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The importance of sponges and mangroves in supporting fish communities in degraded coral reefs in Caribbean Panama

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Fish communities associated with coral reefs worldwide are threatened by overexploitation and other human impacts such as bleaching events that cause habitat degradation. We assessed the fish community on coral reefs on the Caribbean coast of Panama, as well as those associated with mangrove and seagrass habitats, to explore the influences of habitat cover, connectivity and environmental characteristics in sustaining biomass, richness and trophic structure in a degraded tropical ecosystem. Overall, 94 % of all fishes across all habitat types were of small body size (≤11 cm), with communities dominated by fishes that usually live in habitats of low complexity, such as Pomacentridae (damselfishes) and Gobiidae (gobies). Moreover, total fish biomass was very low, small fishes from low trophic levels were over-represented, and top predators were under-represented relative to other Caribbean reefs. For example, herbivorous/omnivorous/detrivorous fishes (trophic level 2-2.7) comprised 37 % of total fish biomass, with the diminutive parrotfish *Scarus iseri* comprising 72 % of the parrotfish biomass. However, the abundance of sponges and proximity of mangroves were found to be important positive drivers of reef fish richness, biomass and trophic structure on a given reef, presumably by promoting functional processes of ecosystems. The masked goby (*Coryphopterus personata*) was a strong indicator of reef degradation, apparently benefiting from the reduced density of large predators on local reefs. The damselfish *Abudefduf saxatilis* was more common on reefs with high sponge cover, and also to proximity to mangroves. Our study suggests that a diverse fish community can persist on degraded coral reefs, and that the availability of habitat forming organisms other than corals, including sponges and mangroves, and their arrangement on the landscape, is critical to the maintenance of functional processes in these ecosystems.

The importance of sponges and mangroves in supporting fish communities in degraded coral reefs in Caribbean Panama

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Keywords

Overfishing, reef degradation, trophic imbalance, mangrove connectivity, sponges

Abstract

Fish communities associated with coral reefs worldwide are threatened by overexploitation and other human impacts such as bleaching events that cause habitat degradation. We assessed the fish community on coral reefs on the Caribbean coast of Panama, as well as those associated with mangrove and seagrass habitats, to explore the influences of habitat cover, connectivity and environmental characteristics in sustaining biomass, richness and trophic structure in a degraded tropical ecosystem. Overall, 94 % of all fishes across all habitat types were of small body size (≤11 cm), with communities dominated by fishes that usually live in habitats of low complexity, such as Pomacentridae (damselfishes) and Gobiidae (gobies). Moreover, total fish biomass was very low, small fishes from low trophic levels were over-represented, and top predators were under-represented relative to other Caribbean reefs. For example, herbivorous/omnivorous/detrivorous fishes (trophic level 2-2.7) comprised 37 % of total fish biomass, with the diminutive parrotfish *Scarus iseri* comprising 72 % of the parrotfish biomass. However, the abundance of sponges and proximity of mangroves were found to be important positive drivers of reef fish richness, biomass and trophic structure on a given reef, presumably by promoting functional processes of ecosystems. The masked goby (*Coryphopterus personata*) was a strong indicator of reef degradation, apparently benefiting from the reduced density of large predators on local reefs. The damselfish *Abudefduf saxatilis* was more common on reefs with high sponge cover, and also to proximity to mangroves. Our study suggests that a diverse fish community can persist on degraded coral reefs, and that the availability of habitat forming organisms other than corals, including sponges and mangroves, and their arrangement on the landscape, is critical to the maintenance of functional processes in these ecosystems.

Introduction

Recent research has revealed ongoing degradation of coral reef fish communities from habitat destruction and other human impacts (Hughes et al. 2003; Knowlton and Jackson 2008; Wilkinson et al. 2008; Jackson et al. 2014). Human disturbances to coastal ecosystems, including pollution, sedimentation, degradation of water quality and climate change, are causing the decline of hard coral cover (Hughes 1994; Jackson et al. 2001; Aronson et al. 2003). In particular, the mass mortality of hard corals from regular coral bleaching, hypoxia events and storms has led to a structural collapse (Beukers and Jones 1998; Wilson 2006; Alvarez-Filip et al. 2009; Wilson et al. 2010; Altieri et al. 2017). Consequences for biodiversity and ecosystem functioning are visible in a declining fish density (Wilson et al. 2010) and diversity (Bell and Galzin 1984; Jackson et al. 2001; Kuffner et al. 2007; Alevizon and Porter 2015; Mora 2015).

At the same time, reef fish populations are apparently declining, as a result of unsustainable reef fisheries and the increasing demand for fish products for a growing population (Hodgson 1999; Jackson et al. 2001; Zaneveld et al. 2016). The negative effects of subsistence and commercial fisheries compound and affect fish population structure, growth, and reproduction, with indirect effects on non-target fish or invertebrate populations and their reef habitats also possible (Saila et al. 1993; Jennings and Lock 1996). The ultimate outcomes of these processes are overexploitation, trophic shifts in the food web, and a decline in reef fish biomass (Berkes 2001; McClanahan et al. 2009). The disproportionate targeting and depletion of larger size classes and high trophic levels can also contribute to trophic imbalance in the reef fish community (Pauly et al. 1998). These negative impacts on fish populations threaten livelihoods and food security, given that reef fishes provide a major food source for coastal communities across the tropics (Cesar et al. 2003).

An additional important factor affecting the reef fish community is the connectivity to, and integrity of, other associated habitats. Nearshore estuarine and marine ecosystems (i.e. seagrass meadows, marshes and mangrove forests) have a very high primary and secondary productivity and support a great abundance of fish biodiversity (Beck et al. 2001). Mangroves and seagrass typically support greater densities of organisms than unvegetated substrates (Nagelkerken et al. 2000; Mumby et al. 2004). The nursery-role concept suggests that many reef fishes (e.g. families Lutjanidae, snappers; Serranidae, groupers; Haemulidae, grunts) have life cycles that include seagrass meadows and mangroves as nursery and feeding grounds (Beck et al. 2001; Nagelkerken et al. 2002; Unsworth et al. 2008; Ley 2014; Serafy et al. 2015).

