

**FISH ASSEMBLAGES OF CARIBBEAN CORAL REEFS:  
EFFECTS OF OVERFISHING ON CORAL COMMUNITIES UNDER CLIMATE  
CHANGE**

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## **ABSTRACT**

Abel Valdivia-Acosta: Fish assemblages of Caribbean coral reefs:  
Effects of overfishing on coral communities under climate change  
(Under the direction of John Bruno)

Coral reefs are threatened worldwide due to local stressors such as overfishing, pollution, and diseases outbreaks, as well as global impacts such as ocean warming. The persistence of this ecosystem will depend, in part, on addressing local impacts since humanity is failing to control climate change. However, we need a better understanding of how protection from local stressors decreases the susceptibility of reef corals to the effects of climate change across large-spatial scales. My dissertation research evaluates the effects of overfishing on coral reefs under local and global impacts to determine changes in ecological processes across geographical scales. First, as large predatory reef fishes have drastically declined due to fishing, I reconstructed natural baselines of predatory reef fish biomass in the absence of human activities accounting for environmental variability across Caribbean reefs. I found that baselines were variable and site specific; but that contemporary predatory fish biomass was 80-95% lower than the potential carrying capacity of most reef areas, even within marine reserves. Second, I examined the effect of current native predatory reef fishes on controlling the invasion of Pacific lionfish across the Caribbean. Native predators and lionfish abundance were not related, even when predatory capacity was relatively high within certain marine reserves. Third, as herbivorous fishes may facilitate coral recovery after warming events by controlling competitive macroalgae, I evaluated whether major benthic groups, such as hard corals, crustose coralline algae, and macroalgae, were associated with these fish assemblages across Caribbean and Pacific reefs. Although,

macroalgae abundance was negatively related to herbivorous fishes across geographical regions, contemporary coral cover showed no association with herbivores abundance after a recent history of thermal stress. Finally, I analyzed the relationship between ~30 years of thermal stress anomalies and coral assemblages in the Caribbean and suggest that recent warming has partially promoted a shift in coral-community composition across the region that compromise reef functionality. My dissertation research highlights the complex interactions among functional groups in coral reefs, local stressors, and environmental variability across geographical scales, and provides novel insights to reevaluate conservation strategies for this ecosystem in a rapidly changing world.

To my wife and love of my life, I couldn't have done this without you.  
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## CHAPTER 1

### Reconstructing baselines for Caribbean predatory reef fishes<sup>1</sup>

#### Abstract

The natural, pre-human, abundance of most large predators is unknown due to the lack of historical data and the poor understanding of the natural factors that control their populations. We assessed the relationship between the biomass of predatory reef fishes and several anthropogenic and environmental variables to (1) attribute among site variability in predator abundance to both human impacts and natural factors, and (2) estimate historical baselines of fish predator biomass in the absence of humans. We hypothesized that predatory fish abundance declines with human influence but is also strongly influenced by natural environmental variability. We assessed the biomass structure of reef fishes at 39 sites over three years across the greater Caribbean. Using generalized linear mixed effect models, we examined the relationships between the biomass of predatory reef fishes and a comprehensive set of 29 anthropogenic, physical, spatial, biotic, and management-related covariates. We used the best explanatory models to predict the biomass of fish predators in the absence of humans. Predatory reef fish biomass was higher in marine reserves but strongly negatively related to human impacts, especially coastal development. Over 50% of the variability in predator biomass, however, was also explained by non-human factors including reef complexity, ocean productivity, and prey

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<sup>1</sup> A version of this chapter is in review in *ECOLOGY* as Valdivia, A., C.E. Cox., J.F. Bruno. Reconstructing baselines for Caribbean predatory reef fishes

abundance. Comparing site-specific predicted values to field observations suggests predatory reef fish biomass has declined by 80-95% in most sites, even within most marine reserves. Bottom-up forces are critical (yet often overlooked) drivers of reef fish predators across strong gradients of human exploitation. This suggests that we could underestimate historical biomass at sites that provide ideal conditions for predators or greatly overestimate that of seemingly predator-depleted sites that may have never supported large predator populations due to suboptimal environmental conditions. We highlight areas that are natural “hot spots” of predator biomass that can be targeted for strategic protection and restoration.

**Keywords:** baselines, predatory reef fish, fish biomass, human impacts, coastal development, marine reserves, overfishing, habitat complexity, trophic levels

## **Introduction**

Overharvesting and habitat degradation have caused the loss of countless large predator species from most of the world’s biomes (Jackson et al. 2001, Estes et al. 2011). For example, population levels of grey wolves in North America (Ripple et al. 2001), tigers in India’s forests (Jhala et al. 2008), and sharks in the Northwest Atlantic (Myers et al. 2007) have declined to <20% of their historical values. Their widespread depletion has indirectly modified (or eliminated) species interactions, redistributed the flow of energy, altered ecosystem functioning and services (Terborgh and Estes 2010, Estes et al. 2011), and even caused trophic cascades resulting in the loss of entire fisheries (Myers et al. 2007). Historical analysis suggest that extensive reduction of predators often preceded their population evaluations, making it difficult to establish natural baselines (Jackson et al. 2001, Pandolfi et al. 2003, Lotze and Worm 2009)

Restoring predator populations and communities requires, at minimum, ending overharvesting and the restoration of their habitats (Myers and Worm 2005). Additionally, knowledge of the natural state of predator assemblages – the baseline – gives managers reasonable science-based restoration goals to evaluate the efficacy of management. Baselines, however, vary with environmental context (Bruno et al 2013). Therefore, to assess the degree to which human activities have altered communities and to estimate local and regional baselines, we need a better understanding of the factors that control the structure and composition of unexploited communities. We know surprising little about the natural abundance and distribution of predator assemblages across landscapes and regions (Worm et al. 2005, Sinclair et al. 2010, Terborgh and Estes 2010, Estes et al. 2011). We tend to assume that predators used to be ubiquitous – present at all locations – (Jackson et al. 2001, Lotze and Worm 2009) but knowledge of natural spatial-temporal distribution and abundance is limited. Given their dependence on the presence of prey species (Sims et al. 2008, Sinclair et al. 2010) and disparate response to environmental variability (Friedlander et al. 2003, Richards et al. 2012, Nadon et al. 2012), natural predator populations were likely patchy in space and time.

Natural predator assemblages in heterogeneous environments are influenced by resource distribution and limitation (i.e., bottom-up regulation) (Terborgh and Estes 2010). For example, in the Serengeti ecosystem of East Africa, predator (e.g., canid and felid) abundance and composition respond positively to the biomass, accessibility, diversity and body size of their ungulate prey (Sinclair et al. 2010). Foraging patterns of several marine predators (e.g., sharks, tuna, and turtles) also respond to their prey accessibility and density distribution (Sims et al. 2008). Predator responses can also be influenced by other predators, competitors, temperature,



and habitat structural complexity (Worm et al. 2005, Hunsicker et al. 2011). Yet in exploited ecosystems, bottom-up forcing can be difficult to detect because predators are affected by pronounced geographic and temporal variations in top-down regulation by humans (i.e., hunting or fishing) that obscures any response of the community to environmental variability (Worm et al. 2005, Frank et al. 2007, Terborgh and Estes 2010).

Fishing alone has reduced the biomass of predatory fishes in pelagic ecosystems by as much as 90% (Myers and Worm 2003, Lotze and Worm 2009). Although overfishing is severe in many regions, quantifying its extent has proven challenging because we generally lack quantitative spatially replicated baseline data on the pre-exploited state of fish assemblages (Jackson et al. 2001). Furthermore, most regional to global scale evidence of extensive predatory fish depletion is based on fisheries-dependent data (i.e., derived from commercial catch or effort data) (e.g., Baum et al. 2003, Myers and Worm 2003, Baum and Myers 2004, Worm et al. 2005). But these data are biased towards commercial species and can be prone to misreporting, gear related changes, and differential effort distribution (Hampton et al. 2005). In contrast, assessments through fisheries-independent data (i.e., scientific surveys) provides standardized abundance, size, and life history information of target and non-target species (Ferretti et al. 2008, Lotze and Worm 2009, Stallings 2009, Ward-Paige et al. 2010). However, both type of data have collected decades to centuries after exploitation began and thus likely underestimates the real impacts of fishing (Lotze and Worm 2009). Historical records such as photographs, catch records, and logbooks hint at severe predator losses even before official records started in the mid-20th century (Jackson et al. 2001, McClenachan 2009, Lotze and Worm 2009). Yet, such information does little to help establish quantitative targets for modern fisheries management as

they generally cannot be translated into a metric such as biomass per unit area to estimate natural spatial variability in predator assemblages.

An alternative approach is to study spatial gradients of human impacts, using “quasi-pristine” areas with minimal disturbance, to evaluate exploitation effects on more disturbed areas (DeMartini et al. 2008, Sandin et al. 2008, Williams et al. 2011). These rare undisturbed sites should reflect pre-exploitation levels that can approximate historical baselines (Lotze and Worm 2009). Gradients of human disturbance, however, are imbedded in other physical-oceanographic gradients that may influence predator abundance. For example, in coral reefs of the central Pacific, sea surface temperature and primary productivity cause differences in reef shark abundances within regions under the same human impact levels (Nadon et al. 2012). In the western Pacific, fishing pressure can explain ~26-60% of the variability in diversity and biomass of large-bodied reef fish, while ~19-53% can be explained by factors including atoll position, temperature, depth, wave energy, distance to deep water, and topography complexity (Mellin et al. 2008, Richards et al. 2012). Thus, the assumption that all sites and regions have the potential, in the absence of fishing, to sustain fish communities similar to “quasi pristine” baseline sites (Sandin et al. 2008) may be unfounded. Instead, variation at local, landscape, and regional scales of the site characteristics and resource availability can be at least as influential as fishing. To gain insights into the original state of predatory fish populations we need to understand species responses to both anthropogenic stressors and environmental patterns that are often overlooked at regional scales.

The primary purpose of this study was to quantify how human impacts (e.g., fishing and other related activities) have altered predatory reef fish biomass by reconstructing site-specific

potential baselines at 39 reefs across the central-western Caribbean. First, we quantified reef fish community structure at each site over a three years period. Second, we determined the relationship between the biomass of predatory reef fishes (e.g., sharks, groupers, and snappers) and 29 anthropogenic, physical, biotic, and management-related variables known to influence fish abundance. We used generalized linear mixed effect models to identify the factors that best explained the variability of fish predator assemblages among sites. Third, we used these models to predict natural predatory reef fish biomass at each reef in the absence of humans (i.e., the estimated baseline). Finally, we compared the site-specific predicted baselines to observed values to calculate the degree of predator losses locally and regionally. Our results not only indicate severe depletion of predatory fish biomass on Caribbean reefs, but also suggest that natural predator abundance varies greatly among sites due to the influence of resource availability and abiotic factors like habitat heterogeneity. These findings have implications for reef management and expectations for predatory reef fish restoration.

## **Materials and Methods**

### ***Study sites***

Surveys were performed on slope and spur-and-groove fore-reefs 10-15m deep, usually dominated by the corals *Montastraea* and *Orbicella*, across 39 sites in The Bahamas, Cuba, Florida (USA), Mexico, and Belize (Fig. 1.1, Table S1.1). We selected sites to maximize the range of total fish biomass in each sub-region by including reefs inside and outside marine reserves (i.e., no-take zones where fishing is prohibited), except at Dry Tortugas where only a reserve site was surveyed. Four sites in Gardens of the Queen marine reserve in Cuba (Fig. 1.1,

Table S1.1) were chosen *a priori* because there were reputed to have relatively high predator biomass with fairly intact fish communities (Newman et al. 2006). To minimize seasonal variability, we conducted all surveys during the summer months of May to July, 2010-2012 (Table S1.1).

### ***Fish Abundance***

Underwater visual censuses, with methods modified from Lang et al. (2010), were used to characterize the fish assemblages. At each site we randomly placed six to eight belt transect sets parallel to the spur-and-groove habitat or along the reef-slope formation following constant isobaths. In each transect, we recorded fish species, number, and estimated body size. Fish total length (TL) was binned by 10 cm size intervals, except for individuals <10 cm TL, for which two 5 cm intervals were used. As a transect tape was positioned, a diver counted fish of medium size (5-40 cm TL) in a 30 x 2 m belt area, followed by a 15 x 1 m belt to estimate small fish <5 cm TL. A second diver counted fish > 40 cm TL within a 50 x 10 m belt to account for more mobile and large-bodied fish (e.g., sharks) (McCauley et al. 2012a). The two smaller transects were contained within the largest transect to create a transect set. Each transect set was surveyed in ~15 minutes, covered the entire visible water column, and were at least 10 m apart.

Biomass was calculated through the allometric length-weight conversion formula,  $W = aTL^b$ , where  $W$  is body mass in grams,  $TL$  is the total length of each fish in cm (mid-point of the 5 or 10 cm interval estimates), and the parameters  $a$  and  $b$  are species-specific selected from geographic areas close to our study region (Froese and Pauly 2013). When these parameters were unavailable, we used estimates for congeneric species of similar morphology and size (Table

S1.2). For all the analysis, we used fish biomass because it is often used as a comprehensive indicator of fish assemblages status across disturbance gradients (Newman et al. 2006).

Fish species were assigned to a functional group based on six trophic guilds: apex predators, piscivore-invertivores, invertivores, planktivores, omnivores, and herbivores following reported dietary information (Froese and Pauly 2013). For the purpose of this study, we considered “fish predators” apex predators and/or piscivore-invertivores because both feed on fish. That is, apex predators consume mostly fish and piscivore-invertivores feed on fish and invertebrates; invertivores only feed on invertebrates; omnivores consume marine plants and invertebrates; and herbivores only feed on marine plants (Table S1.2).

### *Covariates*

For each reef site, we gathered a data set of 29 anthropogenic, physical, biotic, and management-related variables that are known to explain variability of predatory fish abundance (for detailed justification see Table S1.3 & Appendix 1.1). The best explanatory variables were then used to predict baselines in the absence of humans (see data analysis section). Direct and accurate measures of anthropogenic impacts are scarce for the study sites. For example, fishing pressure could not be accurately estimated for each site because of the lack of information on fishing activities. Therefore, we assumed that several human population parameters were adequate indicators of anthropogenic impacts (e.g., harvesting intensity, pollution, sedimentation) as the number of people are positively correlated with fishing pressure (Newton et al. 2007, Stallings 2009, Ward-Paige et al. 2010, Williams et al. 2011, Nadon et al. 2012). As such, the actual mechanisms related to anthropogenic impacts will remain open to discussion.

Anthropogenic variables included: coastal development (electrical power), number of humans, and area of cultivated land (proxy of terrestrial runoff or pollution) and were measured within 50 km of each site. This radius of influence has been adequate in detecting human effects in the region (Mora 2008). Additionally, we measured number of humans and distance to the nearest population settlement per site (as a proxy for fish demand and distance traveled to markets) (Table S1.3, Appendix 1.1). Physical and spatial covariates included: average and minimum average of sea surface temperature (2002-2011), average oceanic net primary productivity (2002-2012), wave exposure, depth, reef structural complexity, reef area (within 5 and 10 km), distance to deep water, distance to reef breaks, and distance to mangrove (Table S1.3, Appendix 1.1). Biotic factors were mangrove perimeter (within 5 km and 10 km), coral cover, algae cover, gorgonian abundance, and biomass of lower trophic fish groups. Reef area and mangrove perimeter were calculated at multiple scales to determine the influence of landscape extend on fish predators (Table S1.3, Appendix 1.1). Management related variables included protection level (none; marine protected areas or MPAs; and no-take zones or NTZs), reserve size and age, and poaching levels (low or high) inside reserves (Table S1.3, Appendix 1.1). For detailed descriptions and measurements of each covariate refer to Appendix 1.1.

### ***Data Analysis***

To explore the variability of fish predator biomass in relation to strict protection (e.g., reserve and non-reserve) and country, we used a linear mixed-effect model in which fish biomass was predicted by those two factors, and grouped by sites. We analyzed differences between factors using Bonferroni-corrected pairwise comparisons. To analyze the covariates that

influence predatory fish biomass, we first evaluated collinearity among all explanatory variables using a Spearman's rank ( $r_s$ ) correlation matrix for all sites and for sites within marine reserve (Table S1.4). Several covariates were sufficiently correlated ( $-0.5 > r_s > +0.5$ ) to compromise interpretation when modeled together (Graham 2003). For example, reef area ( $r_s = 0.83$ ) and mangrove perimeter ( $r_s = 0.93$ ) were highly correlated within 5 and 10 km, as were the log values among most of the human-related variables ( $r_s > 0.5$ ) (see Table S1.4 for other correlations). Thus, we first ran generalized linear models with related covariates (e.g., human related) to examine the best supporting covariates using the weights of Akaike's Information Criterion corrected for small samples ( $AIC_c$ ) (Table S1.5). Improvement in fit was evaluated with analysis of deviance among models (Zuur et al. 2009).

