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

Janina Seemann[1*], Alexandra Yingst[2], Rick D. Stuart-Smith[3], Graham J. Edgar[3], Andrew H. Altieri[1]

[1]MarineGEO, Smithsonian Tropical Research Institute, Panamá, Republic of Panama

[2] University of Pittsburgh, Pittsburgh, Pennsylvania, United States

[3] Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia

Email: seemannja@gmail.com~~seemannj@si.edu~~

Abstract

Fish communities associated with coral reefs worldwide are threatened by habitat degradation and overexploitation. We assessed coral reefs, mangrove~~mangroves~~ fringes, and seagrass meadows on the Caribbean coast of Panama to explore the influences of habitat cover, ~~connectivity~~ proximity, and environmental characteristics in sustaining biomass, species richness and trophic structure of fish communities in a degraded tropical ecosystem. We found 94 % of all fish across all habitat types were of small body size (≤10 cm), with communities dominated by fishes that usually live in habitats of low complexity, such as Pomacentridae (damselfishes) and Gobiidae (gobies). Total fish biomass was very low, with small fishes from low trophic levels over-represented, and top predators under-represented, compared to coral reefs elsewhere in the Caribbean. For example, herbivorous and omnivorous fishes (trophic level 2 – 2.7) comprised 37 % of total fish biomass, and the small parrotfish *Scarus iseri* comprised 72 % of the parrotfish biomass. We~~For the reef-associated fish community, we~~ found evidence that non-coral biogenic habitats support reef-associated fish communities.~~provided a mechanism of resilience.~~ In particular, the abundance of sponges on a given reef and proximity of mangroves were found to be important positive ~~factors for the~~correlates of~~drivers of~~ reef fish species richness, biomass, abundance and trophic structure. Our study indicates that a diverse fish community can persist on degraded coral reefs, and that the availability and arrangement within the seascape of other habitat-forming organisms, including sponges and mangroves, is critical to the maintenance of functional processes in such ecosystems.

Introduction

Coral reef fishes are useful model communities for exploring drivers of species diversity at landscape and regional scales (Galzin et al. 1994; Fabricius et al. 2005; Knowlton et al. 2010; Wilson et al. 2010). They are sensitive to changes in habitat and anthropogenic impacts – a particular concern given that fishes play an important role in coral reef ecosystems, and declines of coral reef fishes threaten people's livelihoods and food security (Cesar 2000; Cesar et al. 2003; Bellwood et al. 2004; Paddack et al. 2009). A variety of human impacts are responsible for coastal degradation, including habitat destruction, eutrophication, and sedimentation (Hughes 1994; Jackson et al. 2001; Aronson et al. 2003). Climate change has additionally contributed to ecosystem decline through coral die-off from bleaching, hypoxia events and storms (~~Beukers and Jones 1998;~~ Wilson 2006; Alvarez-Filip et al. 2009; Wilson et al. 2010; Altieri et al. 2017). The consequences of these ~~processes~~ events are~~is~~ structural collapses and habitat homogenization in coral reefs, effects which have a variety of potential direct and indirect implications for ~~the~~ resident organisms ~~that reside there~~ (Bell and Galzin 1984; Jackson et al. 2001; Kuffner et al. 2007; Wilson et al. 2010; Alevizon and Porter 2015; Mora 2015).

Additional factors contributing to declining reef fish abundances are unsustainable fisheries and increasing demand for fish products for a growing human population (Hodgson 1999; Jackson et al. 2001; Zaneveld et al. 2016). The overexploitation and disproportionate targeting of large size classes and high trophic levels affects fish population structure, growth, and reproduction, and contributes to a trophic imbalance and shifts in trait composition in the reef fish community (Hixon~~Pauly~~ et al. 2014).~~1998; Mumby et al. 2006).~~ This, in turn has led to further changes in habitat structure, phase shifts from coral to algal communities, and decreasing ecosystem stability (Saila et al. 1993; Jennings and Lock 1996; White and Jentsch 2001).

Reef fish populations have also been negatively affected by the loss of coastal habitats~~,~~ ~~which~~that provide important ~~as~~ nurseries (Nagelkerken et al. 2000). 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). Seagrass meadows and mangrove forests have high primary and secondary productivity relative to unvegetated substrates, and support high diversity and abundances of reef fishes (Nagelkerken et al. 2000; Beck et al. 2001; Mumby et al. 2004). Many fish species on coral reefs therefore depend on the connectivity to, and integrity of, associated habitats.