Our study system, Bocas del Toro on the Caribbean coast of Panama, is affected by multiple threats within a strongly connected coastal reef-seagrass-mangrove habitat system (Rawlins et al. 1998; Guzmán 2003; Cramer et al. 2012; Cramer 2013; Seemann et al. 2014). Bocas del Toro is a semi-lagoon system composed of six major islands and the mainland, which surround Almirante Bay with large coastal swamps and mangrove forests. Mangrove islands are also scattered across the bay (Collin 2005). Several rivers, creeks and oceanic inlets discharge sediments and nutrients into the bay (Collin 2005). Additionally, human population growth, which is strongly connected to agriculture (banana industry) and tourism (Seemann et al. 2014), exacerbates degradation of water quality and physical destruction (Guzmán and Jiménez 1992; Collin 2005; D'Croz et al. 2005; Aronson et al. 2014). Global impacts also cause degradation of coral reefs, as described elsewhere across the world (Smith and Buddemeier 1992; Hughes 1994; Riegl et al. 2009; Sammarco and Strychar 2009). Bleaching and low oxygen events in 2010, in particular, killed up to 95% of the hard coral cover (Seemann et al. 2014; Altieri et al. 2017).

The persistence of invertebrate communities on these degraded reefs suggests that some resilience mechanisms are operating (Nelson et al. 2016; Kuempel and Altieri 2017). Whereas most studies focus on documenting the negative drivers that cause the loss of fish biomass and diversity, our study takes the alternative perspective by investigating the positive factors that maintain fish communities in a degraded ecosystem. We investigated the extent to which the fish communities have been affected by over-exploitation, and how the remnant fish communities at degraded reef sites are supported by habitat quality and connectivity. Specific questions we address include: Does this southwestern Caribbean fish community show signals of reef degradation and over-fishing? Is the reef fish community affected by proximity to other biogenic coastal habitats (e.g. seagrass beds and mangroves)? Do reef organisms other than hard corals support the biomass and structure of the fish community? Which factors support fish species richness, biomass and trophic structure?

Answers to these questions are needed to improve future research and conservation efforts on degraded coral reefs in the Caribbean and beyond.

Methods

In order to place results within the wider Caribbean context, visual fish surveys were conducted at reefs inside and outside marine protected areas with different management restrictions on fishing in five different ecoregions within the Caribbean. Additional fish surveys using the same methodology were conducted in adjacent seagrass and mangrove fringe areas in Bocas del Toro, where benthic surveys were also conducted and water quality measured for all sites and habitat types.

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Fish surveys. Firstly, we conducted visual fish surveys from 2012 to 2015 using the Reef Life Survey (RLS) protocol method 1 (Edgar and Stuart-Smith 2014) at reefs in the southwestern Caribbean, Southern Caribbean, Greater Antilles, Floridian and Bahamian ecoregions (Spalding et al 2007) at 61 sites, including Bocas del Toro and Kuna Yala (Panama), Archipelago of San Andres, Providencia and Santa Catalina (Colombia), Bonaire (Netherlands Antilles), Florida (US), Turks and Caicos Islands and Cayman Islands (British Overseas Territory). Each survey was repeated 2-6 times in depth ranges between 1 and 35 m (see Appendix), with fish surveys conducted at the same time by two divers averaged.

These data were used to identify the fisheries impacts in relation to protection status. Sites inside and outside marine protected areas with different management restrictions were described using the criteria of Edgar et al. (2014) as NTZ (no take zones, n=27), RZ (restricted zones, which still allows local fishing, n=19) and OZ (open zones, n=8), and these data compared to data from Bocas del Toro (OZ, n=9).

At Bocas del Toro the same RLS method was applied in seagrass and mangrove habitats located adjacent to the reef sites (≤250 m distance). Seagrass sites ranged in depth from 1 m to 4 m (see Appendix), whereas mangrove fringe root systems had maximal depth of 2 m. All individual fish sighted were counted, and their size was estimated along a 50 m x 5 m belt transect (250 m^2). Mangrove surveys were conducted facing the mangroves prop roots at the uppermost fringe line to the water. All fishes were identified to the highest taxonomic resolution possible. If an individual could not be identified on-site, a photograph was taken for later identification. Abundance, size and species identity were used to estimate biomass in kg m^{-2} (Edgar and Stuart-Smith 2014).

Fish community factors. The reef fish community was characterized using a variety of metrics including total abundance, abundance within size classes (10 cm size bin and below; 12.5-20 cm size bins; 25 cm size bin and above), total biomass, biomass of fishes ≤11 cm, and total species richness.

We also calculated the mean trophic level (community trait) of the reef fish community by multiplying the trophic level of each species by their log abundance, summing these values across species recorded on a transect, and dividing by the log abundance of all fish on the transect.

The classification of the trophic level (2-5) for each species was based on the feeding strategies: herbivores and detritivores (2-2.1), omnivores (2.2-2.7), low-level carnivores (2.8-3.4), mid-level carnivores (3.5-3.9) and high-level carnivores (4-4.5) (values obtained from www.fishbase.org).

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We also calculated the resilience factor (values obtained from www.fishbase.org) of each fish species, which was estimated from the population doubling time (low, medium, high).

Habitat assessment. Reef fish communities in Bocas del Toro (Fig.1) differed due to variation in structural complexity and other potentially-important factors, including amount of live coral cover, hard substrata, sponge cover and distance to nearest mangrove forest (Table 1). Reefs were typically dominated by *Porites furcata* in the shallow (1-4 m) and *Agaricia* spp. (>3 m) in the deeper areas. The associated seagrass meadows were dominated by *Thalassia testudinum* (turtlegrass). Mangrove fringes were exclusively shaped by *Rhizophora mangle* (red mangrove). To characterize the different habitats and their connectivity, benthic surveys were conducted for reefs and seagrass beds. In addition, the distance between reef sites surveyed and nearest mangrove was measured using GPS coordinates. Reef benthos was analyzed with 20 photo quadrats of 0.5 m^2 along a 50 m transect at each sampling site. Photos were analyzed via point counting using the Coralnet annotation tool (coralnet.ucsd.edu). A total of 25 points were randomly distributed on each photo. Substratum categories for the analyses comprised: healthy hard coral, bleached hard coral, recently-dead coral, anemones, soft coral, sponges, worms, zoanthids, rubble, sand, rock, calcifying algae, seagrass and macroalgae.