We evaluated the effect of the selected set of variables on the biomass of predatory reef fish (apex predators, piscivore-invertivores, and total predators) with generalized linear mixed effect models (GLMMs, Zuur et al. 2009) fitted by maximum likelihood (Laplace approximation), in which reef sites, region, and year of survey were nested and coded as random effects, and the explanatory variables as fixed effects. The biomass of total predators and piscivore-invertivores was modeled with a Gaussian distribution, while apex predators with an inverse Gaussian error structure, both models with log link. All fish groups were  $\log(x+1)$  transformed to improve homogeneity of variance and model fit. Numerical covariates were standardized and centered (mean of zero and standard deviation of one) to aid in model comparisons. Meaningful interactions and quadratic terms were included in exploratory models.

We modeled separately those covariates that were correlated (Table S1.4), eliminating factors that did not improve model fit. We created two sets of global models: A) for all reef sites

considering protection level and B) for the subset of sites within marine reserves (Table 1.1). To verify the lack of multi-collinearity among covariates, we calculated the variance inflation factors (VIF) after fitting the models. We sequentially removed and modeled separately each covariate for which the VIF value was above 2 (Graham 2003).

The variables included in the best models were selected through a multi-model inference approach and model averaging based on  $AIC_c$  weights ( $\Delta AIC_c < 2$  where  $\Sigma AIC_c$  weights  $> 0.95$ ) (Burnham and Anderson 2002) (Table 1.1). For final models, a coefficient of determination (pseudo adjusted- $R^2$ ) based on likelihood-ratio test was calculated, which represented the “variance explained” by fixed factors. Finally, using the best explanatory models for total predatory fish, we predicted the expected biomass range in the absence of humans by setting human-related variables to zero and categorizing all sites as no-take zones (i.e., no fishing). Predicted means and 95% confidence intervals per site were obtained by bootstrapping (Appendix 1.2).

Homogeneous and normal distribution errors of final models were confirmed in the plot of residuals against fitted values and by using the normal scores of standardized residuals deviance, respectively (Zuur et al. 2009) (Fig. S1.1). Spline spatial correlograms were plotted to corroborate that the final model residuals were independent and not spatially autocorrelated (Zuur et al. 2009) (Fig. S1.2). All analyses were performed in R v.3.03 (R Core Team 2013) using the package *lme4* v.0.99-2 for GLMMs and *MuMIn* v.1.9.13 for model averaging.



## Results

### *Predatory fish biomass variability*

Among the 39 fore reef sites studied, the average total fish biomass per site (mean  $\pm$  standard error) ranged from  $\sim 58 \pm 8 \text{ g m}^{-2}$  at Mexico Rocks (MR) in Belize to  $\sim 527 \pm 148 \text{ g m}^{-2}$  at Cueva Pulpo (CF) inside the Gardens of the Queen marine reserve in Cuba (Fig. 1.2). Mean total fish biomass was less than  $200 \text{ g m}^{-2}$  on  $\sim 80\%$  of unprotected reefs compared with over  $300 \text{ g m}^{-2}$  on selected marine reserves (Fig. 1.2; Fig. S1.3). The mean biomass of apex predators and piscivore-invertivores combined (hereafter “predators”) ranged from  $\sim 4 \pm 1 \text{ g m}^{-2}$  at Ebano (EB) to  $\sim 441 \pm 139 \text{ g m}^{-2}$  at Cueva Pulpo (CF), both sites in Cuba (Fig. 1.2). Although there was high variability among reefs within countries and protection levels, total fish and predator biomass was higher within the marine reserves of Abaco, Cuba, and Mexico than in reserves of Belize (Fig. 1.2; Fig. S1.3). The proportion of trophic guilds varied across sites (Fig. 1.2; Fig. S1.4), but the biomass of all lower trophic levels, were slightly and positively correlated with predator biomass ( $r_s \sim 0.20-0.35$ ,  $p=0.000$ , Fig. S1.5). For detailed description of fish biomass variability see Appendix 1.4.

### *Predatory fish biomass models*

All the human-related variables, except “distance to population centers”, explained some of the variability of predatory fish biomass in the single variable models (Table S1.5). The “log of coastal development within 50 km” (hereafter “coastal development”) yielded better goodness of fit (i.e., lowest  $AIC_c$  and highest weights) when considering all sites. For the subset of sites within marine reserves, however, the “log of humans within 50 km” (hereafter “human

population”) showed higher weights for total predators and piscivore-invertivore biomass, while the “log of cultivated land within 50 km” (hereafter “cultivated land”) had the highest weights for apex predators. We selected “minimum monthly sea surface temperature” (hereafter “temperature”), “reef area within 5 km” (hereafter “reef area”), and “mangrove perimeter within 5 km” (hereafter “mangrove”) because they had highest AIC<sub>c</sub> weights (Table S1.5). We discarded “wave exposure”, “depth”, “distance to deeper water”, “minimum distance to mangrove”, “distance to reef breaks”, and “macroalgae cover”, because they did not contribute to model fit in exploratory models. Different combinations of non-correlated variables were considered candidate predictors for predatory fish biomass.

The combination of top models ( $\Delta\text{AIC}_c < 2$  where  $\Sigma w\text{AIC}_c > 0.95$ ) in set A (all sites) included “coastal development” as the predictor with the strongest negative effect among the human-related variables for all predator groups (Table 1.1, Fig. 1.3). This was in concordance with the results of the single covariate models (Table S1.5). “Human population” was not selected on the top models, although improved goodness-of-fit in exploratory models (Table 1.1). For apex predators, “cultivated land” was also selected in the top models (Table 1.1) and had a negative effect (Fig. 1.3). Among the physical cofactors (Table 1.1), “ocean productivity” had a small positive effect on apex predator, while the quadratic term of “temperature” improved model fit and had a slightly positive effect on piscivore-invertivores (Fig. 1.3). In contrast, “reef complexity” had a positive effect on the biomass of both apex predators and piscivore-invertivores that was reflected on total predators (Table 1.1, Fig. 1.3).

Most biotic variables improved model fit and had a positive effect on predators (Table 1.1, Fig. 1.3). “Mangrove perimeter”, however, had a slight positive effect only on apex

predators. Unexpectedly, “coral cover” and “gorgonian abundance” had a slight negative effect on the biomass of apex predators and piscivore-invertivore, respectively (Fig. 1.3). Lower trophic fish groups (except planktivores) were important in predicting the biomass of piscivore-invertivores from which invertivores and omnivores had the strongest positive effects (Table 1.1, Fig. 1.3). Yet, only piscivore-invertivores were good predictors for apex predators (Table 1.1, Fig. 1.3). Therefore, only omnivores and invertivores had a positive effect on total predators (Fig. 1.3).

The effect of protection level (e.g., none, MPA, and NTZ) was different for both fish predator groups. NTZs (i.e., no fishing) had only a positive effect on apex predator biomass (Fig. 1.3). In contrast, MPAs (i.e., some fishing is allowed) had no effect on apex predators, but showed strong negative effect on piscivore-invertivores biomass thus total predators (Fig. 1.3). No-protection was used to set the comparisons for the NTZ and MPA categories. Overall, these models (set A) “explained” ~50%, ~57%, and ~61% of the variability in the biomass of apex predators, piscivores-invertivores and total predators, respectively (Table 1.1).

Within marine reserves (model set B), the top models ( $\Delta AIC_c < 2$  where  $\sum w AIC_c > 0.95$ ) included “coastal development” and “human population” for both predator groups, and “cultivated land” for apex predators (Table 1.1). These variables had the strongest negative effect of all predictors (Fig. 1.3). Among the physical cofactors, “ocean productivity” was only selected for apex predators (Table 1.1) with a positive effect on their biomass (Fig. 1.3). In contrast to all sites, “temperature” did not improve model fit for any group within marine reserves (Table 1.1, Fig. 1.3). “Reef complexity” was also selected in the top models for all predators (Table 1.1) showing a positive effect on their biomass (Fig. 1.3). Among the biotic predictors, “mangrove”

had a positive effect on the biomass of apex predators, showed no effect on piscivore-invertivores, and did not improve model fit for total predators within marine reserves (Table 1.1, Fig. 1.3). “Coral cover” improved models fit (Table 1.1) but showed no effect on predator biomass (Fig. 1.3). “Gorgonian” abundance was only selected for apex predators (Table 1.1) but showed no effect on their biomass (Fig. 1.3). Piscivore-invertivores had a positive effect on apex predator biomass (Table 1.1, Fig. 1.3). In contrast, “invertivores” and “omnivores” were the only fish groups selected in the top models for piscivore-invertivores and showed a positive effect on their biomass within marine reserves (Table 1.1, Fig. 1.3). Finally, higher “poaching levels” within marine reserves contributed to model fit for all predator groups (Table 1.1) with a slightly negative effect on apex predator biomass (Fig. 1.3). Surprisingly, reserve age and size were not important for any predator group in our study (Table 1.1). Within marine reserves, all these covariates explained ~ 43% of the variability of apex predators, ~56 % for piscivore-invertivores, and ~58 % for total predators (Table 1.1).

To visualize some of these relationships across all sites and survey years we plotted the mean total predator biomass per site versus “coastal development”, “ocean temperature”, “reef complexity”, and “invertivores” as the trend was similar for apex predators and piscivore-invertivores (Fig. 1.4a-d). We also plotted the mean apex predator biomass per site versus “productivity” and “mangrove” (Fig. 1.4e-f). Additionally, we overlaid the expected predatory fish biomass as a function of the plotted predictor by holding other covariates at a representative value for each site (Fig. 1.4). The predicted total predator biomass followed a steeply declining power function because a small increase in coastal development (based on light pixels) was associated with a drastic 75-95% decline in predator biomass (Fig. 1.4a). Temperature predicted piscivore-invertivore biomass with high variability at lower values, peaking at ~23°C and

declining towards 27°C (Fig. 1.4b). Most survey sites, however, exhibited minimum average temperatures over 24°C and the scarce number of sites with temperature below this value hinders a meaningful interpretation of our patterns. In contrast, reef structural complexity increased 10 fold the predicted values for total predator biomass from the lowest to the highest score (Fig. 1.4c). This landscape-scale index of reef complexity had stronger positive effect on apex predators and piscivore-invertivores than on the rest of the trophic guilds (Fig. S1.6). Among the lower trophic levels with positive effects on total predator biomass, for example, an increase in invertivore biomass ( $\sim 145 \text{ gm}^{-2}$ ) was associated with a similar increase ( $\sim 140 \text{ gm}^{-2}$ ) in the predicted total predator biomass (Fig. 1.4d). However, an increase of  $200 \text{ gm}^{-2}$  of piscivore-invertivores was only associated with a  $20 \text{ gm}^{-2}$  increase in the biomass of apex predators. Finally, an increase of  $\sim 1400 \text{ mg C m}^{-2} \text{ day}^{-1}$  in productivity and over 150 km of mangrove perimeter was associated with a  $\sim 5 \text{ g m}^{-2}$  increase in apex predator biomass (Figs. 1.4e-f).

### ***Reconstructing baseline biomass for reef fish predators***

Considering the effect of all these variables in the absence of humans, our analysis suggests that three out of four reefs (30 out of 39 sites), even within marine reserves, have lost between 80-96% of predatory fish biomass due to human activities associated with coastal development (Fig. 1.5, see Table S1.6 for values). Populations of apex predators such as sharks, jacks, barracudas, tarpon, and large-bodied groupers have declined severely by over 98% in median biomass ( $94 \pm 4 \%$ , mean  $\pm 95\%$  CI). We estimated that piscivore-invertivore of medium-bodied size such as jacks, snappers, and groupers, have lost  $\sim 88\%$  in median biomass across sites (mean  $82 \pm 4 \%$ ). Few sites, mostly within reserves, showed less loss (Fig. 1.5, Table S1.6). For example, in the Gardens of the Queen reserve in Cuba, Cueva Pulpo (CF) and Pipin

(PP) have lost in average ~7% and ~39% of the total predator fish biomass, respectively. Other reserves such as Dry Tortugas (LG) in Florida and Hol Chan (HC) in Belize may have lost ~53% and 62%, respectively (Fig. 1.5, Table S1.6). On average, sites within NTZs showed ~ a 66% decline in predatory fish biomass, while loss was ~88% at sites with no protection and within MPAs.

## **Discussion**

Predatory reef fishes have been overexploited and depleted globally in a general sense, but we know little about their historical baselines and how they varied in space (Nadon et al. 2012). The evidence for widespread predatory fish loss in coral reefs are based on historical data (Jackson et al. 2001, McClenachan 2009), analysis of presence/absence from citizen science data (Stallings 2009, Ward-Paige et al. 2010), indirect measures of fish gradients and size-spectra as proxy of fishing pressure (Graham et al. 2005, Newman et al. 2006) or by considering responses to gradient of human impacts (Hawkins and Roberts 2004, Newton et al. 2007, DeMartini et al. 2008, Sandin et al. 2008, Williams et al. 2011, Richards et al. 2012). We built on these approaches by modeling current predatory fish abundances across gradients of both exploitation and environmental variability to reconstruct local-specific and regional baselines across the Caribbean.

Overall, human-related variables had the strongest negative influence on predatory fish biomass while habitat structural “complexity”, prey availability, and protection from fishing (e.g., marine reserves) had the strongest positive effects. Other physical and biotic variables such as ocean “productivity”, “temperature”, “mangrove”, “coral cover”, and “gorgonian abundance”

had weak or undetectable effects but contributed to model fit. Understanding how these natural and anthropogenic covariates simultaneously affect predatory fish biomass was crucial to reconstructing the potential baselines for local assemblages. We estimated that the magnitude of predatory reef fish biomass losses is 80-96% across most of our sites, which is concordant with similar patterns in other coastal and oceanic systems (Baum et al. 2003, Myers and Worm 2003, 2005, Ferretti et al. 2008, Lotze and Worm 2009, Nadon et al. 2012). Our simulations also support the hypothesis that the baseline for reef fish predators is highly variable and context specific.

### ***Response of predatory fish biomass to human impacts and environmental factors***

The estimated total fish biomass in our study varied by approximately nine fold (over 460 g m<sup>-2</sup>), a finding consistent with other large spatial-scale reef studies across gradients of human impact. Our range (58-527 g m<sup>-2</sup>) fell within the wider range (15-596 g m<sup>-2</sup>) observed in similar areas of the Caribbean (Newman et al. 2006) and elsewhere. In the Western-Central Pacific, for instance, fish biomass gradually increased from 13 g m<sup>-2</sup> on reefs of the heavily populated island of Guam to 348 g m<sup>-2</sup> on the isolated Kure atoll (Williams et al. 2011), and up to 527 g m<sup>-2</sup> on the remote Kingman atoll (Sandin et al. 2008). This generalized gradient of fish biomass across large spatial-scales is assumed to have been caused largely or entirely by spatial variation in fishing intensity due to proximity to human settlements (Sandin et al. 2008, Williams et al. 2011).

Predatory fishes represented a substantial portion (over 40%) of the total fish biomass at relatively isolated reefs and inside well-enforced marine reserves (Fig. 1.2). In these areas, reef fish assemblages resembled the trophic structure of remote and less human-populated Pacific

islands (DeMartini et al. 2008, Sandin et al. 2008, Williams et al. 2011). Large predators could dominate the biomass structure of the fish assemblage inside well-enforced, larger and older reserves (Babcock et al. 2010). This is because fishing pressure differentially affects species with dissimilar life-history traits (DeMartini et al. 2008), leading to disparate recovery rates of different trophic guilds in response to protection (Russ and Alcala 2003, Babcock et al. 2010). As large predators recover more slowly than species of lower trophic levels (due to slow growth and low fecundity rates) they can reach larger sizes over time (Graham et al. 2011). In response, the proportions of less intensely targeted lower trophic groups tend to decrease or stabilize over time. Thus, the differences in the proportion of trophic guild biomass at each reef site may be in part associated with the removal of large predators as documented in other regions (DeMartini et al. 2008).

Human-related activities associated with coastal development and population density had strong negative effect on reef fish predators, as seen in other large-scale studies (Stallings 2009, Ward-Paige et al. 2010, Nadon et al. 2012). Most protected reefs had higher total fish and predator biomass (Fig. 1.2), and the abundance of apex predators, such as sharks, groupers, snappers, and jacks, sharply declined across a gradient of human impact (Fig. 1.4a). In fact, most of these predators were entirely absent from unprotected sites (Fig. 1.2), a finding concordant with presence/absence surveys performed by citizen scientists (Stallings 2009). Large reef predators are rare throughout the Caribbean and occupy only a small fraction of sites due to selective targeting by fisherman (Stallings 2009, Ward-Paige et al. 2010). Although we could not directly assess the relative role of fishing and other human impacts, we suspect fishing was the main proximate cause of predator depletion. The ultimate causes include coastal development, increased human populations, and economic growth.



