattern when looking at the relationship between predators,

habitat availability and the local abundance of *S. planifrons* across 5 Caribbean locations (Florida, the Bahamas, Jamaica, Cayman Islands and Belize) where habitat availability rather than predator abundance best predicted the local abundance of *S. planifrons*. However, those observations and the ones presented here are not mutually exclusive.

Bonaire ranks highest in terms of biomass of predatory fishes of all the locations covered in both studies

(Fig. 4). When populations of predators are reduced or extinct, previously suppressed prey populations, such as those of *S. planifrons*, can increase in size (Rayner et al. 2007), and local resources such as food or shelter become more important in determining their local abundance (e.g. Crowder & Cooper 1982, Sandin et al. 2008). McClanahan (2005) also observed that predatory fish reduced the number of damselfish in Belize, the site with the next highest abundance of predators considered here (Fig. 4). Combined with our data and those of Precht et al. (2010), this suggests that *S. planifrons* abundance is regulated by predators when such predators are abundant (for example on Bonaire and Belize), and

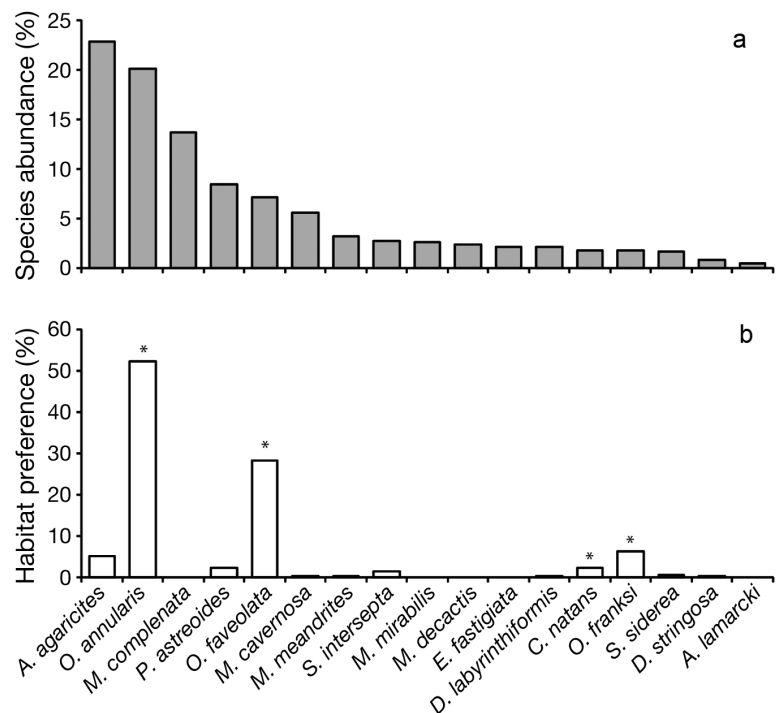


Fig. 3. (a) Relative abundance of the 17 most abundant coral species on Bonaire. (b) Distribution of *Stegastes planifrons* across the most common coral species. *Significantly preferred by *S. planifrons*

by resources such as habitat availability when predators are rare. The data presented here in combination with those of Precht et al. (2010) strongly suggest the existence of a 'switch' whereby the relative importance of one controlling factor of *S. planifrons* abundance (habitat availability) overtakes another (predator abundance) as predator abundance decreases locally.

Because territorial damselfish such as *S. planifrons* actively promote algal growth within their territories, often at the cost of living coral, their increased abundance comes with consequences for the reef communities in which they occur. *S. planifrons* creates 'algal territories' from which it feeds on algae and small animals (Randall 1967, Dromard et al. 2013), but rather than depleting this food source, it actively maintains and expands it. In some cases, *S. planifrons* must kill live coral tissue to create space for its territory, but does not feed on coral tissue in significant amounts (Randall 1967). Because *S. planifrons* defends its territory against herbivorous fish and urchins, it further reduces local levels of herbivory, accelerating the local rate of algal proliferation (Williams 1980, Precht et al. 2010). Thus, the effect of *S. planifrons* on benthic community composition is largely mediated through its own behavior (making

territories) or by changing the behavior of other ecosystem engineers (chasing away herbivorous fish and sea urchins). Besides the direct negative effect of their gardening behavior on coral cover, increased damselfish abundance is also positively correlated with the occurrence of diseased coral colonies (Casey et al. 2014). Coral disease is associated with increased (turf) algal cover inside the damselfish territories (e.g. Harvell et al. 2004, Casey et al. 2014) and coral disease and disease-like symptoms may be induced or mediated by bacteria harbored on or fueled by neighboring algae (Nugues et al. 2004, Smith et al. 2006).