Water quality monitoring. Water quality was assessed by quantifying temperature (°C), salinity (psu), water depth (m), total dissolved solids (TDS, mg L^{-1}), dissolved oxygen (mg L^{-1}), pH, turbidity (FNU), chlorophyll (µg L^{-1}), blue-green alga concentrations (µg L^{-1}), and dissolved organic matter (fDOM, RFU) with an Exo2 multiparameter sonde (YSI, Xylem brand) (Snazelle 2015). The sonde was positioned ~10 cm above the bottom in each habitat (reef, seagrass and mangrove fringe). Measurements were recorded at intervals of 1-6 min over a time period of at least 30 min during the habitat surveys.

Data analyses. First, we identified significant correlations across all sites between environmental factors (including coral reef and seagrass cover, distance to mangroves and water quality) and fish community metrics (biodiversity, fish traits, biomass, size structure, abundances of individual fish species). Data were analyzed using a scatterplot matrix (see appendix) based on a nonparametric test (Spearman's test) for pairwise correlation probabilities. For all statistical analyses, fish abundance data were log-transformed to down-weight the extremely high abundance of a few fish species (i.e. *Coryphopterus personatus*) at some sites (Edgar et al. 2014).

Second, we performed multiple regression analyses to better understand the combined impact of several environmental parameter on particular fish community metrics. Our predictor variables were derived from the habitat assessment and water quality parameters, whereas the response variables were biodiversity metrics, fish traits, biomass and size structure of the fish community. Variables were included only if they showed a significant correlation ($P \leq 0.05$) with one of the fish community metrics identified in the scatterplot matrix.

Third, a principal component analysis (PCA) on correlations was used to identify fish species that were indicative of strong environmental trends in fish community structure. Fish were considered only if abundance >3 and abundances were significantly ($P \leq 0.05$) correlated with one of environmental factors identified in the scatterplot matrix (Appendix).

Last, mean values for different fish metrics were compared using one-way ANOVA or a Student's *t-test*. All statistical analyses were conducted using JMP Software 13.01.

Results

Characteristics of the fish community. A total of 61 fish species was recorded across all reef sites. This number was low compared to other Caribbean locations surveyed using RLS methods (total of 196 species) and also relative to coral reef locations world-wide (Stuart-Smith et al. 2013; Edgar and Stuart-Smith 2014). Total fish biomass in Bocas del Toro was also lower than at other Caribbean reefs, in no-take zones and those with restriction status (ANOVA, $P=0.02$ and 0.001, respectively) (Fig. 2a). The proportion of total biomass comprised by herbivores/omnivores/detrivores (2-2.7) was higher in Bocas del Toro, whereas the proportion of high-level carnivores (4-4.5) was generally lower than at other Caribbean reefs, albeit not significantly for either (Fig. 2b). The abundance of fishes within the smallest size class (≤11 cm) was significantly higher in Bocas del Toro than other Caribbean reefs (ANOVA, $P<0.0001$), whereas the abundances of medium- (12-22 cm) and large- (≥23 cm) sized fishes were significantly lower (ANOVA, $P<0.0001$) (Fig. 2c).

The biomass of herbivorous/omnivorous/detrivorous fishes (trophic level 2-2.7) was 37% of the total biomass (76% of all fish counted, Fig. 2b), with herbivorous members comprising 27% ± 3.5% (versus 10% ± 4% across the wider Caribbean), Pomacentridae (damselfishes) and Scarinae (parrotfishes) being predominant. *Scarus iseri* (striped parrotfish) contributed 72% of the parrotfish biomass. High-level carnivores contributed 22% ± 3.5% of total fish biomass, versus 31 ± 4 % elsewhere in the Caribbean. Dominant high-level carnivores were *Carangoides ruber* (bar jack), *Cephalopholis cruentata* (graysby), *Hyplopectrus nigricans* (black hamlet) and *Scomberomorus regalis* (cero).

A total of 94% of all fishes observed across all habitat types (reef, seagrass, mangrove) were in the smallest size class (≤11 cm length). Fishes ≤11 cm represented 59% of the total biomass within the reefs.

Relationships between environmental factors and fish community composition

Eight environmental and habitat factors were found to be significantly correlated with fish community metrics (Table 2, Appendix): sponge cover, distance to mangroves, the cover of recently-dead corals, calcifying algae, seagrass cover, sand cover in seagrass, chl *a* values, and fDOM values. These factors were not independent, as sponge cover was negatively correlated to the distance to mangroves and positively to chl *a* (R^2=0.60 and R^2=0.70, respectively, $P<0.01$). Mangrove fish richness was positively correlated to reef fish richness (R^2=0.76, P=0.02), and mean trophic level of the reef fish community was significantly correlated with sponge cover and mangrove fish richness (R^2=0.91 P=0.0007, multiple-regression analysis). The three sites without mangroves in close proximity and low sponge cover (Salt Creek, Popa, Hospital Point) showed lower biomass and fish richness (Table 1). The proportion of carnivores was significantly higher at the sites closer to the mangroves (ANOVA, $P<0.01$). However, the sites with a medium distance to mangroves (STRI, Juan Point, Coral Cay) revealed a significantly higher proportion of top-level carnivores (Fig. 3, ANOVA, $P<0.01$). The site (Hospital Point) without either mangroves or seagrass nearby showed the lowest fish diversity.

The highest abundances of all fish observed were recorded for Pomacentridae (damselfishes) and Gobiidae (gobies). However, Gobiidae were only abundant at the sites connected to mangroves. *Coryphopterus personatus* (masked goby) dominated these sites, with abundances up to 13 individuals m^{-2}. RLS surveys conducted in other places i.e. the close by San Andres Achipelago, Colombian Caribbean, revealed much lower densities (0.2 individuals m^{-2}). *Abudefduf saxatilis* (sergeant major) was significantly correlated to sponge cover (R^2=0.62, p=0.0027).