Few site-specific characteristics strongly modulated the variability of reef fish predator abundance and must be considered to explain observed patterns and predict baselines (Mellin et al. 2008, Richards et al. 2012, Nadon et al. 2012). For example, reef complexity was one of the most important predictors of predatory fish biomass. Although a positive relationship between landscape reef complexity and density of large-bodied reef fish (Richards et al. 2012) or reef sharks (Nadon et al. 2012) is not always evident (Hixon and Beets 1993), sites with higher structural complexity may attract relative large resident and transient predators that take advantage of greater prey availability (McCauley et al. 2012b). In fact, lower trophic levels were also strong predictors of total predator biomass especially for piscivore-invertivores. The higher the biomass of lower trophic levels, the greater the biomass of predators tended to be. Predator dependence on prey is common within large terrestrial reserves (Sinclair et al. 2010) and positive associations among reef fish trophic guilds may increase with protection (Newman et al. 2006, Babcock et al. 2010). Thus, in our study, the variability of predicted predator populations in the absence of humans greatly respond to resource availability (i.e., habitat complexity and prey abundance) and other environmental variables such as productivity, temperature, and connectivity with other systems, played a less important role. For a full discussion of the relationships between predatory fish biomass and cofactors and their potential underlying mechanisms refer to Appendix 1.5.

Our models explained more than 50% of the variability observed in predator biomass due to human impacts and environmental variability which are crucial to assess differences across space and predict historical baselines. We caution that there are likely additional variables we did not consider. For example, larval supply (Caley et al. 1996), intra-guild competition and predation (Hixon and Beets 1993, Hixon and Carr 1997), and habitat connectivity (Mumby et al.

2004, McCauley et al. 2012b) may also regulate predatory fish populations. These variables, however, are species-specific and could be considered for species-specific predictions.

### ***Reconstructing predatory reef fish biomass baselines***

Simulated predatory reef fish biomass in the absence of humans suggests severe losses (80-96%). Although other studies have suggested similar declines for reef fish assemblages (Lotze and Worm 2009), the relative magnitude of these losses across space has not been thoroughly investigated (but see Nadon et al. 2012). The predicted baseline for predators does not necessarily translate into higher number of individuals but may also be related to body size increments in the absence of fishing (Shackell et al. 2010). These striking declines (Fig 1.5, Table S1.6), not previously reported for the entire assemblage of Caribbean predatory reef fishes, coincides with other large spatial and temporal scale studies that show losses of over 90% of the original baselines in coastal and oceanic waters across the globe, primarily due to overfishing (Baum et al. 2003, Myers and Worm 2003, 2005, Myers et al. 2007, Nadon et al. 2012). Unlike most of those studies, however, our analysis was based on fisheries-independent that accounts for environmental variability.

Based on our models, some reef sites are potential hotspots for predatory fish biomass with predicted values over  $\sim 800\text{-}1500\text{ gm}^{-2}$  if human-related activities are eliminated and fishing regulations are better enforced. For example, Columbia Reef (CR) within the marine reserve of Cozumel, Mexico, could support ten times the current levels of predator biomass ( $\sim 891\text{ gm}^{-2}$  in average) (Fig. 1.5, Table S1.6). The central and north sites of Banco Chinchorro in Mexico could hold average predator fish biomass of  $\sim 1067\text{-}1562\text{ gm}^{-2}$ . Currently these sites showed  $\sim 10\%$  of predicted values (Fig. 1.5, Table S1.6). Surprisingly, non-protected sites such as Bacunayagua

(BA) in the northern site of Cuba and Rocky Point (RP) in the south tip of Abaco, Bahamas, could potentially reach ten and five times higher biomass than current levels, respectively (Fig. 1.5, Table S1.6). This information can be used by local managers to better tailor conservation efforts for strategic protection and restoration.

## **Conclusion and implications**

The analysis of broad spatial gradients of exploitation and environmental variability provides insight into the magnitude of anthropogenic stressors and the natural factors that regulate predator assemblages at regional scales. Current predatory reef fish abundances are partially driven by these two opposing forces. Without taking this in consideration we could underestimate historical exploitation levels in areas that provide ideal conditions for predators, or greatly overestimate that of seemingly predator-depleted sites as some areas may have never supported large predator populations due to suboptimal physical and biological conditions. This in turn makes it difficult to determine appropriate baselines and restoration targets to evaluate the extent and consequences of predator depletion at local and regional scale. The baseline for predatory fish biomass, therefore, should be variable and site-specific, and proposed global baselines derived from remote sites with unique oceanographic features (e.g., Sandin et al. 2008) are unlikely to provide an accurate representation of historical conditions in most locations. Restoring predatory fish biomass would require an intensive ecosystem-level effort tailored at reducing exploitation of these species and their prey, strengthening enforcement in marine reserves, and identifying and protecting additional hotspots that could potentially support higher biomass.

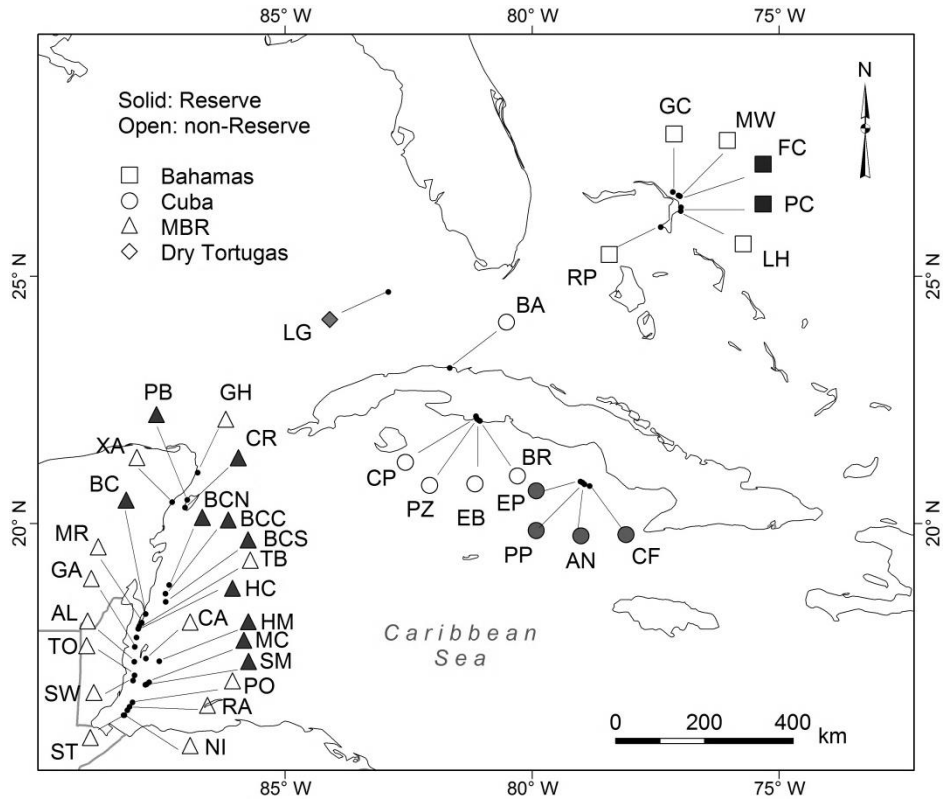
**Table 1.1 Summary of generalized linear mixed effect model comparisons using Akaike’s information criterion corrected for small sample sizes (AICc) for apex predators, piscivore-invertivores, and total predators.** Only the null model, an exploratory model that outperformed the null model, and final models ( $\Delta AIC_c < 2$  where  $\Sigma wAIC_c > 0.95$ ) are shown. Model sets A and B include all sites and sites within reserves, respectively. Parameters are model maximum log-likelihood (LL), degrees of freedom (*df*), change in AIC<sub>c</sub> ( $\Delta AIC_c$ ), AIC<sub>c</sub> weights (*wAIC<sub>c</sub>*), and the pseudo adjusted coefficient of determination based on likelihood ratio test ( $R^2$ ). Models are ordered by increasing *wAIC<sub>c</sub>*. Table footnote shows variable codes.

Models	LL	<i>df</i>	$\Delta AIC_c$	<i>wAIC<sub>c</sub></i>	$R^2$
<b>Set A Apex predators</b>					
<b>Null</b>	-234.6	5	10.27	0.00	0.00
<b>Cd + Tp<sup>2</sup> + Ma + Co + Go + Pi + Pr</b>	-221.3	13	0.52	<b>0.21</b>	0.51
<b>Cd + Tp<sup>2</sup> + Ru + Ma + Co + Go + Pi</b>	-222.2	12	0.18	<b>0.25</b>	0.50
<b>Cl + Tp<sup>2</sup> + Ma + Co + Pi + Pr</b>	-222.2	12	0.17	<b>0.25</b>	0.50
<b>Cl + Pp + Tp<sup>2</sup> + Ru + Ma + Co + Pi</b>	-222.1	12	0.00	<b>0.28</b>	0.50
<b>Set B</b>					
<b>Null</b>	-115.4	5	8.40	0.00	0.00
<b>Cd + Ru + Ma + Co + Go + Pi + In + Om + Ag</b>	-104.6	14	8.21	0.00	0.44
<b>Cl + Ma + Co + Go + Pi + Po</b>	-105.9	11	1.26	<b>0.14</b>	0.43
<b>Ru + Ma + Co + Pi + Po</b>	-105.9	10	0.88	<b>0.17</b>	0.43
<b>Cd + Ru + Co + Go + Pi</b>	-105.8	10	0.62	<b>0.19</b>	0.43
<b>Hu + Co + Go + Pi</b>	-106.7	9	0.14	<b>0.24</b>	0.42
<b>Pp + Ru + Co + Pi + Po</b>	-105.5	10	0.00	<b>0.26</b>	0.42
<b>Set A Piscivore - Invertivore</b>					

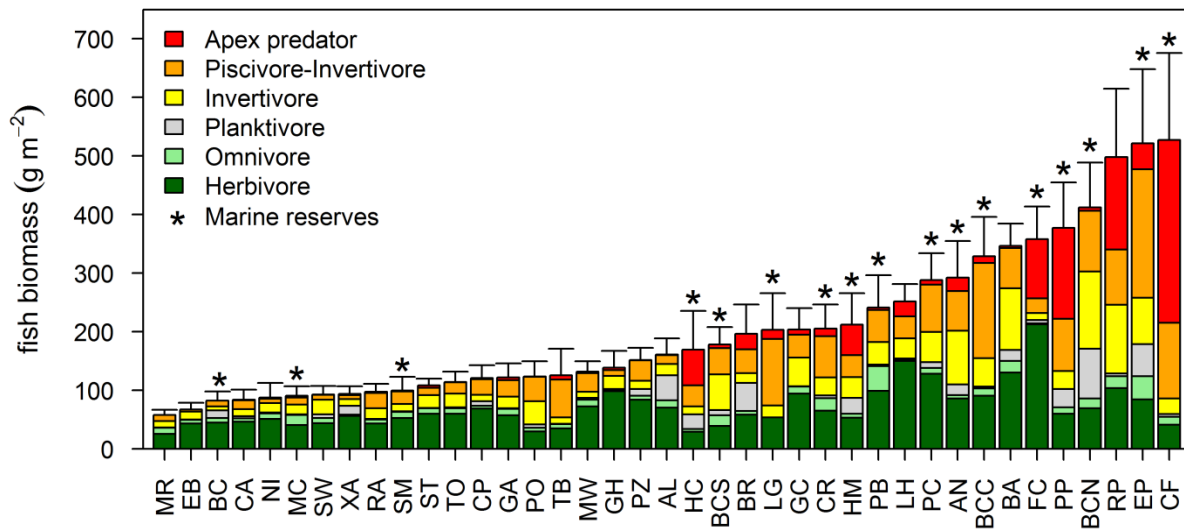
<b>Null</b>	-249.0	5	63.29	0.00	0.00
<b>Cd + Pp + Tp<sup>2</sup> + We + Ru + Ma + Co + Al + Go + In + Om + Pl + He + Pr</b>	-204.5	20	6.50	0.04	0.58
<b>Cd + Tp<sup>2</sup> + Ru + Co + Go + In + Om + Pl + He + Pr</b>	-205.7	16	0.00	<b>0.96</b>	0.57
Set B					
<b>Null</b>	-83.84	5	17.30	0.00	0.00
<b>Cd + Tp<sup>2</sup> + We + Ru + Co + Go + In + Om + Pl + He + Po</b>	-64.10	17	8.39	0.01	0.59
<b>Hu + Ru + Ma + Co + In + Om + Po</b>	-66.54	12	0.12	<b>0.48</b>	0.55
<b>Cd + Ru + Co + In + Om + Po</b>	-67.72	11	0.00	<b>0.51</b>	0.56
<hr/>					
Set A Total Predators					
<b>Null</b>	-250.0	5	46.37	0.00	0.00
<b>Cd + Pp + Tp<sup>2</sup> + We + De + Ru + Db + Dm + Ma + Co + Al + Go + In + Om + Pl + He + Pr</b>	-218.6	21	18.00	0.00	0.60
<b>Cd + Tp<sup>2</sup> + Ru + Co + Go + In + Om + Pl + He + Pr</b>	-215.2	16	0.00	<b>1.00</b>	0.61
Set B					
<b>Null</b>	-88.41	5	24.21	0.00	0.00
<b>Cd + Ru + Ma + Co + Go + In + Om + Pl + He + Si + Ag + Po</b>	-73.66	17	13.28	0.00	0.59
<b>Hu + Ru + Co + In + Om + Po</b>	-75.54	11	1.58	<b>0.31</b>	0.57
<b>Cd + Ru + Co + In + Om + Po</b>	-74.75	11	0.00	<b>0.69</b>	0.58

*Model covariates include: Cd, Coastal development within 50 km; Pp, net primary production; Tp<sup>2</sup>, quadratic term of minimum monthly mean sea surface temperature; We, Wave exposure; De, Depth; Ru, reef complexity; Db, Distance to reef break; Dm, Distance to mangrove; Ma, mangrove perimeter within 5km; Co, Corals; Al, Algae; Go, Gorgonians; Pi, piscivore-invertivores; In, invertivores; Pl, planktivores; Om, omnivores; He, herbivores; Ra, reef area within 5km; Pr, Protection level; Si, reserve size; Ag, reserve age; Po, poaching level within reserve. See Table S1.3 for units.*

**Figure 1.1 Distribution of survey locations.** For site abbreviations, survey dates, coordinates, and protection level refer to Table S1.1. MBR, Mesoamerican Barrier Reef. No-take zones and minimum fished marine protected areas are represented with solid symbols.