Our study region, the Caribbean Sea, has experienced declining reef fish populations as a result of pollution, ecosystem degradation and unsustainable reef fisheries (Hughes 1994; Gardner et al. 2003; Bellwood et al. 2004; Paddack et al. 2009). These problems appear particularly prominent at our focal study area in Bocas del Toro on the Caribbean coast of Panama, where rapid human population growth connected with agriculture (banana industry) and tourism has accelerated the decline of water quality, and the physical destruction of reefs, and has increased the fishing pressure (Guzmán and Jiménez 1992; Collin 2005; D'Croz et al. 2005; Cramer 2013; Aronson et al. 2014; Seemann et al. 2014). Bocas del Toro encompasses a coastal coral reef-seagrass-mangrove system in a semi-enclosed lagoon. It is composed of six major islands and the mainland, which surrounds the Almirante Bay, and includes mangroves fringing the mainland and mangrove islands scattered across the bay (Collin 2005; Guzmán et al. 2005). Reefs are typically dominated by corals with a high stress tolerance, including *Porites furcata* in shallow (1-4 m) and *Agaricia* spp. (>3 m) in the deeper areas (Seemann 2013; Aronson et al. 2014; Seemann et al. 2014). Associated seagrass meadows are dominated by *Thalassia testudinum* (turtlegrass). Mangrove fringes are comprised of *Rhizophora mangle* (red mangrove). Several rivers, creeks and oceanic inlets discharge sediments and nutrients into the bay (Beulig 1999; Collin 2005). Bleaching and low oxygen events occur regularly due to lagoonal characteristics including retention of warm water and depletion of oxygen (Kaufmann and Thompson 2005; Seemann et al. 2014; Altieri et al. 2017). Bocas del Toro reefs potentially represent a model system for improving predictions relevant throughout the region due to their exposure to common stressors, such as high terrigenous run off, nutrient levels, and overfishing, that are afflicting other coral reefs in the Caribbean (Riegl et al. 2009; Sammarco and Strychar 2009; Leinfelder et al. 2012; Aronson et al. 2014).

This study aims to characterize the ecosystem attributes that facilitate the maintenance of essential functions, biodiversity and biomass of coral reef fish communities in a degraded ecosystem. Specifically, we (1) quantify the fish community at 67 sites in 5 bioregions of the Caribbean to assess the status of our focal study system in Bocas del Toro along a gradient of ecosystem degradation and over-fishing, (2) examine the effects of proximity of mangroves and seagrass for fish communities on coral reefs, and (3) identify characteristics of coral reef habitat that are positively related to biomass, abundance and structure of the fish community. Addressing these objectives contributes to a better understanding of how landscape-scale features underlie the resilience of degraded coastal habitats.

Methods

Study system

To place results within the wider regional context, we conducted fish surveys at reefs with different fishery management restrictions in different Caribbean ecoregions.
In our focal study areas of Bocas del Toro on the Caribbean coast of Panama (Fig. 1), we also conducted comprehensive surveys of fish communities, benthic surveys, and water quality measurements in adjacent seagrass and mangrove fringe areas. All data from Bocas del Toro were collected from May to July 2015. Data for the other Caribbean regions were collected from 2012 to 2015.

Research was conducted under a Scientific Permit from the Ministry of the Environment Panama (MiAmbiente) and Autoridad de los Recursos Acuáticos de Panamá (ARAP) with the Number: SE/APO-1-15 & 10b.

Caribbean Data Set

Fish surveys. We conducted visual fish surveys using the Reef Life Survey (RLS) method 1 protocol (Edgar and Stuart-Smith 2014) at reefs at 67 sites in the following five ecoregions (Spalding et al. 2007): Southern Caribbean (14 sites, Bonaire), Southwestern Caribbean (31 sites, Bocas del Toro, Kuna Yala, Archipelago of San Andres), Greater Antilles (1 site, Grand Cayman), Floridian (17 sites, Florida Keys) and Bahamian (4 sites, Turks and Caicos Islands). Surveys involved underwater visual censuses by scuba divers at reef sites (each with 2-6 replicate transects) in depths of 1 to 35 m. Divers counted and assigned all fish species observed within binned size-classes along a 50 x 5 m belt transect (250 m^2). All fishes sighted on each transect were recorded on a waterproof datasheet as the diver swam along the transect at approximately 2 m min^{-1}. We identified fish species to the highest taxonomic resolution possible, and estimated body length for each individual. The order of priority for recording accurately was to first ensure all species observed along transects were included, then individuals of larger or rare species were accurately counted, then estimates made of abundances of common species. If an individual could not be identified underwater, a photograph was taken for later identification. Abundance, size and species identity were used to estimate biomass in kg

ha^{-1} using conversion factors provided by Fishbase (www.fishbase.com), as described by Edgar and Stuart-Smith (2014).