Generally, fishes with life cycles closely associated with hard corals (Lewis 1997), such as Pomacanthidae (angelfishes), were present in very low numbers (<1 per transect). Other reef fishes typically associated with hard substrates with a high complexity such as Balistidae (triggerfishes), Apogonidae (cardinalfishes), Muraenidae (moray eels), Sciaenidae (drums), Pseudochromidae (dottybacks) and Serranidae (grouper) were scarce within the bay (<1 per transect). Fishes of low and very low resilience, including those at higher trophic levels, such as *Diodon hystrix* (porcupinefish), *Ginglymostoma cirratum* (nurse shark), *Gymnothorax funebris* (moray eel), *Lutjanus jocu* (dog snapper), *Ocyurus chrysurus* (yellowtail snapper), *Pomacanthus arcuatus* (gray angelfish) were only found in reefs with mangroves in closer proximity (≤ 250 m), a result associated with the higher biomass of high-level carnivores at sites closely associated with mangroves (Fig. 3).

The PCA revealed a clustering of fishes based on the identified environmental factors (Fig. 4). Component 1 was primarily influenced by sponge cover, distance to mangrove, chl *a* and fDOM. Component 2 was influenced by recently dead corals (Table 3). Sampling sites characterized by high sponge cover, high seagrass cover, high fDOM and low distance to mangroves were

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associated with fishes such as *Abudefduf saxatilis*, *Hypoplectrus nigricans*, *Coryphopterus personatus* and *Coryphopterus glaucofraenum*. Fishes such as *Thalassoma bifascicatum and Acanthurus chirurgus* were associated with greater distances from mangroves and calcifying algae. Fishes as *Scarus iseri*, *Stegastes partitus* and *Cephalopholis cruentatus* were associated with recently dead corals. However, the cover of dead coral was negatively correlated with the abundance of most fish species.

Discussion

Our surveys revealed that the local fish fauna is depauperate in richness and biomass by Caribbean standards. We found further evidence that the fish community is representative of a degraded ecosystem as the fish community was dominated by small fishes typical of habitats of low complexity, such as Pomacentridae and Gobiidae, with few representatives of fish families more closely associated with high-relief coral reefs. Nevertheless, sponges and close proximity of mangroves were found to be positively correlated with fish richness, biomass and trophic level, suggesting that these habitat -forming organisms underpin resilience through presence on reefs and connectivity across the landscape.

Some fish species could be identified as indicator species. Extremely high abundances of a goby which forms schools above the bottom (*Coryphopterus personatus*) suggest that predation rates, and therefore predator abundances, are depleted in our study system. *Coryphopterus personatus* had 65-fold higher abundances than at sites 500 km distant in the San Andres Achipelago. Moreover, fish surveys in our study area in 2002 revealed densities an order of magnitude lower at 1.2 individuals m^{-2} (Dominici-Arosemena and Wolff 2005). We suggest this species represents an indicator species for degraded reefs in the Caribbean by benefiting from loss of predatory fishes that historically kept their local densities lower. *Scarus iseri* was considered as a keystone species given its role as the predominant herbivore, and is likely important for supporting the growth of sponges by cropping competing macroalgae. These functional roles of *S. iseri* had little redundancy in terms of other species potentially filling the same role if populations decline. *Abudefduf saxatilis* was identified as an indicator for sponge cover, a factor that could be positively correlated to fish richness, biomass and relatively high mean community trophic levels.

A degraded fish community in Bocas del Toro is evidenced by overrepresentation of biomass at low trophic levels and high abundance of small fishes, both classic symptoms of over-fishing (Pauly et al. 1998; Myers and Worm 2003). Exploitation thus appears to have contributed substantially to the patterns observed in the fish community at Bocas del Toro (Guzmán et al. 2005; Cramer 2013).

Herbivores, detritivores and omnivores were overrepresented in the fish community, with the proportion of herbivorous fishes much higher than at other Caribbean reef sites (Fig. 2b). Even though most herbivorous fish were in the smallest size category (<11 cm), this group has the potential to control the growth of macroalgae (Kuempel and Altieri 2017).

Another plausible reason for low total fish biomass is the degradation of hard corals (Turner et al. 1999; Wilson et al. 2010), which reduced fish species that are known to associate with hard substrata. This was indicated by significant correlations between the proportions of recently-dead corals and the biomass of fishes. The trophic imbalance of the fish community in Bocas del Toro furthermore can be related to the degradation and loss of coastal habitats, with associated loss of shelter, and nursery and feeding grounds (Turner et al. 1999; Alevizon and Porter 2015). Instead, fishes known to live on habitats of low complexity (particularly Pomacentridae and Gobiidae) occurred in very high abundances.

Sponges covered up to 20% of substrata, and thus provide considerable physical structure on the Bocas del Toro reefs (Diaz and Rützler 2001). In the absence of high cover of hard corals, sponges probably play an important role in supporting richness and biomass of the depauperate fish community in our study system. They are major determinants of the rugosity and height of the reef (Diaz and Rützler 2001), which in turn were found to be the most important predictors for fish abundance and species richness in a prior study (Gratwicke and Speight 2005). Sponges also comprise an important food source for spongivorous reef fishes, such as some members of Pomacentridae (Sammarco et al. 1987; Souza et al. 2011), Pomacanthidae and Scarinae (Dunlap and Pawlik 1996; Pawlik 1998). The pomacentrid *A. saxatilis* has been identified to have a functional dependency with sponges, through either shelter or other aspects of habitat complexity that sponges provide (Gratwicke and Speight 2005).