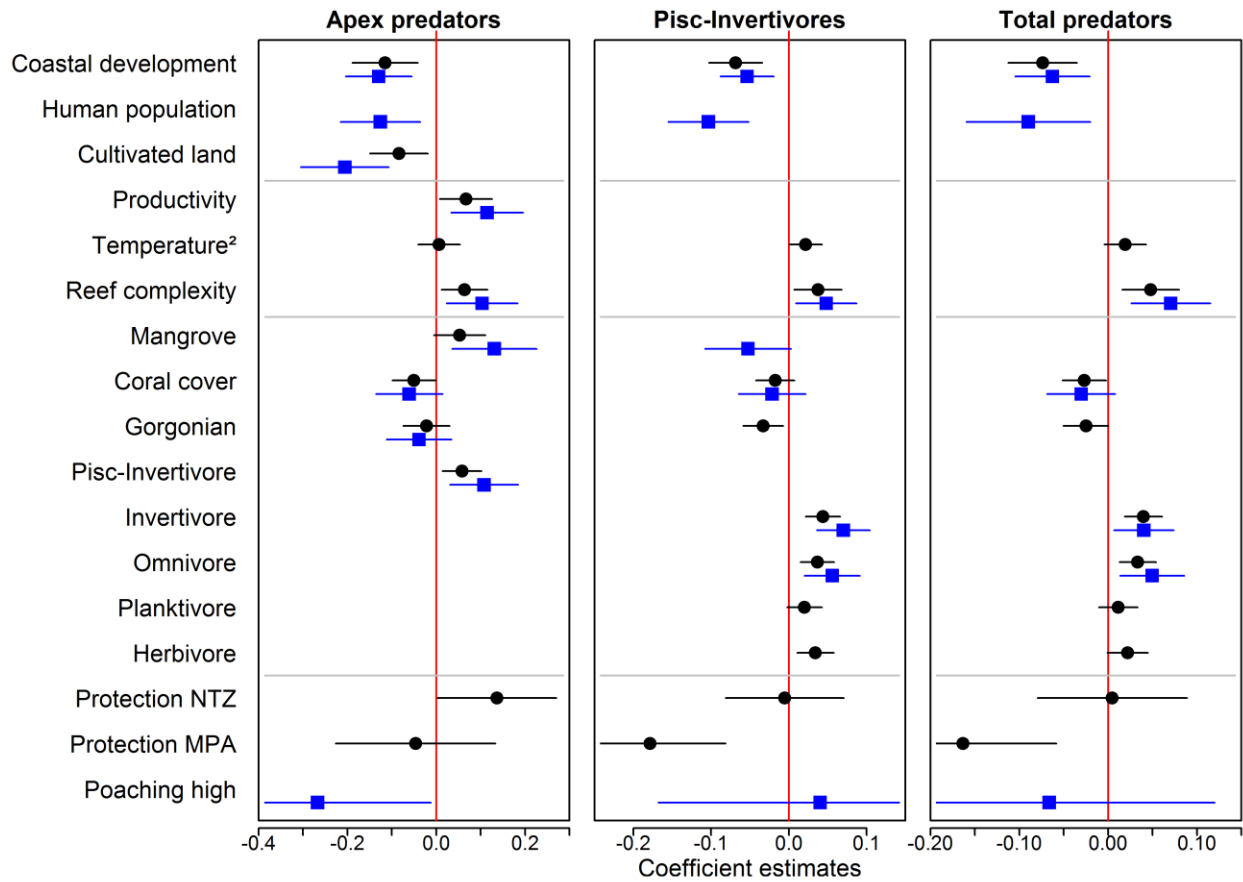


**Figure 1.2 Mean biomass of trophic guilds per reef site +1 standard error for total fish biomass.** Sites are organized from low to high total fish biomass. Trophic categories were based on dietary information (Froese and Pauly 2013). For site abbreviations see Table S1.1. For species list in each group see Tables S1.2. No-take zones and minimum fished marine protected areas are noted as reserves (\*), but for detailed protection level information is in Table S1.1.



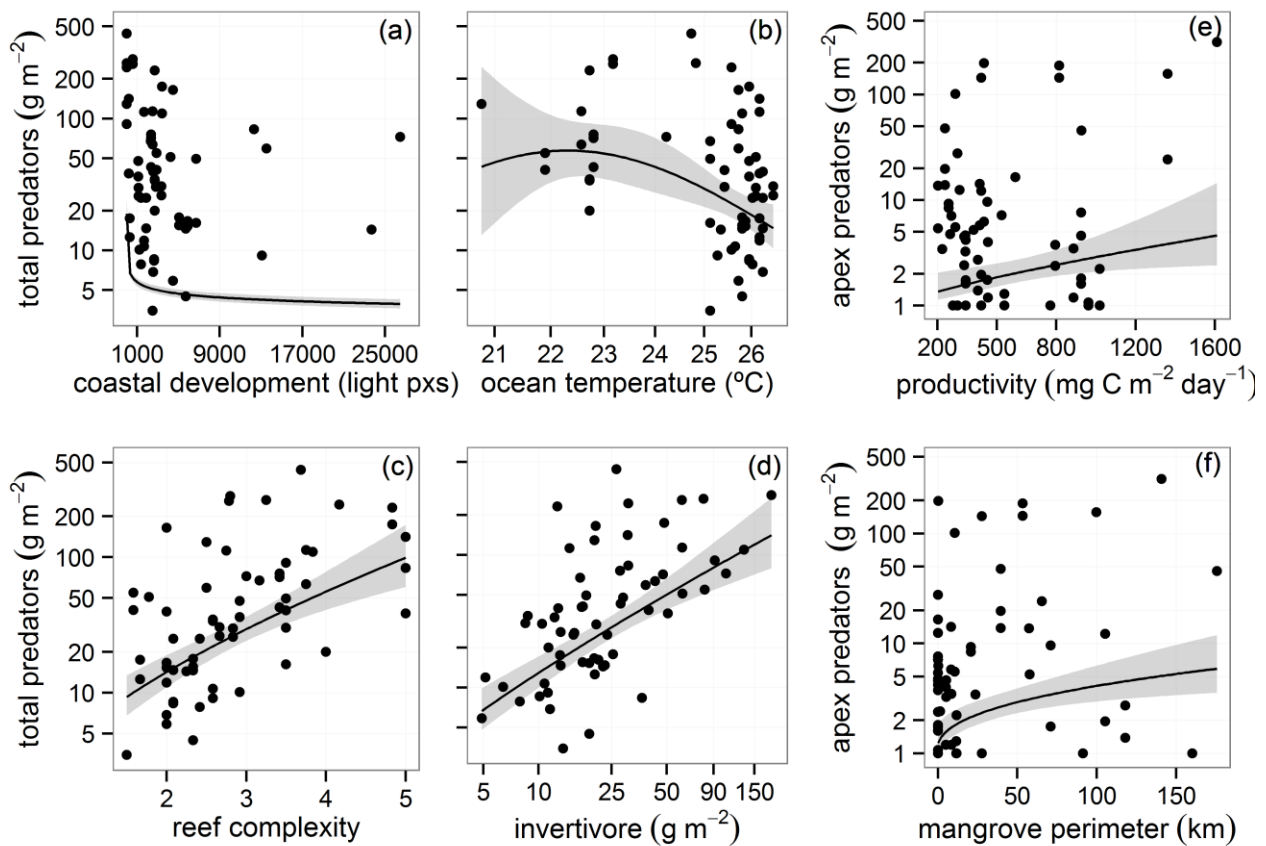
**Figure 1.3 Mean coefficient estimates ( $\pm$  95% confidence interval) of top models ( $\Delta$ AICc < 2 where  $\Sigma$  wAICc > 0.95) for apex predators, piscivore-invertivores, and total predators.**

Black and blue circles include all study sites and sites within marine reserves, respectively. *NTZ*, no-take zones; *MPA*, marine protected areas; *poaching high*, high level of poaching. Only estimates that improved model fit are shown. Grey horizontal lines divide variables by anthropogenic, physical, biotic, and management categories. Longer confidence intervals are truncated for improved visualization.

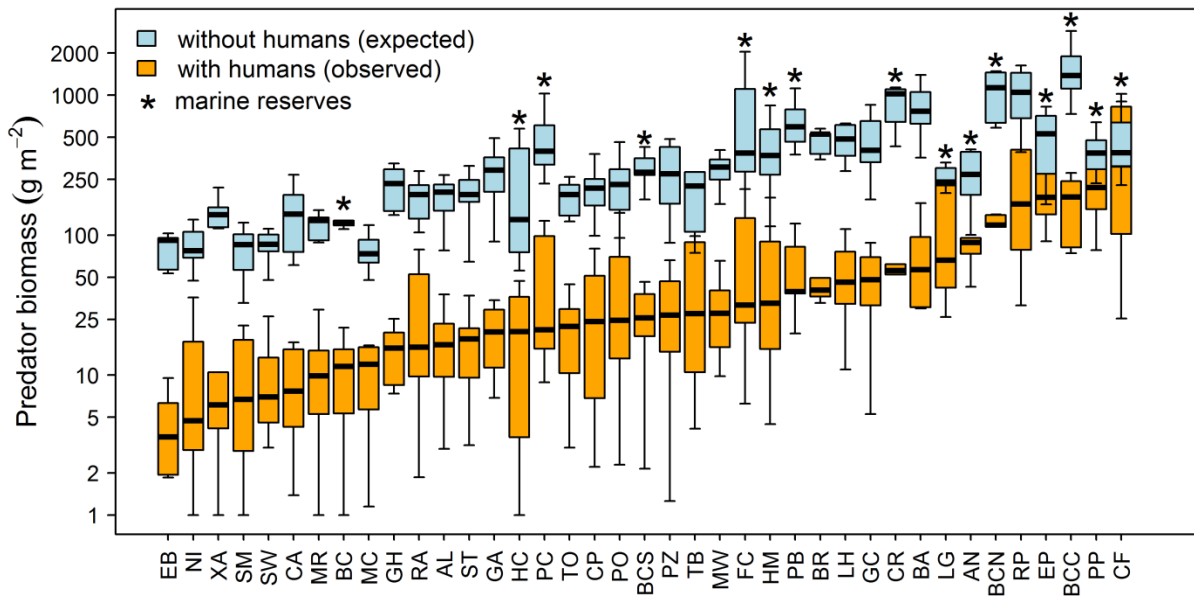




**Figure 1.4 Relations between total predator and apex predator biomass and six individual covariates:** (a) coastal development within 50 km in light pixels; (b) minimum monthly mean sea surface temperature; (c) reef structural complexity; (d) invertivore biomass; (e) ocean productivity, and (f) mangrove perimeter within 5 km. Black dots are means per site. Black line is the mean ( $\pm$  95% confidence interval) of the predicted predator biomass as a function of a given covariate, calculated by holding other covariates at a representative value for each reef.



**Figure 1.5** Boxplot of the observed (orange) and predicted (light blue) median (50% and 99% quartiles) of predatory reef fish biomass across survey sites (ordered from lowest to highest biomass). Predicted biomass was based on the best explanatory model given no coastal development within 50 km (i.e., in the absence of humans) and every site considered as no-take zone (i.e., no fishing). Based on the predictive models three out four reefs have lost 80-95% of the potential predatory fish biomass. No-takes zones and marine protected areas with minimum fishing are noted as marine reserves (\*). For better representation Y axis is in log scale. For site codes see Table S1.1.



## References

- Babcock, R. C., N. T. Shears, A. C. Alcala, N. S. Barrett, G. J. Edgar, K. D. Lafferty, T. R. McClanahan, and G. R. Russ. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences* 107:18256–18261.
- Baum, J. K., and R. A. Myers. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters* 7:135–145.
- Baum, J. K., R. A. Myers, D. G. Kehler, B. Worm, S. J. Harley, and P. A. Doherty. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299:389–392.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. 2nd edition. Springer New York.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27:477–500.
- DeMartini, E. E., A. M. Friedlander, S. A. Sandin, and E. Sala. 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series* 365:199–215.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. *Science* 333:301–306.
- Ferretti, F., R. A. Myers, F. Serena, and H. K. Lotze. 2008. Loss of Large Predatory Sharks from the Mediterranean Sea. *Conservation Biology* 22:952–964.
- Frank, K. T., B. Petrie, and N. L. Shackell. 2007. The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology & Evolution* 22:236–242.
- Friedlander, A. M., E. K. Brown, P. L. Jokiel, W. R. Smith, and K. S. Rodgers. 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305.
- Froese, R., and D. Pauly. 2013. FishBase. <http://www.fishbase.org>.
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815.

- Graham, N. A. J., P. Chabanet, R. D. Evans, S. Jennings, Y. Letourneur, M. Aaron MacNeil, T. R. McClanahan, M. C. Öhman, N. V. C. Polunin, and S. K. Wilson. 2011. Extinction vulnerability of coral reef fishes. *Ecology Letters* 14:341–348.
- Graham, N., N. Dulvy, S. Jennings, and N. Polunin. 2005. Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. *Coral Reefs* 24:118–124.
- Hampton, J., J. R. Sibert, P. Kleiber, M. N. Maunder, and S. J. Harley. 2005. Fisheries: Decline of Pacific tuna populations exaggerated? *Nature* 434:E1–E2.
- Hawkins, J. P., and C. M. Roberts. 2004. Effects of artisanal fishing on Caribbean coral reefs. *Conservation Biology* 18:215–226.
- Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77–101.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946–949.
- Hunsicker, M. E., L. Ciannelli, K. M. Bailey, J. A. Buckel, J. Wilson White, J. S. Link, T. E. Essington, S. Gaichas, T. W. Anderson, and R. D. Brodeur. 2011. Functional responses and scaling in predator–prey interactions of marine fishes: contemporary issues and emerging concepts. *Ecology letters* 14:1288–1299.
- Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, Jon Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.
- Jhala, Y. V., R. Gopal, and Q. Qureshi. 2008. Status of tigers, co-predators and prey in India. National Tiger Conservation Authority, Govt., of India, New Delhi and Wildlife Institute of India, Dehradun. TR 2011/003.
- Lang, J. C., K. W. Marks, P. A. Kramer, P. Richards Kramer, and R. N. Ginsburg. 2010. AGRRA Protocols version 5.4 Atlantic and Gulf Rapid Reef Assessment Program. University of Miami, Florida.
- Lotze, H. K., and B. Worm. 2009. Historical baselines for large marine animals. *Trends in Ecology & Evolution* 24:254–262.
- McCauley, D. J., K. A. McLean, J. Bauer, H. S. Young, and F. Micheli. 2012a. Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations. *Ecological Applications* 22:385–392.

- McCauley, D. J., H. S. Young, R. B. Dunbar, J. A. Estes, B. X. Semmens, and F. Micheli. 2012b. Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications* 22:1711–1717.
- McClenachan, L. 2009. Documenting loss of large trophy fish from the Florida Keys with historical photographs. *Conservation Biology* 23:636–643.
- Mellin, C., J. Ferraris, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, and T. L. de Loma. 2008. Natural and anthropogenic influences on the diversity structure of reef fish communities in the Tuamotu Archipelago (French Polynesia). *Ecological Modelling* 218:182–187.
- Mora, C. 2008. A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society B: Biological Sciences* 275:767–773.
- Mumby, P. J., A. J. Edwards, J. E. Arias-González, K. C. Lindeman, P. G. Blackwell, A. Gall, M. I. Gorczynska, A. R. Harborne, C. L. Pescod, H. Renken, C. C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427:533–536.
- Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–1850.
- Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283.
- Myers, R. A., and B. Worm. 2005. Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360:13–20.
- Nadon, M. O., J. K. Baum, I. D. Williams, J. M. Mcpherson, B. J. Zgliczynski, B. L. Richards, R. E. Schroeder, and R. E. Brainard. 2012. Re-creating missing population baselines for Pacific reef sharks. *Conservation Biology* 26:493–503.
- Newman, M. J. H., G. A. Paredes, E. Sala, and J. B. C. Jackson. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters* 9:1216–1227.
- Newton, K., I. M. Côté, G. M. Pilling, S. Jennings, and N. K. Dulvy. 2007. Current and future sustainability of island coral reef fisheries. *Current Biology* 17:655–658.
- Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems. *Science* 301:955–958.
- R Core Team. 2013. R: A Language and Environment for Statistical Computing, Vienna, Austria. V. 3.03. <http://www.R-project.org>.

- Richards, B. L., I. D. Williams, O. J. Vetter, and G. J. Williams. 2012. Environmental factors affecting large-bodied coral reef fish assemblages in the mariana archipelago. *PLoS ONE* 7:e31374.
- Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102:227–234.
- Russ, G. R., and A. C. Alcala. 2003. Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983-2000. *Ecological Applications* 13:1553–1565.
- Sandin, S. A., J. E. Smith, E. E. DeMartini, E. A. Dinsdale, S. D. Donner, A. M. Friedlander, T. Konotchick, M. Malay, J. E. Maragos, D. Obura, O. Pantos, G. Paulay, M. Richie, F. Rohwer, R. E. Schroeder, S. Walsh, J. B. C. Jackson, N. Knowlton, and E. Sala. 2008. Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE* 3:e1548.
- Shackell, N. L., K. T. Frank, J. A. D. Fisher, B. Petrie, and W. C. Leggett. 2010. Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proceedings of the Royal Society B: Biological Sciences* 277:1353–1360.
- Sims, D. W., E. J. Southall, N. E. Humphries, G. C. Hays, C. J. A. Bradshaw, J. W. Pitchford, A. James, M. Z. Ahmed, A. S. Brierley, M. A. Hindell, D. Morritt, M. K. Musyl, D. Righton, E. L. C. Shepard, V. J. Wearmouth, R. P. Wilson, M. J. Witt, and J. D. Metcalfe. 2008. Scaling laws of marine predator search behaviour. *Nature* 451:1098–1102.
- Sinclair, A. R. E., K. Metzger, J. S. Brashares, A. Nkwabi, G. Sharam, J. M. Fryxell, J. Terborgh, and J. A. Estes. 2010. Trophic cascades in African savanna: Serengeti as a case study. *Trophic cascades: predators, prey and the changing dynamics of nature*, Island Press, Washington, DC, USA:255–274.
- Stallings, C. D. 2009. Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities. *PLoS ONE* 4:e5333.
- Terborgh, J., and J. A. Estes. 2010. *Trophic cascades : predators, prey, and the changing dynamics of nature*. Island Press, Washington DC.
- Ward-Paige, C. A., C. Mora, H. K. Lotze, C. Pattengill-Semmens, L. McClenachan, E. Arias-Castro, and R. A. Myers. 2010. Large-scale absence of sharks on reefs in the Greater-Caribbean: a footprint of human pressures. *PLoS ONE* 5:e11968.
- Williams, I. D., B. L. Richards, S. A. Sandin, J. K. Baum, R. E. Schroeder, M. O. Nadon, B. Zgliczynski, P. Craig, J. L. McIlwain, and R. E. Brainard. 2011. Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western pacific. *Journal of Marine Biology* 2011, 14 pages.