Algae represent only a quarter of *S. planifrons*' diet (Randall 1967) and algal abundance increases more due to *S. planifrons*' 'farming behavior' than it decreases through *S. planifrons*' consumption of algae. The foremost effect of increased *S. planifrons* abundance on lower trophic levels (primary producers) is thus behavioral; such predator–prey interactions are commonly referred to as 'trait-mediated indirect interactions' (Stallings 2008). Qualifying the dynamic discussed here (i.e. fewer predators → more damselfish → more algae) as a trophic cascade across 3 trophic levels (Sandin et al. 2010) would be inaccurate given the missing trophic link between the abundance of damselfish and (turf) algae. The dynamic is better regarded as an example of 'prey release' between 2 trophic levels (predators and *S. planifrons*), confirming similar findings from Australian and Pacific reefs (Ceccarelli et al. 2006). The lower abundance of predators has indirect effects on lower trophic levels (i.e. increased abundance of primary producers), but this effect is largely behaviorally mediated as *S. planifrons* farms, rather than consumes, benthic algae and chases away reef herbivores.

We propose that the structuring influence of predatory fish on the abundance of *S. planifrons* disappears when predator abundance falls below $\sim 40 \text{ g m}^{-2}$. *S. planifrons*' destructive behavior (with respect to the corals) is comparable to the destructive behavior of other organisms (mostly echinoderms) that are increasing in abundance on present-day reefs that have seen the large-scale removal of the predators of such species. Because our findings are solely based on observations made on Bonaire, our con-

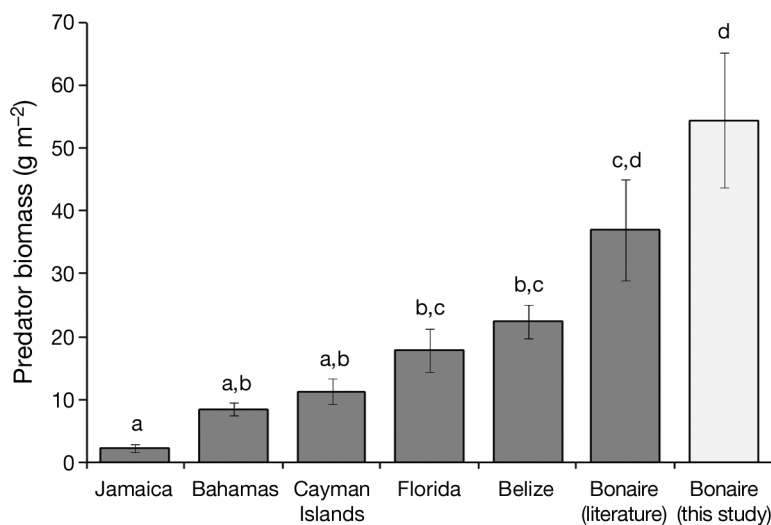


Fig. 4. The abundance of predatory fishes (members of the families Lutjanidae, Haemulidae, Aulostomidae, Serranidae, Carangidae, and Synodontidae) for all locations considered in this study (Bonaire) and in Precht et al. (2010). White bar, this study; grey bars, previously published data — Jamaica: 74 sites (Newman et al. 2006, Marks & Lang 2007); Bahamas: 26 sites (Marks & Lang 2007); Cayman Islands: 34 sites (Marks & Lang 2007); Florida: 28 sites (Newman et al. 2006, Marks & Lang 2007); Belize: 8 sites (Newman et al. 2006); Bonaire: 10 sites (Marks & Lang 2007, Sandin et al. 2007). Error bars represent standard error; letters above the bars indicate significant differences ($p < 0.05$) based on ANOVA followed by post-hoc tests (Tukey)

clusions should be experimentally tested, for example by using changes in the protection status of certain sites (from open to no-take or vice versa) in a BACI (before–after, control–impact) design. The fact that altered trophic interactions within reef communities are primarily documented through the increased abundance and activity of obviously destructive species (such as bioeroding sea urchins, corallivorous starfish and algal-farming damselfish) makes one wonder how many subtle changes in reef trophic dynamics remain presently unnoticed.

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