Bocas del Toro Data Set

Fish surveys. The RLS method employed on coral reefs in five ecoregions was also applied in seagrass and mangrove habitats located within 250 m of reef sites in Bocas del Toro. Seagrass sites ranged in depth from 1 m to 4 m, whereas mangrove fringe root systems had maximal depth of 2 m. Mangrove surveys were conducted amongst the mangroves prop roots below the upper intertidal fringe with counts and size estimates made for all fishes in a 5 m wide belt within the mangrove root system. Two 50 m transects were laid end-to-end along the mangrove fringe given that side-by-side replicate transects typical of the RLS protocol could not be applied within mangrove root habitats.

Habitat assessment. We conducted benthic surveys to characterize coral reef and seagrass bed habitats. Reef and seagrass benthos were analyzed with 20 photo quadrats (0.5 m^2), which were taken every 2.5 m along the 50 m long transects at each 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 and categorized. Substratum categories for analyses were: healthy hard coral, bleached hard coral, recently-dead coral, anemones, non-calcifying corals (including hexacorals and octocorals), sponges, sessile worms (tube worms, mostly polychaetes), zoanthids, rubble, sand, rock, calcifying algae, seagrass and macroalgae. If sessile organisms were too small for identification or obscured by dark shadows, then they were excluded from the dataset.

In addition, the distance between reef sites surveyed and nearest mangrove was measured using GPS coordinates (table 1).

Water quality measurements. 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 algae 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 fish surveys, and constrained to the mid-day hours between, hence measurements were subject to the daily variability of weather conditions or tidal cycles.

Data analyses.

The Caribbean reef fish data set was used to characterize the fish community in relation to the protection status of the sites. All 67 sites from the five different ecoregions were individually classed by management type using the criteria of Edgar et al. (2014): NTZ (no take zones, n=27), RZ (restricted zones that allow local fishing within an MPA, n=19) and OZ (open zones where fishing is unrestricted, n=12). These data were compared to data from Bocas del Toro (OZ, n=9). Replicated surveys from each site were averaged.

Data from the fish surveys were used to calculate fish community metrics, including total abundance (density), abundance of major fish families within size bins (≤10 cm; >10 – 20 cm; >20 cm), total biomass, biomass of fishes ≤10 cm, and total species richness. We also calculated the mean trophic level as an abundance weighted mean 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 total log abundance of all fishes on the transect. The classification of the trophic level (2 – 5) for each species was based on feeding strategy: 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) (classification and values obtained from Fishbase; www.fishbase.org). We also compared preferred substrate types and resilience factors (values obtained from Fishbase) of the fish species, the latter estimated from population doubling time (low, medium, high). Fish community metrics were averaged ~~across sites~~ within~~ a~~ sites and compared among regions for significant differences using one-way ANOVA or a Student's *t-test*.

For the Bocas del Toro dataset only, we assessed whether mangroves and seagrasses provided juvenile or alternative habitat to coral reefs by comparing the abundance (log transformed) and composition of fishes in the different habitat types. We assumed that higher abundances of fishes amongst mangroves and seagrasses compared to reefs, and high species similarity, indicates ~~high migration and exchange rates, indicates~~ higher likelihood and magnitude of migration and exchange rates. We excluded small-bodied species (maximum total length ≤12.5 cm), which are presumably non-migratory fish species (Dahlgren et al. 2006), such as *Apogon townsendi* (belted cardinalfish), *Canthigaster rostrata* (caribbean sharpnose-puffer) and *Coryphopterus* spp. A principal component analysis (PCA) on correlations (fish abundance log transformed, only fish >12.5 cm) was used to compare differences and to define distances in the fish communities between reefs at different distances to mangroves and ~~mangroves and~~ seagrass.

We also tested for correlations between environmental factors and the reef fish community metrics across all sites. Environmental factors included reef cover, cover of the seagrass benthos, distance to mangroves and water quality parameters. Fish metrics included species richness~~biodiversity~~, fish traits, biomass, size structure and the abundances of individual fish species. Data were characterized using a scatterplot matrix (see appendix) and nonparametric Spearman's tests 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 (Edgar et al. 2014). All statistical analyses were conducted using JMP Software 13.01.

Results

Characteristics of the fish community.

We recorded a total of 77 fish species across all habitats in Bocas del Toro, of which 61 species were found on coral reefs. The average mean richness per transect was 29 ± 7

(SD) species. This value was low compared to our other Caribbean survey sites which had a mean richness per transect of 52 ± 4 species (with a cumulative total of 196 species recorded in the whole Caribbean) (Stuart-Smith et al. 2013; Edgar and Stuart-Smith 2014). Fish biomass on Bocas del Toro reefs (71 ± 63 kg ha^{-1}) was also lower than on other Caribbean reefs, in both no-take zones and MPAs with restricted fishing (ANOVA, P=0.02 and 0.001, respectively), although the difference was not significantly lower for open zones (P>0.05) (Fig. 2a). Moreover, the range of total observed fish biomass in Bocas del Toro (30 – 1350 kg ha^{-1}) represents the lowest numbers found amongst fish surveys conducted in the Caribbean, which were 140 - 5930 kg ha^{-1} elsewhere.