Worm, B., M. Sandow, A. Oschlies, H. K. Lotze, and R. A. Myers. 2005. Global patterns of predator diversity in the open oceans. *Science* 309:1365–1369.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer.

## CHAPTER 2

### Re-examining the relationship between invasive lionfish and native grouper in the Caribbean<sup>1</sup>

#### Abstract

Biotic resistance is the idea that native species negatively affect the invasion success of introduced species, but whether this can occur at large spatial scales is poorly understood. Here we re-evaluated the hypothesis that native large-bodied grouper and other predators are controlling the abundance of exotic lionfish (*Pterois volitans/miles*) on Caribbean coral reefs. We assessed the relationship between the biomass of lionfish and native predators at 71 reefs in three biogeographic regions while taking into consideration several cofactors that may affect fish abundance, including among others, proxies for fishing pressure and habitat structural complexity. Our results indicate that the abundance of lionfish, large-bodied grouper and other predators were not negatively related. Lionfish abundance was instead controlled by several physical site characteristics, and possibly by culling. Taken together, our results suggest that managers cannot rely on current native grouper populations to control the lionfish invasion.

**Key words:** biotic resistance, coral reef, invasive species, lionfish, grouper, Caribbean

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## Introduction

Biotic resistance describes the capacity of native or resident species in a community to constrain the success of invasive species (Elton, 1958). While there are several examples of native species controlling invasive populations, especially invasive plants (Reusch & Williams, 1999; Mazia et al., 2001; Magoulick & Lewis, 2002; Levine et al., 2004; Mitchell et al., 2006), less clear are the ecological mechanisms that allow heterogeneous communities to resist invasion (Lockwood et al., 2005; Melbourne et al., 2007), and whether these processes are strong enough to compromise invasion success on a large scale (Byers & Noonburg, 2003; Davies et al., 2005). Especially elusive is whether native predators or competitors can constrain the expansion of exotic predator species at large spatial scales (but see, deRivera et al., 2005). Although biotic resistance substantially reduces the establishment of invaders, there is little evidence that species interactions such as predation completely prevent invasion (Levine et al., 2004; Bruno et al., 2005)

The invasion of Pacific lionfishes (*Pterois volitans* and *Pterois miles*) into the Caribbean basin (Schofield, 2009) over the past ten years provides an example of biotic interactions within a system that have been unable to reduce exotic invasion at a regional scale (Hackerott et al., 2013). Lionfish have spread to every shallow and deep habitat of the Western North Atlantic and the Caribbean (Whitfield et al., 2007; Betancur-R et al., 2011) including fore reef and patch reef environments (Green & Côté, 2009; Albins & Hixon, 2011), seagrass meadows (Claydon et al., 2012), mangrove root forests (Barbour et al., 2010), estuarine habitats (Jud et al., 2011), and even depths of ~90 meters (Green, pers. obs.). Lionfish dissemination in the region has added additional stress (Albins & Hixon, 2011; Lesser & Slattery, 2011; Côté et al., 2013) to an already disturbed coral reef ecosystem (Paddack et al., 2009; Schutte et al., 2010). Their voracious

appetite threatens small reef fish and juveniles of depleted fish populations including commercially important species such as groupers and snappers, and keystone grazers such as parrotfishes (Albins & Hixon, 2008; Green et al., 2012). The failure of the system to constrain invasion success may be associated in part to the lack of native predatory capacity due to overfishing (Carlsson et al., 2009; Mumby et al., 2011), or weak biotic resistance by the native predators and competitors (Levine et al., 2004).

The first study to investigate the potential for biotic control of lionfish by native predators found an inverse relationship between the biomass of native groupers and lionfish on reefs at the Exuma Cays Land and Sea Park (ECLSP) in the Bahamas (Mumby et al., 2011). Specifically, Mumby et al. (2011) found that grouper biomass could explain ~56% of the variability in lionfish biomass, and concluded that large-bodied groupers can constrain lionfish abundance if a series of cofactors at the site level are kept constant (i.e., reef complexity, larval supply, habitat characteristics). To examine whether this relationship holds true at a scale that reflects the heterogeneity of Caribbean reefs, Hackerott et al. (2013) gathered data on lionfish and grouper abundance from 71 sites across multiple regions in the Caribbean. When accounting for several site-specific covariates, Hackerott et al. (2013) did not find a relationship between the abundance of lionfish and native predators/competitors at a broad spatial scale in the Caribbean.

Aside from the suite of variables considered by Hackerott et al. (2013), several other covariates that are known to affect fish community structure, but vary across the region, could mask the effect native predators have on lionfish abundance. Accounting for spatial scale and potential cofactors is essential when evaluating the importance of any single variable in a spatial comparative study (MacNeil et al., 2009). In particular, fishing mortality, larval dispersal, habitat quality, connectivity, reef structural complexity, depth, ecological interactions, and a myriad of

other factors control the population dynamics of reef fish species (Sale, 2002). Here we re-evaluated the relationship between large-bodied grouper and other predators and lionfish abundance, accounting for a broader set of covariates than those included by Hackerott et al. (2013) that may mediate the interaction between predators and the invader (Mumby et al., 2013). We also evaluated the grouper bio-control hypothesis proposed by Mumby et al. (2011) and provide new insights into how such biotic resistance is unlikely at the scale of the Caribbean reef system. The issue still remains how to best manage and/or reduce numbers of lionfish where they are currently found, and the only effective solution to date is direct removal by fisherman and divers (Barbour et al., 2011; Frazer et al., 2012; Green et al., 2013 in press).

## **Materials and Methods**

### ***Sites and fish surveys***

Survey methods are explained in detail in Hackerott et al., (2013). In summary, we surveyed 71 coral reefs (3-15 m deep) across three distinct reef habitats (spur-and-grove, slope, and patch reef) in three regions of the Caribbean: The Bahamas, Cuba, and the Mesoamerican Barrier Reef (Belize and Mexico) from 2009 to 2012 (Fig. S2.1, Table S2.1). All these habitats were once dominated by the coral complex *Montastraea/Orbicella* (Edmunds & Elahi, 2007). Reef sites were selected to cover a wide range of reef fish abundance. To survey fish abundance, we conducted underwater visual censuses at each site using belt transects (for spur-and-grove and slopes) or roving survey dives (for patch reef) (see details in Hackerott et al., 2013). Fish biomass was calculated through the allometric length-weight conversion formula (Froese & Pauly, 2013) and scaling parameters for lionfish were obtained elsewhere (Green et al., 2011).

Grouper was defined as the combined biomass of relatively large-bodied species such as Nassau (*Epinephelus striatus*), tiger (*Mycteroperca tigris*), black (*Mycteroperca bonaci*), and yellowfin grouper (*Epinephelus interstitialis*) as defined also by Mumby et al., (2011). These species could potentially prey on lionfish (Maljković et al., 2008; Mumby et al., 2011) and are relatively more abundant than other potential predators in the region (Hackerott et al., 2013). Other predators considered in this study included any species that could potentially prey on lionfish (see Table S2 in Hackerott et al., 2013). To directly compare our study with the generality of the results by Mumby et al. (2011), we overlaid their values of fish biomass on our main biomass plot and added boxplots that described the distribution of both data sets.

### ***Covariates***

The site-specific parameters included as covariates in our statistical model were wind exposure, habitat type, protection status, depth, and time since invasion which are described in detail in Hackerott et al. (2013). We added two new variables to the models that are hypothesized to strongly modulate lionfish abundance (Mumby et al., 2013): human population density/reef area (humans/reef) which is a proxy for fishing effects (Newton et al., 2007; Mora, 2008), and is predicted to be negatively correlated with lionfish density; and reef complexity, which is a proxy for habitat heterogeneity within sites, predicted to have a positive effect on lionfish density (Green et al., 2012). Human population density was calculated as the number of humans within 50 km (maximum number of people living within 50 km radius of each site). We chose 50 km because it is a reasonable range of human influence on Caribbean reefs (Mora, 2008). Estimates of human population counts for the year 2010 were obtained from the Gridded Population of the

World V.3 at 0.25 degree resolution (SEDAC, 2010). Reef area was calculated within 10 km radius of each site, well below the average home range for certain predators species (Farmer & Ault, 2011). Reef area was calculated from the Global Distribution of Coral Reefs (2010) database as available at the Ocean Data Viewer (<http://data.unep-wcmc.org/datasets/13>). This database represents the global distribution of warm-water coral reefs compiled mostly from the Millennium Coral Reef Mapping Project (UNEP-WCMC et al., 2010). All spatial calculations were done in ArcGIS v10.0. Humans/Reef Area (humans/km<sup>2</sup> of reef) was defined as:

$$\text{Number of humans within 50 km} / \text{Reef area within 10 km} / (\pi 10^2) \text{ (km}^2\text{)}$$

To estimate reef complexity we used a rugosity index (0-5) estimated at the transect level, where “0” was a flat substrate with no vertical relief and “5” was an exceptionally complex substrate with numerous caves and overhangs (Polunin & Roberts, 1993). Relief complexity for Eleuthera and New Providence sub-regions was estimated by averaging measurements of reef height (i.e., the vertical distance between the lowest and highest point of the reef structure in cm), taken at five haphazard points within the survey area (either transect or rover diver area) (Wilson et al., 2007). To make reef complexity estimates homogenous for all sites, we transformed the relief complexity estimates taken in Eleuthera and New Providence to the rugosity index, described by Polunin & Roberts (1993), by assigning a gradient of 0 cm to “0” and over 300 cm to “5”. This resulted in a continuous rugosity index for these two sub-regions that was comparable with the rest of the sites.

## *Data analysis*

Before applying the statistical model, we explored the data and determined that a negative binomial or Poisson were the most plausible distributions for lionfish counts. Additionally, we checked for collinearity among covariates. We ran a logistic regression model with all the covariates and examined the variance inflation factor (VIF) for each variable. We used a  $VIF > 2$  as a threshold to determine collinearity (Graham, 2003). Depth was correlated with reef habitat type as shallower sites tended to be dominated by patch reefs. Thus we modeled these two factors separately. However, we found that keeping depth in the full model, together with habitat type, did not compromise fitting or the magnitude of the effects.

We ran a generalized linear mixed-effect model using the Automatic Differentiation Model Builder (glmmADMB) package (Skaug et al., 2013) in R 3.0.2 (R Core Team, 2013). As the lionfish data were over-dispersed and with excess of zeroes (Hackerott et al., 2013), a glmmADMB which accommodates zero inflation was the most adequate model structure (Bolker et al., 2012). We modeled lionfish counts with a negative binomial type 1 distribution and log link because this model performed better than a Poisson distribution based on the Akaike Information Criterion (AIC). Since a negative binomial is a discrete distribution we included an offset in the model to account for survey area (sampling unit level), thus we could effectively analyze the relationship between the density of lionfish and grouper biomass, i.e.:

$$\text{Log (LF Density)} = \text{Log (LF Counts)} - \text{Log (Survey Area)}$$

Because lionfish density and biomass were highly correlated (Pearson's product moment correlation  $\sim 0.96$ ,  $p < 0.0001$ ), the results of the model should be applicable to biomass as well. The rest of the covariates were considered fixed. We standardized and centered the numerical

covariates to aid in comparison of the coefficient estimates. To account for spatial autocorrelation we nested sites within sub-regions and used them as random effects (see Table S2.1 for sub-regions). To validate the model we corroborated that no patterns were found on the plot of the model residuals versus fitted values.

Moran's I similarity spline correlograms constructed from the residuals of the glmmADMB model (Zuur et al., 2009) graphically indicated that our mixed-effect modeling framework successfully accommodated the spatial autocorrelation observed in the raw data (Fig S2). Additionally, we used Mantel tests (Mantel, 1967) to confirm the lack of spatial autocorrelation between the Pearson residuals of the model and the lag distance (in km) between sites (i.e., whether sites that are closer together were more similar), and found that the overall correlation coefficient for the model was low ( $r = 0.073$ ,  $p = 0.0001$ ). We performed the autocorrelation analyses using the spatial nonparametric covariance function (ncf) package version 1.1-5 (Bjørnstad, 2013). All analyses were performed in R version 3.0.2 (R Core Team, 2013). We provide the entire workflow R code (<https://peerj.com/articles/348/#supp-5>) and the master data summary by site level (FigShare, <http://dx.doi.org/10.6084/m9.figshare.899210>).

## **Results and Discussion**

Even when including proxies for fishing and habitat structure in our statistical model, we found no support for an effect of large-bodied grouper or other predator biomass on lionfish abundance (Fig. 2.1, Table S2.2). As in Hackerott et al. (2013), the effects of other covariates in our analysis (namely wind exposure, habitat type, and protection status) (Fig. 2.1) remained the principal factors that appear to influence lionfish abundance. Our analyses suggest that variation

in lionfish density across the region is driven by environmental processes and human activity and not by biotic resistance from native predators.

The absence of a relationship between lionfish and native grouper biomass across a large scale suggests that the results of Mumby et al. (2011), which found a negative association across 12 sites – 5 inside and 7 adjacent to a no-take reserve (ECLSP) – represented a subset of a much broader and complicated relationship driven by other factors (Fig. 2.1 and 2.2). The average biomass of large-bodied grouper in our study of the Caribbean region ( $7.6 \pm 0.8 \text{ gm}^{-2}$ , mean  $\pm$  standard error) was slightly lower (Wilcoxon test,  $W = 1197$ ,  $p = 0.002$ ) than that found by Mumby et al. (2011) at Exuma ( $10.0 \pm 2.6 \text{ gm}^{-2}$ ) (Fig. 2.2). In contrast, the average biomass of lionfish in our study ( $7.8 \pm 0.5 \text{ gm}^{-2}$ ) was ~20 times higher (or ~2 times higher excluding patch reefs, i.e.,  $0.7 \pm 0.1 \text{ gm}^{-2}$ ) than those found at Exuma ( $0.4 \pm 0.1 \text{ gm}^{-2}$ ) by Mumby et al. (2011) (Fig. 2.2). In that study, relatively low lionfish biomass ( $\sim 0.3 \text{ gm}^{-2}$ ) was associated with relatively high grouper biomass ( $\sim 25 \text{ gm}^{-2}$ ). However, across 71 sites in our study, lionfish biomass ranged widely ( $0\text{-}50 \text{ gm}^{-2}$ ) at sites with equivalent grouper abundance (Fig. 2.2). Thus, while predators may negatively impact lionfish under a particular set of local conditions (Mumby et al., 2011), the underlying relationship between lionfish and predator biomass was undetectable on a wide range of heterogeneous sites across the Caribbean region.

In this study, we assume that high predator biomass is indicative of high predatory capacity resulting from a high frequency of large individuals (Fig. 2.3a). Grouper at protected sites were, on average, larger ( $48.6 \pm 1.5 \text{ cm TL}$ , mean  $\pm$  standard error total length) than those at unprotected sites ( $34.7 \pm 1.1 \text{ cm}$ ) ( $t = -7.68$ ,  $p < 0.001$ , Fig. 2.3a). It is unlikely that sites with relatively high grouper biomass have low predatory capacity as a result of more abundant, but smaller, individual fishes. Indeed, the exact opposite pattern is well documented in a wide range



of habitat types for several fish species (Gust et al., 2001; Friedlander & DeMartini, 2002; McClanahan et al., 2007). This seems to also be the case for groupers in our study (Fig. 2.3b). At sites with grouper biomass of at least  $10 \text{ gm}^{-2}$ , which was the minimum biomass per site in the ECLSP (Mumby et al., 2011), there were relatively high frequencies of medium/large individuals (Fig. 2.3b). Medium/large groupers ( $>30\text{cm TL}$ ) have been classified as having potentially high predatory capacity (Mumby et al., 2011). We found relatively lower frequencies ( $<50\%$ ) of small individuals ( $<30 \text{ cm TL}$ ) across all protected sites. Therefore, it is unlikely that a lack of predatory capacity at sites with the highest grouper biomass (Fig. 2.2 and Fig. 2.3b) explains the absence of a relationship between lionfish and grouper in our results.