Connectivity to mangroves was another important positive factor associated with fish communities, as the biomass and richness of fish were greater on coral reefs that were closer to mangroves. Mangroves are well known to provide a nursery ground, shelter and food sources for reef fishes (Laegdsgaard and Johnson 2001; Mumby et al. 2004). Our study suggests that the positive effect of mangroves as nursery and feeding grounds can overcome and compensate some aspects of reef degradation in an ecosystem that has suffered multiple stressors. There are, however, non-linearities in mangrove influences on reefs, with negative influences at distances below 100 m. The reef-mangrove distance driving the highest abundance of carnivores was identified to be between 100 and 250 m.

One possible reason for a negative feedback with distance <100 m is that mangroves increase run-off of nutrients and detritus, providing a food resource for filter feeders (Lee 1995), which can then dominate and flatten the reef substratum. High cover of filter feeders in turn decreases hard coral cover (Granek et al. 2009), resulting in a reduction in fish species associated with high complexity reefs and that depend on hard corals (Beck et al. 2001; Nagelkerken et al. 2002; Unsworth et al. 2008; Ley 2014; Serafy et al. 2015). Nevertheless, lowest fish biodiversity and biomass was found on reefs without seagrass and mangroves in near proximity, presumably because many reef fish species may depend on interconnectivity between habitat types (Ley 2014). Also, the mean trophic level of the fish community declines at locations with no adjacent mangrove forest, probably because of the lack of food sources and nurseries for reef fish in general, and pelagic carnivores in particular (Ley 2014).

Further information on optimal habitat connectivity is critically needed for improved fisheries management and to ensure protection of diversity hotspots in marine protected areas (Linton and Warner 2003; Unsworth et al. 2008). Although fish biomass can be increased through fishing restrictions (Fig. 2a), habitat factors and connectivity of coastal habitats need to be considered to maintain the resilience of fish communities.

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Figure 1

Sampling sites in Bocas del Toro

Three reef sites (Punta Caracol, Casa Blanca, Almirante) possess close connectivity with mangrove habitat (within 100m), three sites (STRI, Juan Point, Coral Cay) represent reef sites further away from mangroves (100 - 250m), and three reef sites (Popa, Salt Creek, Hospital Point) are not closely connected to mangroves (> 750 m). Yellow areas are reefs and green areas are mangroves islands, gray is island, white is ocean, blue is river and blue polygon is poorly enforced MPA.

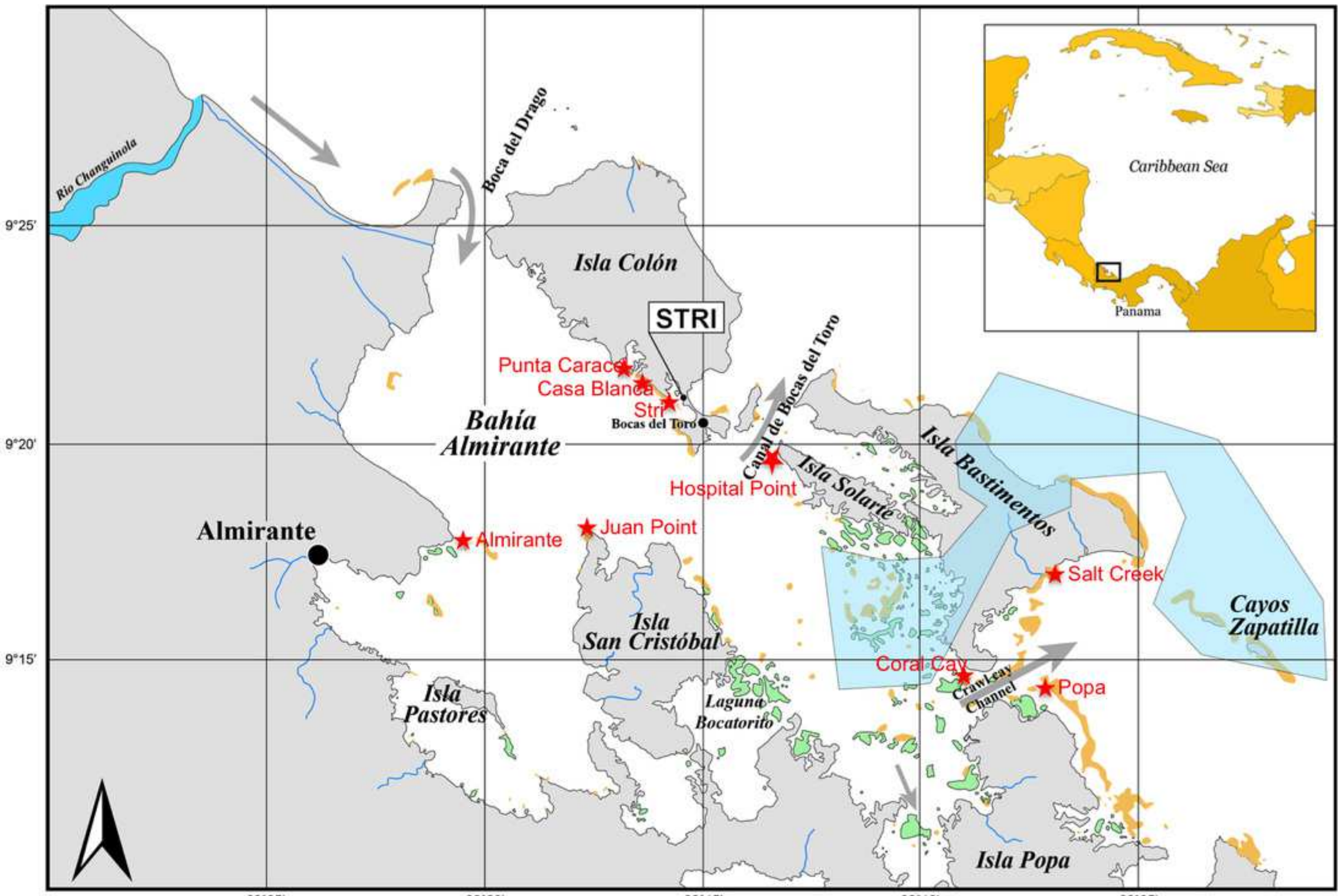

Figure 2

Biomass and composition of the fish community in the Caribbean and Bocas del Toro.