The biomass of herbivorous, omnivorous and detrivorous fishes in Bocas del Toro (trophic level 2 – 2.7) was 37 % of the total biomass and 76 % of all individual fishes counted (Fig. 2b). Herbivores alone comprised 27 % ± 3.5 % (SD) of biomass versus 10 % ± 4 % across the wider Caribbean. Pomacentridae (damselfishes) and Scarinae (parrotfishes) were the predominant taxa in terms of biomass. *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 in Bocas del Toro were *Carangoides ruber* (bar jack), *Cephalopholis cruentata* (graysby), *Hyplopectrus nigricans* (black hamlet) and *Scomberomorus regalis* (cero). There was a trend for fish communities in Bocas del Toro to exhibit a greater proportion of total biomass comprised of herbivores, omnivores and detrivores (trophic level: 2 – 2.7), and a lower proportion comprised of high-level carnivores (trophic level: 4 – 4.5), relative to other Caribbean reefs, although the difference was not significantly different for either group (Fig. 2b).

A total of 94 % of all fishes observed across all habitat types (reef, seagrass, mangrove) in Bocas del Toro were in the smallest size class (≤10 cm length). Fishes ≤10 cm represented 59 % of the total biomass within the reefs. The abundance of fishes within the smallest size class (≤10 cm) was significantly higher in Bocas del Toro than other Caribbean reefs (ANOVA, $P<0.0001$), whereas the abundances of medium- (>10 – 20 cm) and large- (≥20 cm) sized fishes were significantly lower (ANOVA, $P<0.0001$) (Fig. 2c). This pattern was also evident when comparing reef fish families in Bocas del Toro with other Caribbean reefs (table 2).

Relationships between environmental factors and fish community composition

Some environmental parameter and habitat factors were associated with reef fish community metrics in Bocas del Toro. Multiple environmental factors were not independent, as sponge cover was negatively correlated with the distance to mangroves and also positively to chl *a* ($R^2=0.60$ and $R^2=0.70$, respectively, $P<0.01$). The other water parameters were not found to correlate with any fish community or species metrics. Sponge cover was the strongest positive correlate among all environmental parameters for species richness ($R^2=0.5$, $P<0.01$), small fish ≤10 cm biomass ($R^2=0.85$, $P<0.01$), and trophic level of the fish community ($R^2=0.89$, $P<0.01$). The abundance of *Abudefduf saxatilis* (sergeant major) was significantly correlated with sponge cover ($R^2=0.62$, p=0.0027). Survey sites characterized by high sponge cover and low distance to mangroves were characterized by fishes such as *Abudefduf saxatilis* (sergeant major), *Hypoplectrus nigricans* (black hamlet), *Coryphopterus personatus* (masked goby) and *Coryphopterus glaucofraenum* (bridled goby). *Scarus iseri* (striped parrotfish), *Stegastes partitus* (bicolor damselfish) and *Cephalopholis cruentatus* (graysby) had a positive association with recently dead corals, however, the cover of dead corals was negatively correlated with the abundance of most fish species.

Fish species richness on a given reef was positively correlated with ~~fish~~ richness values in nearby mangroves (R^2=0.76, P<0.05). The three reef sites with low sponge cover and without mangroves in close proximity (Salt Creek, Popa, Hospital Point) showed lower biomass, abundances and species richness of fishes (table 1, Fig.3 and Fig. 4). The site without either mangroves or seagrass nearby (Hospital Point) showed the lowest species richness.

Also, distance to mangroves was identified as a factor to influence reef fish communities (Fig. 5), suggesting that mangrove distance has a strong influence on reef community types, likely by mangroves functioning as effective nursery grounds and as alternative complex habitats. The proportion of carnivorous fishes was significantly higher at the sites closer to the mangroves than those sites that were further away (ANOVA, P<0.01, Fig. 4). However, a more detailed look at the carnivorous fishes revealed that the sites at an intermediate distance from mangroves (STRI, Juan Point, Coral Cay) possessed a

Formatted: Font: Not Italic

Formatted: Font: Not Italic

significantly higher proportion of top-level carnivores than sites that were closer or further away (Fig. 4, ANOVA, P<0.01).