While we did not find evidence for an effect of native predators on invasion status, lionfish biomass varied significantly between the reef types we examined. All of our fore-reef sites (slope and spur-and-groove) constituted high-profile habitats and we also included a set of patch reefs, a reef habitat common in the region. In particular, slope and spur-and-groove habitat had a negative effect on lionfish abundance (Fig. 2.1, Table S2.2) with higher average lionfish abundance in patch reef habitats ( $27.5 \pm 2.1 \text{ gm}^{-2}$  vs.  $0.7 \pm 0.1 \text{ gm}^{-2}$ ). However, both lionfish and large-bodied grouper and predators were frequently observed in each of these habitats (Fig. 2.3c). The class size distribution for groupers among reef habitats were similar (Fig. 2.3c). Almost 90% of the patch reef sites had groupers in the 21-40 cm class size range, while ~60 % of slope and spur-and-groove sites had groupers within 31-50 cm total length (Fig. 2.3c). Although, the size distribution of our study sites indicates that grouper  $>30\text{cm TL}$  (deemed 'large-bodied' by Mumby et al. 2011) were frequently (over 50%) observed in patch reef habitats (Figure 2.3c), we caution that other patch reefs across the Caribbean must be surveyed in order to make meaningful extrapolations of the observed patterns in this habitat.

Other variables may also partly explain the variability of lionfish abundance in the region. Wind exposure, specifically whether sites were located on the windward side, had a weak negative effect on lionfish abundance (Fig. 2.1). However, the mechanism behind this association is not well understood and a premature explanation may be misleading. Larval supply, which we did not measure, may contribute to the lack of biotic resistance. As with other reef fish species (James et al., 2002; Cowen & Sponaugle, 2009), differential larval supply could influence site-specific lionfish recruitment (Ahrenholz & Morris, 2010). However, such data is not available for our sites. While measuring larval supply would have been interesting, it was outside the scope of our study due to the large number of sites included and the regional scale of the analysis. Additionally, though larval supply can be predicted by biophysical models that describe oceanographic features such as wind direction, surface temperature, or tidal amplitude, these relationships are often taxon-dependent (Wilson & Meekan, 2001; Vallès et al., 2009).

The question from a management point of view is whether native predators can actually constrain lionfish abundance across the Caribbean, given the heterogeneity of the systems and the factors that seemingly affect lionfish abundance. While we found no evidence that large-bodied grouper or any other large-bodied predators influence lionfish invasion success across the region, this finding is expected based on other systems and examples of invasive predators. For example, there is weak support in the literature for the biotic resistance hypothesis of native species constraining exotic predators in natural ecosystems, and rarely can resident predators constrain the distribution expansion of the invader (Harding, 2003; deRivera et al., 2005). In fact, the exact opposite is typical in systems where native predators are abundant. For example, the successful invasion of the Burmese python (*Python molurus bivittatus*) in the Everglades of South Florida has not been constrained by potential and abundant predators such as alligators

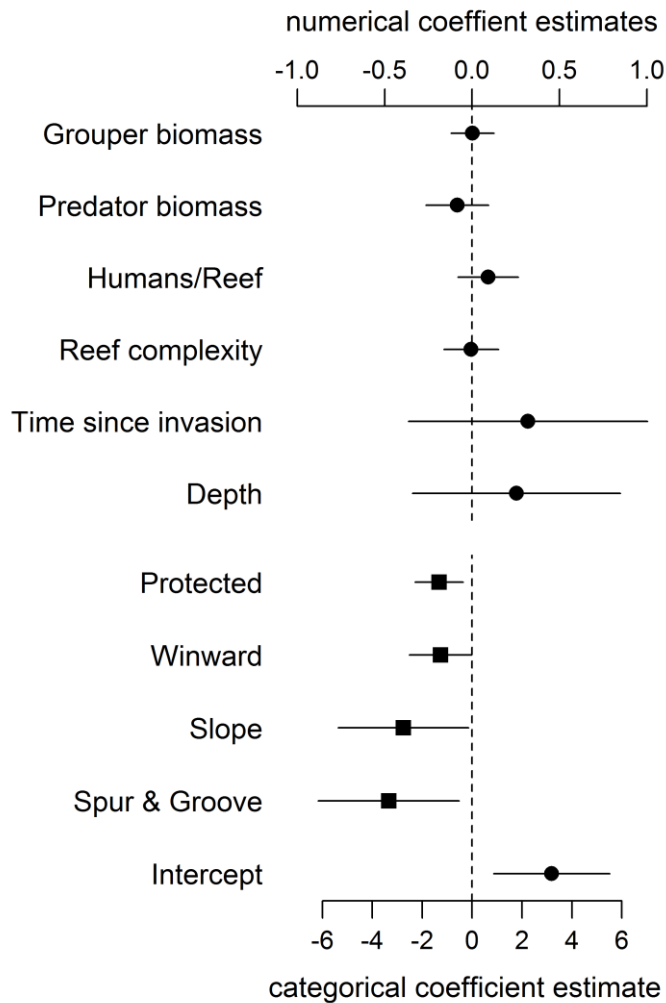
(*Alligator mississippiensis*) (Willson et al., 2011). Moreover, it is common that invasive predators feed on the juveniles of the resident predators and competitors (Snyder & Evans, 2006; MacDonald et al., 2007; Doody et al., 2009; Kestrup et al., 2011; Willson et al., 2011; Côté et al., 2013), further weakening the potential resistance capacity of the system. Ecological interactions, such as predation and competition, seldom enable communities to resist invasion, but instead constrain the abundance of invasive species once they have successfully established (Levine et al., 2004). However, the abundance of lionfish across the region does not appear to be constrained by ecological interactions (Hackerott et al., 2013). In the one published record of grouper eating lionfish (Maljkovic et al., 2008), it could not be determined whether the lionfish were dead or alive when consumed. It is common for divers and tour operators to feed speared lionfish to native predators, including sharks (Busiello, 2011). However, there is no evidence that this practice has changed the natural predatory instincts of resident predators towards the invader and feeding speared lionfish to native predators is now being discouraged due to safety concerns for divers (Whittaker, 2013).

Our results indicate that protection status (i.e., whether sites were located within a marine reserve or not) also had a negative effect on lionfish abundance (Fig. 2.1). This is most likely due to targeted culling in protected areas. Morris and Whitfield (2009) suggested that lionfish removals should be focused on ecologically important areas, including marine protected areas and reserves. Lionfish removals have since occurred in many marine reserves through organized citizen programs (Biggs & Olden, 2011; López-Gómez et al., 2013) and by reef managers (author pers. comm. with Belize Audubon Society). This effort is paying off and has the potential to greatly reduce lionfish abundance, at least temporarily (Barbour et al., 2011; Frazer et al., 2012; Côté et al., 2013). In our dataset, of the six sites with grouper biomass over 20 gm<sup>-2</sup>, five

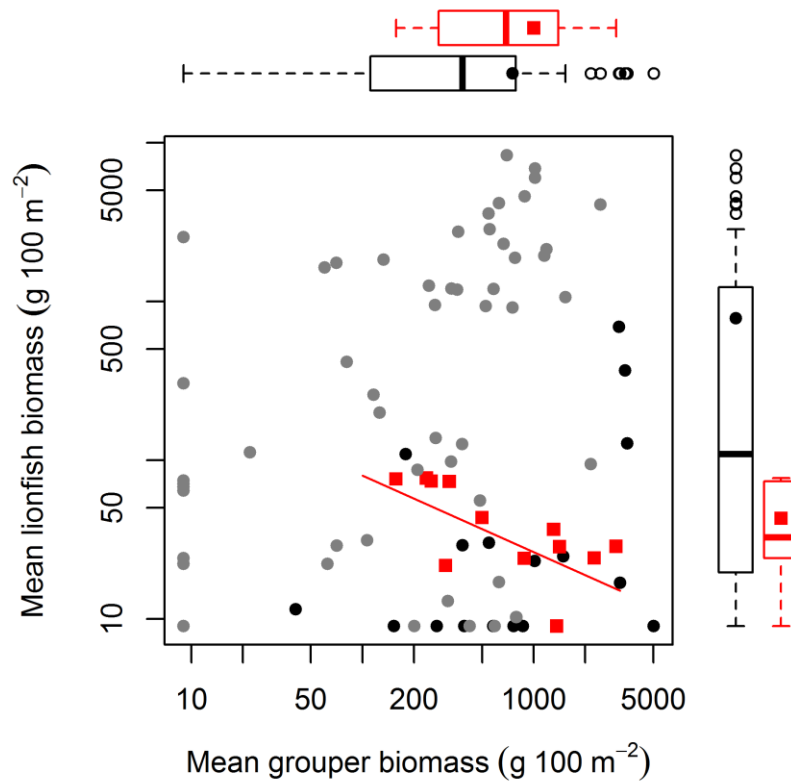
were in protected areas where culling is very likely occurring (Fig. 2.2). This pattern supports the results of our statistical analysis that lionfish abundance is reduced in marine protected areas due to some factor other than predator abundance. The negative effect of protection status on lionfish abundance and lack of effect of grouper or other predator biomass on lionfish abundance indicate that culling within protected areas most likely explains the observed pattern.

This analysis expands our original statistical model of the relationship between invasive lionfish and native grouper species (Hackerott et al., 2013) to include two additional covariates hypothesized to moderate the relationship between these species (Mumby et al. (2013). After accounting for these additional processes, we find that: (a) the biomasses of lionfish and large-bodied grouper (or other predators) are not negatively related, and (b) lionfish biomass is controlled by a number of physical site characteristics, as well as by culling within marine reserves. Our study was motivated by the desire to explore whether the findings and solutions from local case studies will be effective elsewhere, which is key to informed management decisions about the invasion. We conclude that removals are most likely the only feasible mechanism for controlling lionfish at a Caribbean-wide scale.

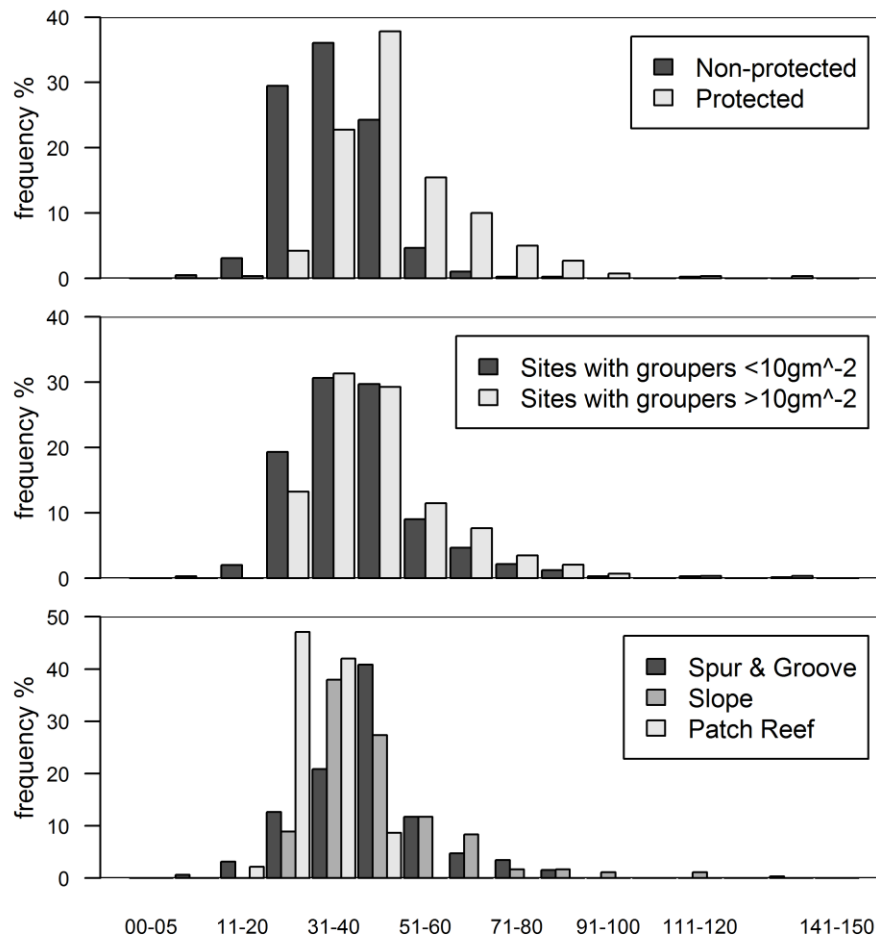
**Figure 2.1 Coefficient estimates ( $\pm$  95% confident intervals) showing the effect of different variables on lionfish abundance.** Lionfish counts were modeled with a generalized linear mixed effect model using the automatic differentiation model builder (glmmADMB) based on a negative binomial distribution type 1 and log link. Abundance values were obtained by adding the log of survey area as offset in the model. Numerical variables (top axis, circles) and categorical variables (bottom axis, squares) are on different scale for easy visual representation as the magnitude effects of the former are relatively smaller. For full summary of the model see Table S2.3.



**Figure 2.2 Relationship between mean grouper and lionfish biomass.** In this study, 71 fore reefs (black dots protected sites, grey dots non-protected sites) were surveyed and analyzed across the Caribbean. For comparison, we included 12 sites (red squares) surveyed at Exuma Cays Land and Sea Park by Mumby et al., (2011). Red fitted line is for the linear regression model by Mumby et al., (2011) that explain 56 % of the variability of lionfish biomass due to grouper abundance. Note that red squares represent ~16 % of all sites. Boxplots are median (vertical or horizontal line), 50 and 90 percentiles for lionfish biomass (right) and grouper biomass (top). Boxplots with black dots (general mean) correspond to our study and boxplots with red squares (general mean) to Mumby et al., (2011). Empty circle are outliers. Axes are in log scale.



**Figure 2.3 Histograms of grouper class size (total length in cm) by categories.** A) Class size distribution for protected and non-protected sites, B) for sites with over and under 10 gm<sup>-2</sup> of grouper biomass, and C) for reef habitat types. Note that over 90% of protected sites and sites with >10 gm<sup>-2</sup> of grouper biomass have individuals >30 cm in total length. Only every other class size has a label for clarity.



## References

- Ahrenholz DW, Morris JA. 2010. Larval duration of the lionfish, *Pterois volitans* along the Bahamian Archipelago. *Environmental Biology of Fishes*. 88(4):305–309.
- Albins M, Hixon M. 2011. Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes*. 1–7.
- Albins MA, Hixon MA. 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series*. 367:233–238.
- Barbour AB, Allen MS, Frazer TK, Sherman KD. 2011. Evaluating the Potential Efficacy of Invasive Lionfish (*Pterois volitans*) Removals. *PLoS ONE*. 6(5):e19666.
- Barbour AB, Montgomery ML, Adamson AA, Díaz-Ferguson E, Silliman BR. 2010. Mangrove use by the invasive lionfish *Pterois volitans*. *Mar Ecol Prog Ser*. 401:291–294.
- Betancur-R R, Hines A, Acero P. A, Ortí G, Wilbur AE, Freshwater DW. 2011. Reconstructing the lionfish invasion: insights into Greater Caribbean biogeography. *Journal of Biogeography*. 38(7):1281–1293.
- Biggs CR, Olden JD. 2011. Multi-scale habitat occupancy of invasive lionfish (*Pterois volitans*) in coral reef environments of Roatan, Honduras. *Aquatic Invasions*. 6(3):447–453.
- BjØrnstad ON. 2013. ncf: Spatial nonparametric covariance functions. *R package version 1.1-5*.
- Bolker B, Skaug H, Magnusson A, Nielsen A. 2012. Getting started with the glmmADMB package.
- Bruno J, Fridley J, Bromberg K, Bertness M. 2005. Insights into biotic interactions from studies of species invasions. *Species invasions: insights into ecology, evolution and biogeography*. 13–40.
- Busiello A. 2011. Pictures: Sharks Taught to Hunt Alien Lionfish. *National Geographic*.
- Byers JE, Noonburg EG. 2003. Scale dependent effects of biotic resistance to biological invasion. *Ecology*. 84(6):1428–1433.
- Carlsson NO, Sarnelle O, Strayer DL. 2009. Native predators and exotic prey –an acquired taste? *Frontiers in Ecology and the Environment*. 7(10):525–532.
- Claydon JAB, Calosso MC, Traiger SB. 2012. Progression of invasive lionfish in seagrass, mangrove and reef habitats. *Marine Ecology Progress Series*. 448:119–129.
- Côté IM, Green SJ, Hixon MA. 2013. Predatory fish invaders: Insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biological Conservation*. 164:50–61.