A) The comparison of the total biomass from RLS conducted across the Caribbean, divided in no take zones, restricted zone and open zones, and open zones in Bocas del Toro, Groups with different letters are significantly different. B) Distribution of trophic guilds based on total biomass: high-level carnivores (trophic level 4-4.5), low and mid-level carnivore 2.8-3.9, herbivores, omnivores and detrivores (trophic level 2-2.7). C) The abundance of fish subdivided in size classes (AVR ± SD), which are indicative of fishing pressure (skew towards smaller body size implies fishing). Asterisk represents significant differences between size abundance data from Bocas and the Caribbean.

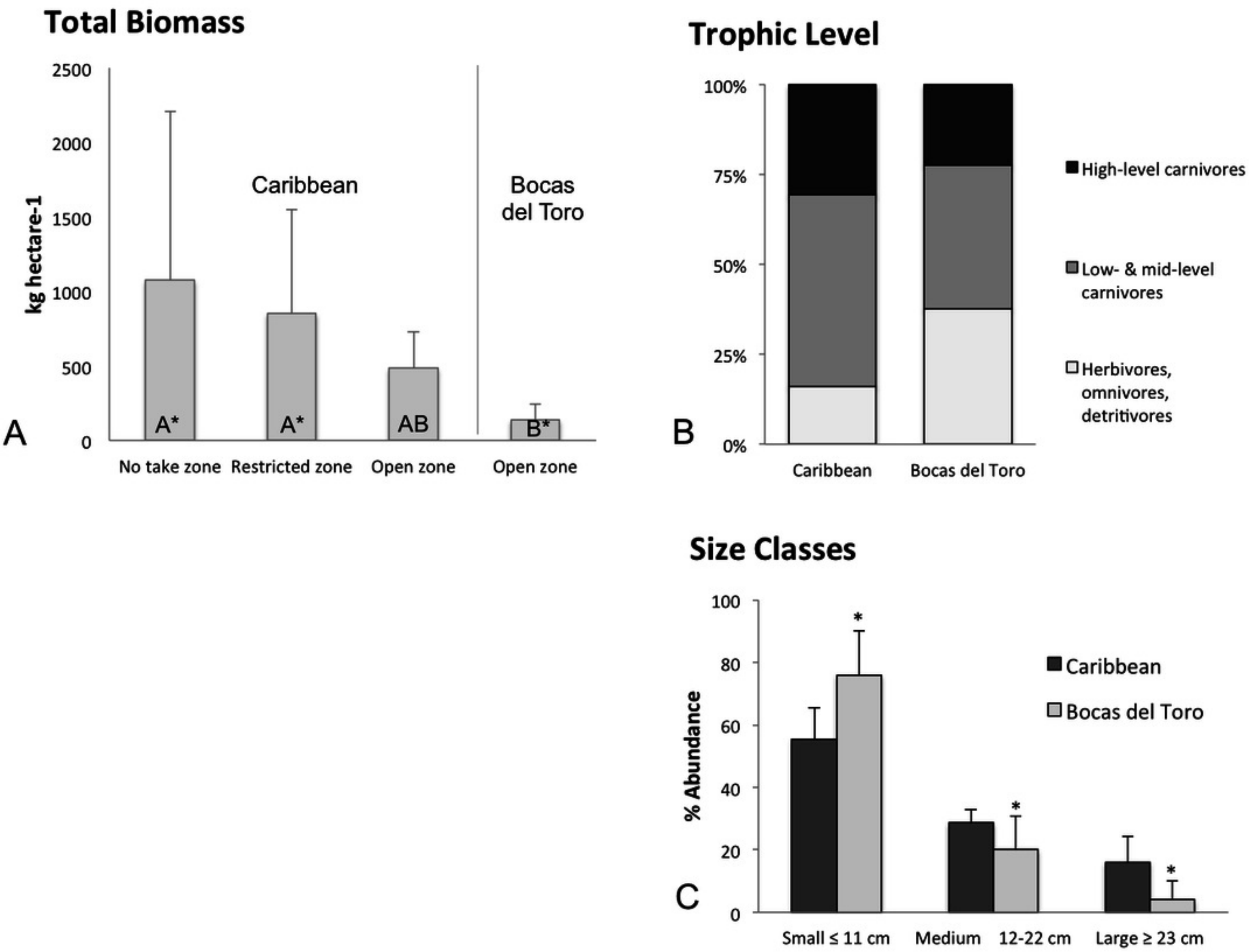
Total Biomass
kg hectare-1
2500
2000
1500
1000
500
0
Caribbean
Bocas
del Toro
A*
A*
AB
B*
A
No take zone
Restricted zone
Open zone
Open zone
Trophic Level
100%
75%
50%
25%
0%
B
Caribbean
Bocas del Toro
High-level carnivores
Low- & mid-level carnivores
Herbivores, omnivores, detritivores
Size Classes
100
80
60
40
20
0
% Abundance
C
Caribbean
Bocas del Toro
Small ≤ 11 cm
Medium 12-22 cm
Large ≥ 23 cm

Figure 3

Biomass of trophic guilds pooled by sites with a similar distance to mangroves.

Sites in distance to mangrove < 100 m (Punta Caracol, Casa Blanca, Almirante), 100 - 250 m (STRI, Juan Point, Coral Cay) and > 700 m (Popa, Salt Creek, Hospital Point) (compare Table 1).