The highest abundances of all fish observed were recorded for families Pomacentridae (damselfishes) and Gobiidae (gobies) (table 2). However, Gobiidae were ~~only~~ abundant only at sites close to mangroves. *Coryphopterus personatus* (masked goby) dominated these sites, with abundances up to 13 individuals m^{-2}. RLS surveys conducted elsewhere in the Caribbean (e.g. San Andres Archipelago, 350 km distant) revealed much lower densities for the same species (0.2 individuals m^{-2}).

Generally, fishes with life cycles closely associated with hard corals (Lewis 1997), such as Pomacanthidae (angelfishes), were present in very low numbers on the reefs of Bocas del Toro (<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). Many fish species ~~of low or very low resilience factors~~, 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~~ observed only on reefs with mangroves in close proximity (≤ 250 m distance).

Discussion

Our surveys revealed that the fish fauna in Bocas del Toro is depauperate in species richness and biomass by Caribbean standards. We found evidence that the fish community is representative of a degraded and overexploited ecosystem, characterized by numerical dominance of fishes that are small bodied and also typical of habitats of low complexity, such as Pomacentridae and Gobiidae, with few representatives of fish families that achieve body sizes targeted by fisheries or that are commonly associated with high-relief coral reefs. Nevertheless, sponge cover and proximity to mangroves were found to be positively correlated with fish species richness, biomass, abundance and trophic level. This pattern suggests that sponges as habitat-forming reef organisms, and mangroves as nursery grounds and alternative habitats, continue to provide critical habitats for the reef fish communities in a degraded ecosystem, and may be an important mechanism of resilience where they are able to therefore counteract some effects of reef degradationsdegradation.

Some fishes appeared to be an indicator species for the overall trends observed at our study site. One example is the goby *Coryphopterus personatus*, which forms schools that hover in a vulnerable position above the bottom in extremely high abundances (65-fold higher abundances than in the San Andres Archipelago). Moreover, fish surveys in our Bocas del Toro study area in 2002 revealed densities an order of magnitude lower at 1.2 individuals m^{-2} (Dominici-Arosemena and Wolff 2005). We suggest that this species goby represents is an indicator species for overfished reefs that benefits from a loss of predatory fishes that historically ~~kept~~ limited their densities. Another ~~example of an~~ indicator species is *Scarus iseri*, which is ~~perhaps an important habitat interactor,~~ecologically important given its role as the predominant herbivorous fish in Bocas del Toro (Kuempel and Altieri 2017). ~~It~~ This species likely plays an important role supporting the growth of sponges and corals by cropping competing macroalgae. Third, *Abudefduf saxatilis* was identified as an indicator for sponge cover, which in turn is a factor positively correlated to fish richness, biomass, abundance and relatively high mean community trophic levels.

A degraded reef fish community in Bocas del Toro is evidenced by low total biomass, under-representation of biomass at high trophic levels, and high abundance of small fishes,~~;~~ all classic symptoms of over-fishing (Pauly et al. 1998; Myers and Worm 2003). Moreover, the range of total observed fish biomass represents the lowest numbers found amongst fish surveys conducted in the Caribbean. High level carnivores and large fishes are depleted in intense fisheries (Cinner and McClanahan 2006; Wilson et al. 2010), causing a skewing of the trophic food web and community size structures. As described ~~in~~ by Wilson et al. (2010), the loss of individuals within the largest size classes, which have the highest per capita reproductive output and produce the majority of juveniles, impacts the recruitment of small size classes ~~containing~~ of juveniles ~~in the~~ reef fish ~~population~~. Accordingly, we observed that small Haemulidae were rare on Bocas del Toro reefs. Exploitation thus appears to have contributed substantially to the distorted fish community patterns observed at Bocas del Toro (Guzmán et al. 2005; Cramer 2013).

Another plausible hypothesis for the low total fish biomass and trophic shifts within the fish community in Bocas del Toro relative to other Caribbean sites is the loss of hard corals (Turner et al. 1999; Wilson et al. 2010). This in turn results in the loss of shelter and feeding grounds (Turner et al. 1999; Alevizon and Porter 2015). This hypothesis was supported by significant negative correlations between the proportions of recently-dead corals and the biomass of fishes, as well as the finding that fish species that are known to associate with hard corals or hard substrate were rare. Instead, fishes known to live on habitats of low complexity (particularly Pomacentridae and Gobiidae) and grazers (particularly Scaridae and Pomacentridae) occurred in very high abundances (Booth and Baretta 1994; Bruggemann et al. 1994).