- Cowen RK, Sponaugle S. 2009. Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science*. 1(1):443–466.
- Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ. 2005. Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. *Ecology*. 86(6):1602–1610.
- deRivera CE, Ruiz GM, Hines AH, Jivoff P. 2005. Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. *Ecology*. 86(12):3364–3376.
- Doody JS, Green B, Rhind D, Castellano CM, Sims R, Robinson T. 2009. Population-level declines in Australian predators caused by an invasive species. *Animal Conservation*. 12(1):46–53.
- Edmunds PJ, Elahi R. 2007. The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecological Monographs*. 77(1):3–18.
- Elton CS. 1958. The ecology of invasions by plants and animals. *Methuen, London*. 18.
- Farmer NA, Ault JS. 2011. Grouper and snapper movements and habitat use in Dry Tortugas, Florida. *Marine Ecology Progress Series*. 433:169–184.
- Frazer TK, Jacoby CA, Edwards MA, Barry SC, Manfrino CM. 2012. Coping with the Lionfish Invasion: Can Targeted Removals Yield Beneficial Effects? *Reviews in Fisheries Science*. 20(4):185–191.
- Friedlander AM, DeMartini EE. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Marine Ecology Progress Series*. 230:253–264.
- Froese R, Pauly D. 2013. FishBase. *World Wide Web electronic publication (version 10/2013)*.
- Graham MH. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology*. 84(11):2809–2815.
- Green S, Côté I. 2009. Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs*. 28(1):107–107.
- Green SJ, Akins JL, Ct IM. 2011. Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Marine Ecology Progress Series*. 433:159–167.
- Green SJ, Akins JL, Maljković A, Côté IM. 2012. Invasive Lionfish Drive Atlantic Coral Reef Fish Declines. *PLoS ONE*. 7(3):e32596.
- Green SJ, Dulvy NK, Brooks ALM, Akins JL, Cooper AB, Miller S, Côté IM. 2013. Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecological Applications*.

- Green SJ, Tamburello N, Miller SE, Akins JL, Côté IM. 2012. Habitat complexity and fish size affect the detection of Indo-Pacific lionfish on invaded coral reefs. *Coral Reefs*.
- Gust N, Choat J, McCormick M. 2001. Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. *Marine Ecology Progress Series*. 214:237–251.
- Hackerott S, Valdivia A, Green SJ, Côté IM, Cox CE, Akins L, Layman CA, Precht WF, Bruno JF. 2013. Native Predators Do Not Influence Invasion Success of Pacific Lionfish on Caribbean Reefs. (F. Guichard, Ed.) *PLoS ONE*. 8(7):e68259.
- Harding JM. 2003. Predation by blue crabs, *Callinectes sapidus*, on rapa whelks, *Rapana venosa*: possible natural controls for an invasive species? *Journal of Experimental Marine Biology and Ecology*. 297(2):161–177.
- James MK, Armsworth PR, Mason LB, Bode L. 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. *Proceedings of the Royal Society of London. Series B: Biological Sciences*. 269(1505):2079–2086.
- Jud ZR, Layman CA, Lee JA, Arrington DA. 2011. NOTE Recent invasion of a Florida (USA) estuarine system by lionfish *Pterois volitans* / *P. miles*. *Aquatic Biology*. 13(1):21–26.
- Kestrup ÅM, Dick JTA, Ricciardi A. 2011. Interactions between invasive and native crustaceans: differential functional responses of intraguild predators towards juvenile hetero-specifics. *Biological Invasions*. 13(3):731–737.
- Lesser MP, Slattery M. 2011. Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biological Invasions*. 13(8):1855–1868.
- Levine JM, Adler PB, Yelenik SG. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*. 7(10):975–989.
- Lockwood JL, Cassey P, Blackburn T. 2005. The role of propagule pressure in explaining species invasions. *Special issue: Invasions, guest edited by Michael E. Hochberg and Nicholas J. Gotelli*. 20(5):223–228.
- López-Gómez MJ, Aguilar-Perera A, Perera-Chan L. 2013. Mayan diver-fishers as citizen scientists: detection and monitoring of the invasive red lionfish in the Parque Nacional Arrecife Alacranes, southern Gulf of Mexico. *Biological Invasions*. 1–7.
- MacDonald JA, Roudez R, Glover T, Weis JS. 2007. The invasive green crab and Japanese shore crab: behavioral interactions with a native crab species, the blue crab. *Biological Invasions*. 9(7):837–848.
- MacNeil MA, Graham NAJ, Polunin NVC, Kulbicki M, Galzin R, Harmelin-Vivien M, Rushton SP. 2009. Hierarchical drivers of reef-fish metacommunity structure. *Ecology*. 90(1):252–264.

- Magoulick DD, Lewis LC. 2002. Predation on exotic zebra mussels by native fishes: effects on predator and prey. *Freshwater Biology*. 47(10):1908–1918.
- Maljković A, Leeuwen TEV, Cove SN. 2008. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs*. 27(3):501–501.
- Maljkovic A, van Leeuwen TE, Cove SN. 2008. Predation on the invasive red lionfish, *Pterois volitans* (Pisces : Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs*. 27:501–501.
- Mantel N. 1967. The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer Research*. 27(2 Part 1):209 –220.
- Mazia NC, Chaneton EJ, Ghera CM, León RJ. 2001. Limits to tree species invasion in pampean grassland and forest plant communities. *Oecologia*. 128(4):594–602.
- McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA. 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in kenya. *Ecological Applications*. 17(4):1055–1067.
- Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H. 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters*. 10(1):77–94.
- Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloom EW, Torchin ME, Vázquez DP. 2006. Biotic interactions and plant invasions. *Ecology Letters*. 9(6):726–740.
- Mora C. 2008. A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society B: Biological Sciences* . 275 (1636 ):767–773.
- Morris JA, Akins JL. 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environmental Biology of Fishes*. 86(3):389–398.
- Mumby PJ, Brumbaugh DR, Harborne AR, Roff G. 2013. On the relationship between native grouper and invasive lionfish in the Caribbean. *PeerJ PrePrints*.
- Mumby PJ, Harborne AR, Brumbaugh DR. 2011. Grouper as a natural biocontrol of invasive lionfish. *PLoS ONE*. 6(6):e21510.
- Newton K, Côté IM, Pilling GM, Jennings S, Dulvy NK. 2007. Current and Future Sustainability of Island Coral Reef Fisheries. *Current Biology*. 17(7):655–658.
- Paddack MJ, Reynolds JD, Aguilar C, Appeldoorn RS, Beets J, Burkett EW, Chittaro PM, Clarke K, Esteves R, Fonseca AC, Forrester GE, Friedlander AM, García-Sais J, González-Sansón G, Jordan LKB, McClellan DB, Miller MW, Molloy PP, Mumby PJ,

- Nagelkerken I, Nemeth M, Navas-Camacho R, Pitt J, Polunin NVC, Reyes-Nivia MC, Robertson DR, Rodríguez-Ramírez A, Salas E, Smith SR, Spieler RE, Steele MA, Williams ID, Wormald CL, Watkinson AR, Côté IM. 2009. Recent region-wide declines in Caribbean reef fish abundance. *Current biology : CB*. 19(7):590–595.
- Polunin NVC, Roberts CM. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology-Progress Series*. 100:167.
- R Core Team. 2013. R: A Language and Environment for Statistical Computing, Vienna, Austria.
- Reusch TB, Williams SL. 1999. Macrophyte canopy structure and the success of an invasive marine bivalve. *Oikos*. 398–416.
- Sale PF. 2002. Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. Academic Press.
- Schofield P. 2009. Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. *Aquatic Invasions*. 4(3):473–479.
- Schutte VGW, Selig ER, Bruno JF. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Mar Ecol Prog Ser*. 402:115–122.
- SEDAC (Socioeconomic Data and Applications Center). 2010. Global rural-urban mapping project – settlement points. Columbia University, New York.
- Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B. 2013. glmmADMB: Generalized linear mixed models using AD model builder. *R package version 0.7.7*. 4.
- Snyder WE, Evans EW. 2006. Ecological Effects of Invasive Arthropod Generalist Predators. *Annual Review of Ecology, Evolution, and Systematics*. 37:95–122.
- UNEP-WCMC, WorldFish Centre, WRI, TNC. 2010. Global distribution of warm-water coral reefs, compiled from multiple sources, including the Millennium Coral Reef Mapping Project. UNEP World Conservation Monitoring Centre. Cambridge (UK).
- Vallès H, Hunte W, Kramer DL. 2009. Variable temporal relationships between environment and recruitment in coral reef fishes. *Mar Ecol Prog Ser*. 379:225–240.
- Whitfield P, Hare J, David A, Harter S, Muñoz R, Addison C. 2007. Abundance estimates of the Indo-Pacific lionfish *Pterois volitans*-miles complex in the Western North Atlantic. *Biological Invasions*. 9(1):53–64.
- Whittaker J. 2013. Hunters warned not to feed lionfish to predators. *CayCompass*.

- Willson JD, Dorcas ME, Snow RW. 2011. Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in Southern Florida. *Biological Invasions*. 13(7):1493–1504.
- Wilson DT, Meekan MG. 2001. Environmental influences on patterns of larval replenishment in coral reef fishes. *Marine Ecology Progress Series*. 222:197–207.
- Wilson S, Graham N, Polunin N. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*. 151(3):1069–1076.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Violation of Independence – Part II. In: *Mixed effects models and extensions in ecology with R*. Springer New York, 161–191.

## CHAPTER 3

### **Reef fish assemblages and resilience of coral reefs to ocean warming across two distinct geographical regions**

#### **Abstract**

The persistence of coral reef ecosystems in the near future will greatly depend on the capacity of the system to resist and recover from global-scale stressors such as ocean warming and acidification. Reducing localized stressors such as overfishing may increase the resilience of the system to tolerate climate-related disturbances. Particularly, increasing the abundance and functional diversity of key herbivores that shift the balance between macroalgae and corals may facilitate coral recovery after warming events. However, the direct link between fish, algae and coral under different thermal stress regimes has never been analyzed across large spatial scales. Here we asked whether reefs with higher abundance of reef fishes were associated with higher contemporary coral cover (as an approximated measure of coral resilience), across two geographically distinct regions, such that those communities may have lost relatively less coral cover after a recent history of thermal anomalies. We found that spatial patterns of coral cover at geographical scales were associated with a myriad of factors, and the relationship of herbivores-algae-cover was complex. Reefs that experienced higher frequency of thermal stress anomalies showed higher coral cover. However, herbivorous fishes were not more abundant in those reefs, although they showed strong negative correlation with macroalgae cover. Our results do not support the hypothesis that current fish biomass, especially herbivorous fishes, has a cascading effect on contemporary coral cover across geographical scales.

**Keywords:** climate change, fish biomass, coral reefs, resilience, Caribbean, Pacific

## **Introduction**

Global climate change such as ocean warming combined with local stressors such as overfishing and pollution have been major drivers of considerable marine ecosystem degradation during the past decades (Gardner et al. 2003, Hughes et al. 2003, Pandolfi et al. 2003, Bellwood et al. 2004, Bruno and Selig 2007, Hoegh-Guldberg et al. 2007). Restoring degraded marine ecosystems will depend on addressing local chronic stressors to increase ecosystem resilience to global effects (Hughes et al. 2003, 2007, McClanahan et al. 2008, Knowlton and Jackson 2008, McLeod et al. 2009) since humanity is failing to control climate change (Victor 2008, Dutt and Gonzalez 2012, IPCC 2013). This approach is based on the premise that reducing local stressors can increase the capacity of an ecosystem to resist and recover from future climate disturbances (Hughes et al. 2003, 2007, Mumby et al. 2014). However, evidence that support such statement is equivocal (Côté and Darling 2010).

No-take marine reserves are currently the best management tool to ameliorate the effects of local-scale stressors (Halpern and Warner 2002, Lubchenco et al. 2003, Edgar et al. 2014). Although they have been mostly effective in restoring fish biomass, increasing biodiversity of a variety of taxa, and protecting critical habitats (Côté et al. 2001, Halpern and Warner 2002, Lester et al. 2009, Gaines et al. 2010), marine reserves are incapable of shielding ecosystems from the effects of climate change (Keller et al. 2009). In coral reefs for example, reserve's boundaries cannot protect reef-building corals from acute thermal stress anomalies that cause widespread bleaching and mortality (Hughes et al. 2003, Graham et al. 2008, Selig et al. 2012), or from ocean acidification that constrains coral calcification (Hoegh-Guldberg et al. 2007, Dove

et al. 2013, Billé et al. 2013). But protection could promote the control of local land-based threats such as sedimentation and pollution, potentially reducing coral's susceptibility to diseases (Bruno et al. 2003) and bleaching (Wiedenmann et al. 2013). Individual marine reserves can also restore fish assemblages that may indirectly promote coral recovery (Mumby et al. 2007a, Mumby and Harborne 2010). Thus, the elimination of these localized stressors are hypothesized to increase the capacity of corals to resist and recover from climate-driven stress anomalies (Hughes et al. 2007, McLeod et al. 2009, Keller et al. 2009, Rau et al. 2012, Graham et al. 2013).

In reality, current conservation efforts in coral reefs rely mostly or entirely on fisheries regulations (Lester et al. 2009, Gaines et al. 2010), because the reduction of local stressors such as pollution or sedimentation is in most cases impractical (McLeod et al. 2009, Keller et al. 2009, Rau et al. 2012). Thus, the restoration of reef fish assemblages within reserves may be the most realistic solution to promote coral resilience under climate change scenarios. But marine reserves can reach disparate levels of fish abundance (Harborne et al. 2008, Babcock et al. 2010, Karnauskas et al. 2011) depending on their oceanographic conditions, placement, configuration, past history, age, size, and enforcement level (Gaines et al. 2010, Edgar et al. 2014). In this context, the actual currency to measure the potential effects of marine reserves on coral resilience must be the abundance and composition of their fish assemblages. A fundamental question remains as whether increasing fish abundance and functional diversity will confer benefits to reef building organisms in the face of climate change, such that coral communities within areas of higher fish abundance will fare better than in areas with less fish.

Reef fish assemblages could increase coral resilience to thermal disturbance through at least two indirect mechanisms. First, through top-down grazing by herbivorous fishes that shift the balance between macroalgae and corals, facilitating coral recovery (McCook et al. 2001,



Mumby et al. 2007a, Hughes et al. 2007). In principle, increasing the abundance and diversity of a whole set of key herbivorous fishes increases grazing pressure on different functional groups of algae (Williams and Polunin 2001, Bellwood et al. 2006, Cheal et al. 2010) that inhibited coral settlement, recruitment, or that smother juveniles and adult corals (McCook et al. 2001, Kuffner et al. 2006, Birrell et al. 2008, Diaz-Pulido et al. 2010, Rasher and Hay 2010). Greater grazing intensity may also promote higher cover of crustose coralline algae (CCA) that facilitate coral settlement (Bak 1976, O'Leary et al. 2012). Second, fish communities may provide coral resilience through bottom-up effects by supplying consumer-mediated nutrients of adequate N:P ratios necessary to maintain healthy coral-endosymbionts relationships (Allgeier et al. 2014). This last mechanism is however, a hypothesis that has yet to be tested at appropriated scales. Thus, more resilient coral reefs may exhibit relatively higher abundance of both calcifying functional groups, corals, and CCA (Vroom 2011) and less macroalgae along a gradient of fish abundance and functional diversity. In theory, both of these top-down or bottom-up controls may promote resilience of coral communities to thermal stress at large spatial scales.

Regardless of the mechanism, there is little evidence that across broad geographical scales increasing fish abundance within marine reserves can benefit corals to counteract the effects of acute thermal disturbance (Keller et al. 2009, Darling et al. 2010, Selig et al. 2012). This lack of clear effects could be explained if protection is insufficient to restore fish to adequate levels to reverse degradation of coral reefs to less degraded states (Côté and Darling 2010, Graham et al. 2013) or because numerous variables affect the mechanisms through which fish can benefit corals. Although most marine reserves have no positive effect on coral communities (Huntington et al. 2011, Toth et al. 2014), some individuals reserves show higher coral species diversity (McClanahan 2008), may prevent coral loss (Selig and Bruno 2010), and

may facilitate coral recruitment and rates of coral recovery by ultimately declining algae abundance (Mumby et al. 2007a, Mumby and Harborne 2010). However, even when marine reserves may promote limited coral recovery, it is not clear whether this pattern can be detected across broad spatial scales because frequent thermal-stress events can outweigh any benefit provided by local protection from fishing (Hoegh-Guldberg et al. 2007, Darling et al. 2013).