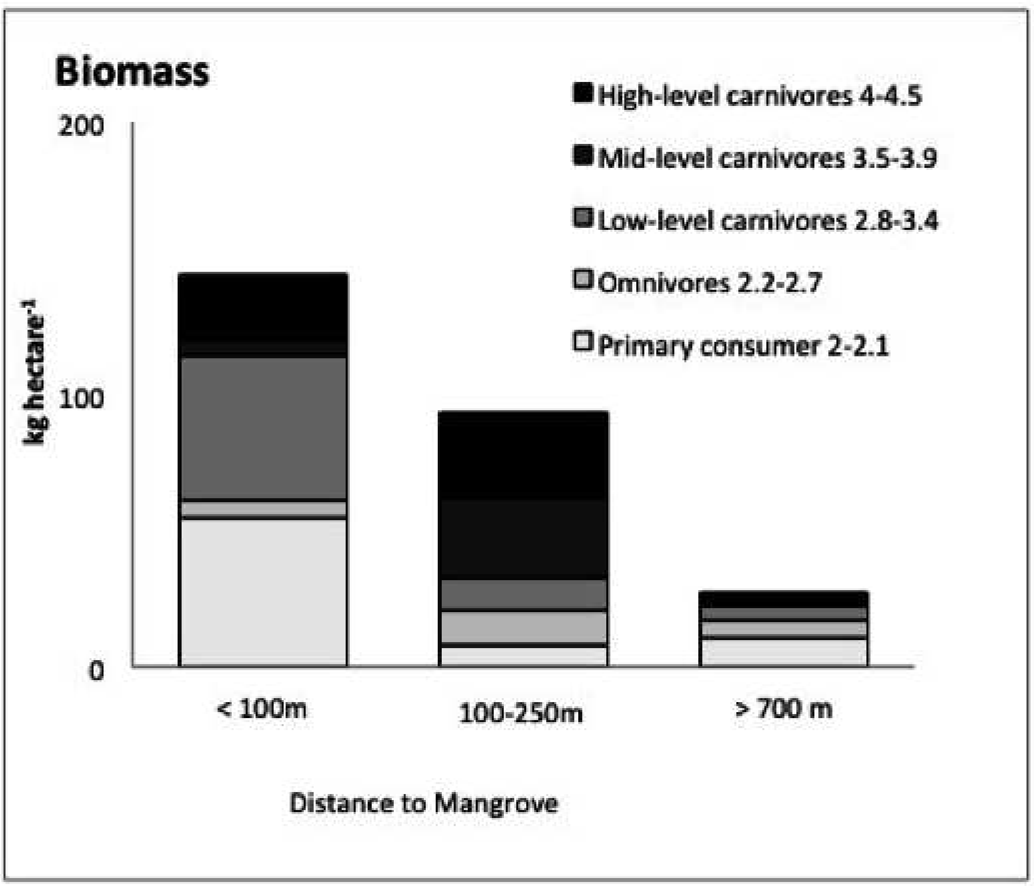

Figure 4

Principal Component Analyses

Principal components by site. The PCA showing clustering of sites with similar fish communities, with overlay vector plot showing major correlations of fish species with defined habitat characteristics. Sites are grouped in close (light green), medium (dark green), and far (black) distance to mangroves. Each site point represents the average of two transects at one timepoint. The strongest environmental trigger for component 1 is sponge cover (-0.96) and distance to mangroves (0.81). For component2 it is calcifying algae (-0.31) and recently killed corals (0.28).

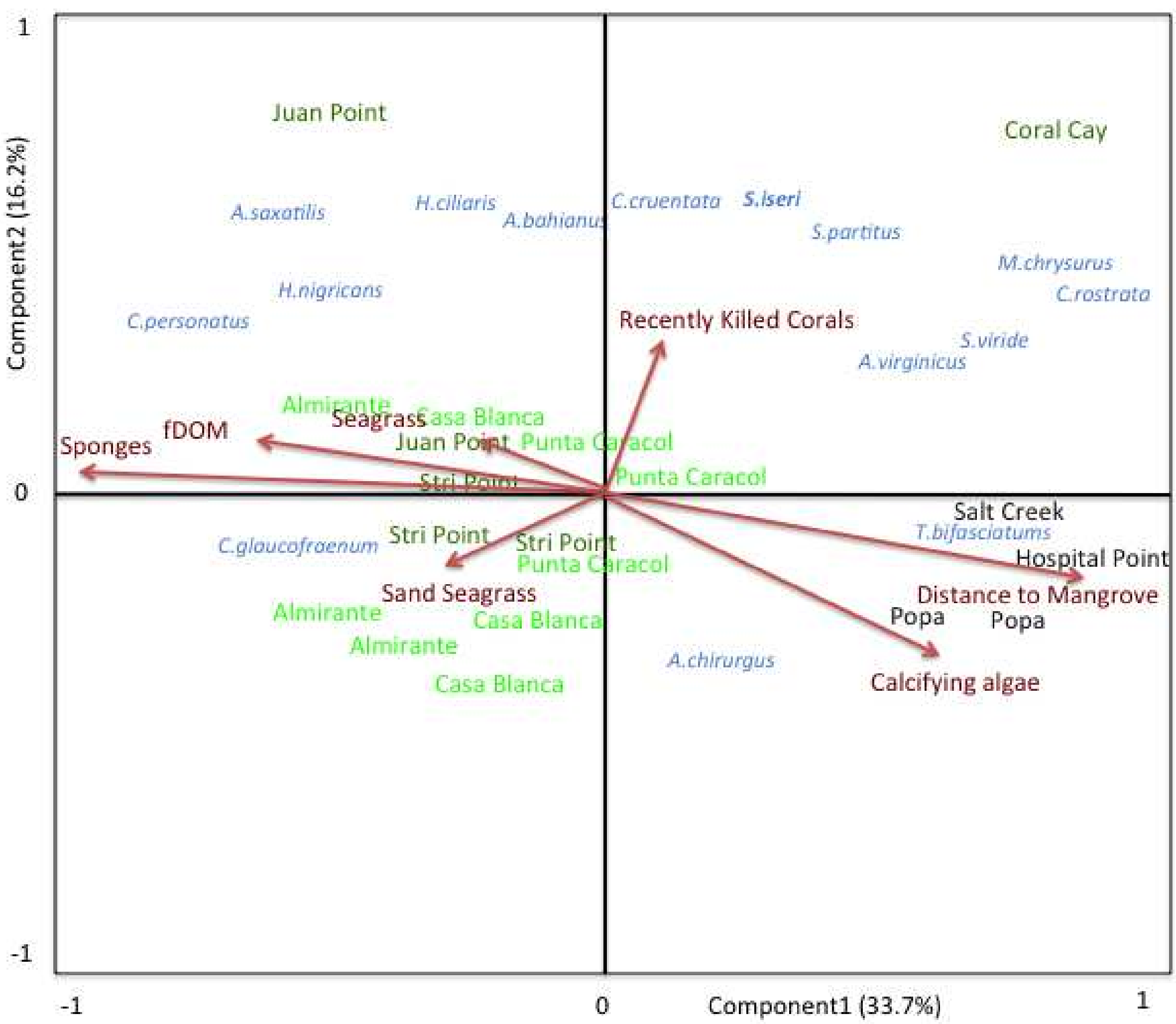

Table 1(on next page)