Herbivores, detritivores and omnivores were overrepresented in the Bocas del Toro fish community compared to elsewhere in the Caribbean. Herbivorous species alone comprised nearly a third of the total fish biomass, which could be explained by a decreased number of predators in the system. Even though most herbivorous fishes were in the smallest size category (≤10 cm), this group has the potential to control the growth of macroalgae and prevent algal phase shifts, particularly in combination with invertebrate herbivores, such as sea urchins, which are abundant in this system (Kuempel and Altieri 2017). However, if the reduction of live coral cover continues, herbivorous fishes may reach their limits for grazing control (Williams and Polunin 2001; Williams et al. 2001). Also, the lack of redundant species within the herbivore functional group is likely to result in low resilience, since a system with a single dominant herbivorous species *Scarus iseri* (72%) is vulnerable to stressors affecting that species (Hughes 1994; White and Jentsch 2001). The reason for the dominance of one herbivore species ~~is probably~~may be attributable to the small body size of *S.iseri*, which matures at ~ 65 mm. It is therefore not a targeted fishery species, and escapes most fishing pressure (Kuempel and Altieri 2017).

Sponges cover up to 20% of substrata, and thus provide considerable physical structure on the Bocas del Toro reefs (Diaz and Rützler 2001; Loh and Pawlik 2014; Loh et al. 2015). In the absence of high cover of hard corals, sponges likely play an important role in supporting richness, biomass and expanded trophic levels of the depauperate fish community in our study system. Results furthermore suggest a positive effect and increased abundance of reef fishes with increased sponge cover. Sponges are major determinants of the rugosity and height of the reef (Diaz and Rützler 2001), thus could be an important driver for fish abundance and species richness in Bocas del Toro as in other Caribbean reef systems (Gratwicke and Speight 2005). Sponges also comprise an important food source for spongivorous reef fishes, such as some members of Pomacentridae and Scarinae (Sammarco et al. 1987; Dunlap and Pawlik 1996; Pawlik 1998; Souza et al. 2011). The pomacentrid *A. saxatilis* has been identified to have a functional dependency on sponges, through either shelter or other aspects of habitat complexity that sponges provide (Gratwicke and Speight 2005).

Proximity to mangroves was another important positive factor associated with fish communities, as the biomass and species richness of fishes were greater on coral reefs in close proximity to mangroves. Mangroves are widely recognized for their functions of providing nursery grounds, 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 alternative habitats is an important factor maintaining diversity and biomass of the reef fish communities, and that this function remains particularly important in a system as degraded as Bocas del Toro. However, we did not find such evidence for seagrass meadows. The closer mangroves are located to reefs, the more effective is their role as nursery or alternative habitat. Lowest fish species richness~~biodiversity~~, biomass and trophic levels ~~was~~ were found on reefs without mangroves in close proximity, presumably because many reef fish species depend on interconnectivity between habitat types (Ley 2014).

Bocas del Toro arguably represents a good model system for reef fish communities that are associated with high levels of anthropogenic stress. Trends suggest that stressed systems are increasingly moving to low diversity, low mean trophic level, and a size distribution skewed to small body size (Pauly et al. 1998). To maintain reef fish communities, resource managers can ~~direct local fisheries and~~ take factors such as sponge cover and proximity~~connectivity~~ to other habitats, including mangroves, into consideration to prioritize protection efforts. Our results suggest that reef sponges and mangroves together can maintain physical structure, act as nurseries, and provide alternative habitats and there by compensate for particular functional losses during coral mortality events. Much more information is nevertheless needed on the role of habitat connectivity if fisheries management is to be optimized and diversity hotspots safeguarded through effective marine protected areas (Linton and Warner 2003; Unsworth et al. 2008).

Acknowledgements

We thank divers who helped with the fish surveys and fish identification or benthic surveys, especially Scott Jones, Zachary Foltz, Ross Whippo, Justin Campbell, Jan Vincente and Seamus Harrison. We thank the people from the Bocas Research Station team for logistical help and for assistance with all aspects of the work, particularly Plinio Gondola. This is contribution number 21~~X~~ from the Smithsonian's MarineGEO network.

References

Alevizon W, Porter J (2015) Coral loss and fish guild stability on a Caribbean coral reef: 1974–2000. Environmental Biology of Fishes 98:1035-1045

Altieri AH, Harrison SB, Seemann J, Collin R, Diaz RJ, Knowlton N (2017) Tropical dead zones and mass mortalities on coral reefs. Proceedings of the National Academy of Sciences

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society of London Series B-Biological Sciences 276:3019-3025

Aronson RB, Hilbun NL, Bianchi TS, Filley TR, Mckee BA (2014) Land use, water quality, and the history of coral assemblages at Bocas del Toro, Panamá. Marine Ecology Progress Series 504:159-170

Aronson RB, Bruno JF, Precht WF, Glynn PW, Harvell CD, Kaufman L, Rogers CS, Shinn EA, Valentine JF (2003) Causes of coral reef degradation. Science 302:1502-1504

Beck MW, Heck Jr KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. Bioscience 51:633-641

Bell J, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. Marine Ecology Progress Series 15:265-274
Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827
Beukers JS, Jones GP (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114:50-59
Beulig A (1999) Relative influence of terrigenous vs. reef carbonate silt on turbidity and coral distribution at Bocas del Toro, Panama. International Conference on Scientific Aspects of Coral Reef Assessment, Monitoring and Restoration
Booth DJ, Beretta GA (1994) Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. Coral Reefs 13:81-89
Bruggemann JH, Kuyper MWM, Breeman AM (1994) Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). Marine Ecology Progress Series 112:51-66
Cesar H, Burke L, Pet-Soede L (2003) The economics of worldwide coral reef degradation. Cesar environmental economics consulting (CEEC)
Cesar HS (2000) Coral reefs: their functions, threats and economic value. Collected essays on the economics of coral reefs:14-39
Cinner JE, McClanahan TR (2006) Socioeconomic factors that lead to overfishing in small-scale coral reef fisheries of Papua New Guinea. Environmental Conservation 33:73-80
Collin R (2005) Ecological monitoring and biodiversity surveys at the Smithsonian Tropical Research Institute's Bocas del Toro Research Station. Caribbean Journal of Science 41:367-373
Cramer KL (2013) History of Human Occupation and Environmental Change in Western and Central Caribbean Panama. Bulletin of Marine Science 89:955-982
D'Croz L, Del Rosario JB, Gondola P (2005) The effect of fresh water runoff on the distribution of dissolved inorganic nutrients and plankton in the Bocas del Toro Archipelago, Caribbean Panama. Caribbean Journal of Science 41:414-429
Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE (2006) Marine nurseries and effective juvenile habitats concepts and applications. Marine Ecology Progress Series 312:291-295
Diaz MC, Rützler K (2001) Sponges: An essential component of Caribbean coral reefs. Bulletin of Marine Science 69:535-546
Dominici-Arosemena A, Wolff M (2005) Reef fish community structure in Bocas del Toro (Caribbean, Panama): gradients in habitat complexity and exposure. Caribbean Journal of Science 41:613-637
Dunlap M, Pawlik JR (1996) Video-monitored predation by Caribbean reef fishes on an array of mangrove and reef sponges. Marine Biology 126:117-123
Fabricius K, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Marine Pollution Bulletin 51:384-398
Galzin R, Planes S, Dufour V, Salvat B (1994) Variation in diversity of coral reef fish between French Polynesian atolls. Coral Reefs 13:175-180
Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958-960
Granek EF, Compton JE, Phillips DL (2009) Mangrove-Exported Nutrient Incorporation by Sessile Coral Reef Invertebrates. Ecosystems 12:462-472
Gratwicke B, Speight M (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66:650-667
Guzmán HM, Jiménez CE (1992) Contamination of coral reefs by heavy metals along the Caribbean coast of Central America (Costa Rica and Panama). Marine Pollution Bulletin 24:554-561

Guzmán HM, Barnes PAG, Lovelock CE, Feller IC (2005) A site description of the CARICOMP mangrove, seagrass and coral reef sites in Bocas del Toro, Panama Caribbean Journal of Science 41:430-440

Hixon MA, Johnson DW, Sogard SM (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science 71:2171-2185

Hodgson G (1999) A global assessment of human effects on coral reefs. Marine Pollution Bulletin 38:345-355

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science 293:629-637

Jennings S, Lock JM (1996) Population and ecosystem effects of reef fishing. In: Polunin NVC, Roberts CM (eds) Reef Fisheries. Springer Netherlands, Dordrecht, pp193-218

Kaufmann KW, Thompson RC (2005) Water temperature variation and the meteorological and hydrographic environment of Bocas del Toro, Panama. Caribbean Journal of Science 41:392-413

Knowlton N, Brainard RE, Fisher R, Moews M, Plaisance L, Caley MJ (2010) Coral reef biodiversity. Life in the World's Oceans: Diversity Distribution and Abundance:65-74

Kuempel CD, Altieri AH (2017) The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. Scientific Reports 7:39670

Kuffner IB, Brock JC, Grober-Dunsmore R, Bonito VE, Hickey TD, Wright CW (2007) Relationships Between Reef Fish Communities and Remotely Sensed Rugosity Measurements in Biscayne National Park, Florida, USA. Environmental Biology of Fishes 78:71-82

Laegdsgaard P, Johnson C (2001) Why do juvenile fish utilise mangrove habitats? Journal of experimental marine biology and ecology 257:229-253