Tables

Table 1: Major habitat characteristics and location of monitoring sites. Sites 7 8 and 9 did not have mangroves in close proximity (≤ 250m); site 9 also did not have a seagrass meadow close to the reef

	Site	Coordinates Lat	Coordinates Long	Depth Reef (m)	Depth Seagrass (m)	Distance Reef-Mangrove (m)	Sponge Cover %	Live Hard Coral Cover %	Hard Substrate %	Reef Fish Biomass kg ha^{-1}	Seagrass Fish Biomass kg ha^{-1}	Mangrove Fish Biomass kg ha^{-1}	Reef Fish Abundance ha^{-1}	Seagrass Fish Abundance ha^{-1}	Mangrove Fish Abundance ha^{-1}	Reef Fish Richness	Seagrass Fish Richness	Mangrove Fish Richness
1	Punta Caracol	9.3757°	-82.2997°	3	2	65	9.5	41.5	33	201	25	111	12929	2820	17423	38	12	21
2	Casa Blanca	9.3588°	-82.2737°	3	1	70	17.5	2.5	71	67	32	47	18741	67660	17570	30	9	16
3	Almirante	9.2900°	-82.3429°	3	2	90	19.5	36.5	71	206	2	202	11105	2560	1202510	28	6	15
4	STRI Point	9.3483°	-82.2625°	3	4	120	19.5	3.0	57	257	24	15	71076	73153	42390	35	15	19
5	Juan Point	9.3003°	-82.2921°	4	1	170	17.6	46.4	69	94	14	32	24045	31760	200660	30	11	10
6	Coral Cay	9.2435°	-82.1478°	5	2	230	2.0	16.0	51	25	12	11	1717	50850	42060	25	7	9
7	Popa	9.2336°	-82.1120°	3	1	700	1.1	26.9	61	60	2		2608	560	17423	24	9	
8	Salt Creek	9.2815°	-82.1012°	6	2	950	0.5	24.8	99	13	0		1688	1290		15	12	
9	Hospital Point	9.3326°	-82.2220°	5.5		900	0.5	96.0	33	12			1946			16		

Table 2: Major fish families (only considering >10 counts ha^{-1} in average in one of the size bins)

	Caribbean			Bocas del Toro								
	Reef			Reef	Seagrass	Mangrove	Reef	Seagrass	Mangrove	Reef	Seagrass	Mangrove
	≤11 cm	12.5-20 cm	≥25 cm	≤11 cm	≤11 cm	≤11 cm	12.5-20 cm	12.5-20 cm	12.5-20 cm	≥25 cm	≥25 cm	≥25 cm
Acanthuridae	317	351	127	113	127	120	233	0	20	0	0	0
Balistidae	100	380	145	0	0	0	0	0	0	0	0	0
Carangidae	296	1078	145	321	20	2593	330	80	100	40	0	0
Clupeidae	11500	0	0	0	46000	278080	0	0	0	0	0	0
Ephippidae	0	80	280	0	0	0	30	0	0	0	0	0
Gerreidae	0	30	20	0	600	155	0	0	20	0	0	0
Gobiidae	6239	0	0	18182	30	80	0	0	0	0	0	0
Grammatidae	434	0	0	0	0	0	0	0	0	0	0	0
Haemulidae	1959	1395	160	379	752	823	457	300	70	20	0	0

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Holocentridae	253	441	50	0	0	0	20	0	0	0	0	0
Inermiidae	300	3444	0	0	0	0	0	0	0	0	0	0
Kyphosidae	463	733	160	0	0	0	0	0	0	0	0	0
Labridae	1749	659	96	254	568	580	252	180	80	0	0	0
Loliginidae	0	240	0	0	0	0	0	0	0	0	0	0
Lutjanidae	263	800	279	80	137	559	80	20	350	0	0	20
Mullidae	245	429	229	50	20	0	20	0	0	0	0	0
Pomacentridae	2145	414	20	618	325	123	110	0	0	0	0	0
Scaridae	741	252	196	494	753	979	333	20	173	80	0	0
Sciaenidae	532	176	40	60	0	0	60	0	0	0	0	0
Serranidae	855	107	208	297	72	40	93	0	0	0	0	0
Sphyraenidae	120	2100	180	0	0	40	0	20	40	0	0	100
Tetraodontidae	247	0	0	193	100	20	0	0	0	0	0	0

Table 3: The most significantly correlated environmental factors found to influence characteristics of the reef fish community using a multivariate pairwise correlation (Spearman's test).

Environmental factors	Fish community factors	P
Sponge cover	Reef fish biodiversity	0.05*
	Mangrove fish biodiversity	0.023*
	Trophic level	0.0003*
	Total biomass	0.050*
	Size class ≤11cm	0.001*
Distance reef-mangroves	Reef fish biodiversity	0.003*
	Mangrove fish biodiversity	0.001*
	Trophic level	0.011*
	% fish that live in medium	0.0001*

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	substrate complexity	
	% fish that live in low substrate complexity	0.047*
	Biomass ≤11cm	0.050*
	Size class ≤11cm	0.013*
	Size class ≤12.5-≥20 cm	0.046*
Seagrass cover %	Seagrass fish biodiversity	0.0009*
Seagrass sand cover %	% fish that live in low substrate complexity	0.016*
Recently killed corals	Biomass ≤11cm	0.033*
Calcifying algae	% fish that live in medium substrate complexity	0.030*
fDOM	Total biomass	0.050*

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