Lee S (1995) Mangrove outwelling: a review. Hydrobiologia 295:203-212

Leinfelder RR, Seemann J, Heiss GA, Struck U (2012) Could 'ecosystem atavisms' help reefs to adapt to the Anthropocene? Proceedings of the 12th International Coral Reef Symposium ICRS2012_2B_2:5

Ley JA (2014) Mangrove connectivity helps sustain coral reef fisheries under global climate change. Interrelationships Between Corals and Fisheries:171

Linton DM, Warner GF (2003) Biological indicators in the Caribbean coastal zone and their role in integrated coastal management. Ocean & Coastal Management 46:261-276

Loh T-L, Pawlik JR (2014) Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. Proceedings of the National Academy of Sciences 111:4151-4156

Loh T-L, McMurray SE, Henkel TP, Vicente J, Pawlik JR (2015) Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. PeerJ 3:e901

Mora C (2015) Ecology of Fishes on Coral Reefs. Cambridge University Press

Mumby PJ, Edwards AJ, Arias-González JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427:533-536

~~Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. science 311:98-101~~

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280-283

Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, Van't Hof T, den Hartog C (2000) Importance of Mangroves, Seagrass Beds and the Shallow Coral Reef as a Nursery for Important Coral Reef Fishes, Using a Visual Census Technique. Estuarine, Coastal and Shelf Science 51:31-44

Nagelkerken I, Roberts C, Van Der Velde G, Dorenbosch M, Van Riel M, De La Moriniere EC, Nienhuis P (2002) How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Marine ecology progress series 244:299-305

Paddack MJ, Reynolds JD, Aguilar C, Appeldoorn RS, Beets J, Burkett EW, Chittaro PM, Clarke K, Esteves R, Fonseca AC (2009) Recent region-wide declines in Caribbean reef fish abundance. Current Biology 19:590-595

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. Science 279:860-863

Pawlik JR (1998) Coral reef sponges: Do predatory fishes affect their distribution? Limnology and Oceanography 43:1396-1399

Riegl B, Purkis SJ, Keck J, Rowlands GP (2009) Monitored and modeled coral population dynamics and the refuge concept. Marine Pollution Bulletin 58:24-38

Saila S, Kocic VL, McManus J (1993) Modelling the effects of destructive fishing practices on tropical coral reefs. Marine Ecology Progress Series 94:51-60

Sammarco PW, Strychar KB (2009) Effects of Climate Change/Global Warming on Coral Reefs: Adaptation/Exaptation in Corals, Evolution in Zooxanthellae, and Biogeographic Shifts. Environmental Bioindicators 4:9 - 45

Sammarco PW, Risk MJ, Rose C (1987) Effects of grazing and damselfish territoriality on internal bioerosion of dead corals : indirect effects. Journal of Experimental Marine Biology and Ecology 112:185-199

Seemann J (2013) The use of 13C and 15N isotope labeling techniques to assess heterotrophy of corals. Journal of Experimental Marine Biology and Ecology 442:88-95

Seemann J, Gonzalez CT, Carballo-Bolaños R, Berry K, Heiss GA, Struck U, Leinfelder RR (2014) Assessing the ecological effects of human impacts on coral reefs in Bocas del Toro, Panama. Environmental Monitoring and Assessment 186:1747-1763

Serafy JE, Shideler GS, Araújo RJ, Nagelkerken I (2015) Mangroves Enhance Reef Fish Abundance at the Caribbean Regional Scale. PloS one 10:e0142022

Souza A, Ilarri M, Rosa I (2011) Habitat use, feeding and territorial behavior of a Brazilian endemic damselfish Stegastes rocasensis (Actinopterygii: Pomacentridae). Environmental Biology of Fishes 91:133-144

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57:573-583

Turner SJ, Thrush SF, Hewitt JE, Cummings VJ, Funnell G (1999) Fishing impacts and the degradation or loss of habitat structure. Fisheries Management and Ecology 6:401-420

Unsworth RK, Salinas De Leon P, Garrard SL, Jompa J, Smith DJ, Bell JJ (2008) High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. MARINE ECOLOGY-PROGRESS SERIES- 353:213

White PS, Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics Progress in botany. Springer, pp399-450

Williams I, Polunin N (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral reefs 19:358-366

Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. Marine Ecology Progress Series 222:187-196

Wilson SK (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global change biology 12:2220-2234

Wilson SK, Fisher R, Pratchett MS, Graham NAJ, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC (2010) Habitat degradation and fishing effects on the size structure of coral reef fish communities. Ecological Applications 20:442-451

Zaneveld JR, Burkepile DE, Shantz AA, Pritchard CE, McMinds R, Payet JP, Welsh R, Correa AMS, Lemoine NP, Rosales S, Fuchs C, Maynard JA, Thurber RV (2016) Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nature Communications 7:11833