Here, we assess the relationship between major functional groups of benthic and reef fish assemblages across broad spatial scales within two biogeographically distinct regions of the world, the Caribbean and US Pacific Islands. These reef regions greatly differ in species diversity, functional redundancy, oceanographic conditions, and ecosystem resilience (Roff and Mumby 2012). Our main objective was to determine whether general and spatial patterns of contemporary coral communities, that have resisted and partially recovered from recent thermal stress anomalies over the past three decades, are associated with current abundance of reef fish functional groups. While several studies have analyzed the relationship between fish and benthic assemblages across space (e.g., Newman et al. 2006, Sandin et al. 2008, Sala et al. 2012), or evaluate the effects of coral loss on fish assemblages and fisheries productivity (Jones et al. 2004, Rogers et al. 2014, Graham 2014), a direct link between reef fishes facilitating coral recovery from thermal stress anomalies has never been established across geographical regions. Thus, we hypothesize that across large spatial scales and independent of geographical regions, higher abundance of reef fishes may be associated with higher resilience of coral assemblages such that those communities may have lost relatively less coral cover due to thermal disturbance (Hughes et al. 2007, Côté and Darling 2010, Mumby et al. 2014). These coral reefs may exhibit relatively higher percentage of coral cover, higher cover of crustose coralline algae, and lower macroalgae abundance. However, whether these patterns can be detected across large

geographical scales is unclear due to a myriad of factors that affect the cascading effects of fish assemblages on benthic communities. Thus, we examined the contemporary response of these benthic coral reef communities across a gradient of fish abundance, thermal stress anomalies, human impact, and environmental variability that may compromise any effect of fish on coral recovery.

## **Materials and Methods**

### ***Caribbean study regions***

Surveys of benthic and fish assemblages were performed on slope and spur-and-groove fore-reefs 10-15m deep, usually dominated by the corals *Orbicella* spp. (formerly named *Monstastrea* spp.), across 38 sites in The Bahamas, Cuba, Florida (USA), Mexico, and Belize (Fig. 3.1a, Table S3.1). We selected sites to maximize the range of total fish biomass in each sub-region by including reefs inside and outside marine reserves (i.e. no-take zones where fishing was prohibited). To minimize seasonal variability, we conducted all surveys during the summer months of May to July, 2010-2012 (Table S3.1).

### ***Pacific study regions and data acquisition***

We used data on coral reef fish and benthic assemblages gathered by the NOAA's Pacific Reef Assessment and Monitoring Program (Pacific RAMP) that survey coral reefs at US flag islands across the Pacific. Surveys were conducted by the NOAA Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Division (CRED) in four major regions, the Hawaiian and Mariana Archipelagos, American Samoa islands, and the Pacific Remote Island Areas (PRIAs). Except for the unpopulated PRIAs, several islands within each region sustain dense

human populations that directly affect their coral reefs through fishing (Williams et al. 2011, Nadon et al. 2012). Islands such as Oahu (Hawaii), Guam (Mariana Archipelago), and Tutuila (American Samoa) are among the most populated in the tropical Pacific (Williams et al. 2011). In contrast, remote islands far from human settlements are mostly free of direct human influence.

We selected data from 36 islands and atolls (hereafter “islands”) surveyed between 2006 and 2010 where both fish and benthic assemblages have been studied in detail (Table S3.2). Reef sites comprised fore reef environments <30 m deep. We exclude from the analysis islands with very different oceanographic conditions (e.g., upwelling episodes, no storms events, high frequency of thermal stress anomalies) (Gove et al. 2013). The extent of differences across these 36 islands for reef fish assemblages and shark populations are quantified in detail in Williams et al. (2011) and Nadon et al. (2012), respectively. Major benthic groups such as corals, macroalgae, and crustose coralline algae are also characterized in Vroom (2011) and Schils et al. (2013).

### ***Fish assemblage surveys***

Underwater visual censuses (UVC) were used to characterize the fish assemblages. Survey design and methodology was characterized in detail in Chapter 1 for the Caribbean, and in Williams et al. (2011) for the Pacific.

For the Caribbean, at each reef site we randomly placed six to eight belt transect sets along the fore reef’s spur-and-groove or slope formations and recorded, identified, and estimated body size of all reef fish species. Each set consisted in a 50 x 10 m transect area to estimate fish  $\geq 40$  cm in total length (TL) (McCauley et al. 2012) and a nested 30 x 2 transect area to estimate fish <40 cm TL (Lang et al. 2010). Fish size was estimated to the nearest 10 cm, except

for fish <10 cm where a 5 cm interval was used. Each transect belt set was surveyed in ~15 minutes, covered the entire visible water column, and were at least ~10 m apart.

For the Pacific, fish data was extracted from Williams et al., (2011) from which two UVC survey methods were used. In the Mariana Archipelago, American Samoa, and PRIA, surveys were performed using stationary point counts (SPCs) as in Ault et al. (2006), while belt transects and SPCs were used in the Hawaiian Archipelago. Both methods give similar estimates of total fish and planktivore biomass (<5% mean difference), but relative to SPCs, belt transects tend to over-represent herbivore (by 19%) and secondary consumer (by 34%) while under-represent piscivores biomass (by 23%) (Williams et al. 2011). Each SPC consisted in a 15 m diameter plot where fish species were identified, counted, and sizes were estimated (total length, TL, to the nearest cm). Detailed description of the SPCs protocol is elsewhere (Ault et al. 2006). For belt transect surveys, fish species were identified, counted and sized (TL to the nearest cm) in two swimming passes along a 25 m long belt transect. Fish  $\geq 20$  cm TL were recorded on 4 m-wide belts during the first pass, while fish < 20 cm TL were recorded on 2 m-wide belts at the return pass (Williams et al. 2011). At each site, two SPC or belt transects were surveyed and both covered the entire visible vertical water column. The number of surveyed sites per island varied and fish biomass was averaged at the island level for analysis.

Fish biomass per unit area (hereafter “biomass”) was used as the currency to analyze fish abundance. Biomass was calculated using the allometric conversion relationship  $W = aL^b$  (Froese and Pauly 2013) where  $W$  is the weight of each fish in grams,  $L$  is the total length ( $TL$ ) or fork length ( $FL$ ) in cm, and the parameters  $a$  and  $b$  are species specific. Length-length conversion parameters were used to convert  $TL$  to  $FL$  for those species that  $L$  was based on  $FL$ . When the

allometric parameters ( $a$  and  $b$ ) were not available we used those values from congeneric species of similar size and shape and of similar geographical range (Froese and Pauly 2013).

Fish species were grouped into four major trophic groups, “primary consumers” (herbivores and detritivores); “secondary consumers” (omnivores and benthic invertivores); “planktivores”; and “piscivores” (e.g., species mostly feed on fish but can also feed on invertebrates) based on dietary information (Froese and Pauly 2013). For fish species classification see Chapter 1, Table S1.2 for the Caribbean and Sandin and Williams (2010) for the Pacific.

### ***Benthic assemblage surveys***

For the Caribbean, current cover data of benthic communities by categories (i.e. coral by species, algae by genus or functional groups, gorgonians, sponges, and other) were measured at each site using point intercepts in 6-8 transect lines (10 m long) (Lang et al. 2010) and/or in 6-8 video transects (50 m long) (Carleton and Done 1995). Point intercept transects (PITs) were used at the Belize sites, while both PITs and video transects were used at the rest of the sites. Both methods provided similar accuracy and results in estimating benthic cover categories in our study. Each benthic transect corresponded to a fish transect set. To estimate percent cover, 100 points per transect was used in PITs (Lang et al. 2010), while ~600 points were extracted from each video transect (Carleton and Done 1995).

Benthic percent cover data for the US Pacific islands were extracted from Vroom et al. (2011). These data was collected via CRED towed-diver surveys (Kenyon et al. 2006) from 2004 through 2009 RAMP research expeditions. The towed-diver survey method characterizes benthic communities at a coarse taxonomic resolution across large spatial scales. As such, benthic

assemblages were divided in several major functional groups (e.g. hard coral, crustose coralline algae, macroalgae, soft coral, sand, rubble, other). For the purpose of our study, however, we only used the average among years for the benthic cover data correspondent to hard corals, crustose coralline algae, and macroalgae as in Vroom et al. (2011). We used five years of data because we were interested on the overall effects of fish communities on the benthic assemblages. For detail description of tower-diver methodology see Kenyon et al. (2006).

### *Covariates*

For each Caribbean site and Pacific islands we created a data set of anthropogenic, oceanographic, physical, and biotic parameters (see supporting information). These variables may directly and indirectly affect the coerture of calcifying organisms (i.e. hard corals and CCA) and macroalgae abundance and therefore may modulate the cascading effect of fish assemblages on benthic communities. Anthropogenic-related parameters included number of humans within 50 km radius of each site for the Caribbean and human population density per island for the Pacific. Oceanographic variables included mean frequency of thermals stress anomalies (TSA), oceanic primary productivity (for the Caribbean) and Chlorophyll-a concentration (proxy for oceanic primary productivity for the Pacific), and average wave exposure. Physical parameters included landscape reef complexity measured on a six-level scale (Polunin and Roberts 1993), reef area around each Pacific island, and maximum island elevation. Biotic parameters included the biomass of aforementioned trophic fish groups. For detail description, measurements and reasoning for using each variable refer to Appendix 3.1.

## *Data analysis*

### *Effect of fish biomass and temperature anomalies on corals and CCA cover*

Our study was based on the premise that increasing fish abundance, especially piscivorous and herbivorous fishes, may have increased the resilience of major calcifying organisms (e.g., corals and CCA) to tolerate warming anomalies, such that the relative contemporary benthic cover of these groups would be higher. Therefore, in our models we assume that fish assemblages affect benthic communities by top down control (Mumby et al. 2007a) and resources supply (Allgeier et al. 2014). In this context, the interactive effects of fish abundance with thermal stress anomalies on benthic communities should be significant. We did not include protection level in the models as MPAs are not a good predictor of coral change (Selig and Bruno 2010, Selig et al. 2012). As such, we avoid problems associated with the effectiveness of MPAs in protecting fish assemblages. Thus, we assumed that a gradient of fish biomass (especially piscivorous and herbivorous fish) may better explain a potential effect on benthic communities.

We evaluated multi-collinearity among all explanatory predictors using a Spearman's rank ( $r_s$ ) correlation matrix and pairs plot based on the mean values for Caribbean sites and Pacific islands (Fig S3.1). Several covariates were sufficiently correlated ( $-0.5 > r_s > +0.5$ ) to compromise the interpretation of coefficient estimates when modeled together (Graham 2003). For example, in the Caribbean, the biomass of herbivorous fishes was negative correlated with macroalgae cover ( $r_s = -0.62$ ), as it was the biomass of piscivorous fishes and reef complexity ( $r_s = 0.60$ ), and macroalgae and turf cover ( $r_s = -0.62$ ) (Fig. S3.1a). In the Pacific, high correlations occurred among several biotic and environmental variables that could not be modeled together (Fig. S3.1b). For the rest of the correlation values among predictors see Fig. S3.1. To avoid



multi-collinearity problems we grouped uncorrelated variables (e.g.,  $-0.5 < r_s < +0.5$ ) and created three model sets for the Caribbean and four model sets for the Pacific (Table S3.3). With this approach we model all potential covariates; however, we cannot differentiate between unique and shared variance contributions of each strongly correlated covariate on the response variable.

### ***Model selection and multi-model averaging***

We used generalized linear mixed-effects models (GLMMs, Bolker et al. 2009) to assess the interaction effect of fish abundance and thermal stress anomalies on benthic assemblages. We created several sets of global models for each response variable (i.e., coral, CCA, and macroalgae cover) at each geographical region. To account for potential spatial autocorrelation we used random intercept models where sites (or islands) were allowed to vary within country and region respectively. A logistic (logit) transformation was applied to the percent cover data and treated the logit as normally distributed (Lessafre et al. 2007). We transformed  $(\log(x+1))$  the biomass values of each fish functional group used as predictors in the models.

For each response variable, we run models fitted by maximum likelihood (Adaptive Gauss-Hermite Quadrature,  $n_{AGO} = 0$ ) with all possible combinations of predictors and hypothesized interactions within the model sets. To compare relative effect sizes of predictors, we standardized our data by centering and dividing by two standard deviations (Zuur et al. 2009). We evaluated the relative importance of each predictor using AICc (for small sample sizes) model selection and incorporated model uncertainty using model averaging for those with  $\Delta AICc < 2$  using the ‘natural average’ method (Burnham and Anderson 2002, Grueber et al. 2011). Average parameter estimates were calculated for each predictor from its weights in the set of top models.

Model validation to assess heterogeneity was performed by examining the error distribution of top models in the plot of normalized residuals against fitted and explanatory values. For normality validation we used the normal scores of standardized residuals deviance (Zuur et al. 2009). Additionally, spline spatial correlograms were plotted to corroborate that the top model residuals were independent and not spatially autocorrelated (Zuur et al. 2009). All analyses were performed in the statistical software R v.3.03 (R Core Team 2013) using the function `glmer()` from package *lme4* v.0.99-2 for GLMMs and *MuMIn* v.1.9.13 for model averaging.

## Results

### *Spatial variation of benthic and fish functional groups in the Caribbean and Pacific*

The average coral cover across the 38 fore reefs in the Caribbean was  $15.6 \pm 1.2$  % (mean  $\pm$  SE) ranging from 1.5 % at Loggerhead (LG, Florida), to 29.5 % at Pampion (PO, Belize). Reefs within and outside protected areas had similar coral cover with  $15.5 \pm 1.6$  % and  $15.7 \pm 2.0$  %, respectively. Across the 36 US Pacific islands, mean coral cover was  $16.7 \pm 1.3$  % and similar to the Caribbean (Welch test,  $df = 71.5$ ,  $p = 0.5336$ ) with the lowest value (2.5 %) at Midway atoll (MID, Hawaiian archipelago), and the highest (36.9 %) at Swains islands (SWA, American Samoa). Overall, populated islands in the Pacific had lower mean coral cover ( $13.9 \pm 1.6$  %) than remote islands ( $18.7 \pm 1.8$  %), however, this apparent difference was not statistically significant ( $F = 3.6$ ,  $df = 34$ ,  $p = 0.0675$ ).

The mean cover of crustose coralline algae (CCA) across the Caribbean was  $7.2 \pm 1.2$  % while across the Pacific islands was significantly higher with  $12.2 \pm 1.5$  % (Welch test,  $df = 67.1$ ,  $p = 0.01$ ). In the Caribbean, CCA cover ranged from 0.7% at Rocky Point (RP) to 36.5% at

Fowls Cay (FC), both sites in the Bahamas. Protected reefs in the Caribbean had slightly higher mean CCA cover ( $9.0 \pm 2.4\%$ ) than reefs outside marine reserves ( $5.9 \pm 1.2\%$ ), but these values were statistically similar ( $F = 1.69$ ,  $df = 36$ ,  $p = 0.2015$ ). Across the Pacific islands, CCA cover was the lowest at Lanai islands (LAN, Hawaiian archipelago) with 2.5% and the highest at Ofu and Olosega islands (OFU, American Samoa) with ~41.0%. Remote and populated islands had similar average of CCA cover with  $12.4 \pm 1.8\%$  and  $12.0 \pm 2.7\%$ , respectively.

Macroalgae cover was twofold higher across the Caribbean than in the Pacific islands. Mean macroalgae cover across the Caribbean was  $39.1 \pm 2.1\%$  while in the Pacific islands was significantly lower with  $20.2 \pm 1.6\%$  (Welch test,  $df = 68.3$ ,  $p < 0.00001$ ). The Caribbean site with the lowest mean macroalgae cover was Paraiso Bajo (PB, Mexico) with 6.2%, while the site with the highest cover was South Water (SW, Belize) with 56.5%. Protected reefs in the Caribbean had lower average of macroalgae cover ( $31.9 \pm 3.3\%$ ) than reefs outside marine reserves ( $43.8 \pm 2.3\%$ ) ( $F = 9.5$ ,  $df = 36$ ,  $p = 0.003$ ). Across the Pacific islands, Farallón de Pájaros (FDP) had the lowest average of macroalgae cover with 2.6% while Tinian (TIN) showed the highest values with 42.7%, both islands are within the Mariana archipelago. Although remote Pacific islands had apparently lower macroalgae cover ( $17.9 \pm 1.6\%$ ) than populated islands ( $23.4 \pm 2.9\%$ ), this difference was not significant ( $F = 3.1$ ,  $df = 34$ ,  $p = 0.089$ ).

Overall, the patterns of benthic cover of major functional groups across protection status in the Caribbean and remote/populated islands in the Pacific were variable and indicated that protection or remoteness was not a good predictor of relative abundance across spatial scales.

### ***Model description for corals***

Contemporary coral cover, showed both similar and disparate response to several anthropogenic and environmental variables across Caribbean sites and Pacific islands (Fig. 3.2). The density of humans per reef area (a proxy of anthropogenic impact) showed no effect on the average coral cover across both geographical regions (Fig. 3.2). Coral cover declined along a gradient of wave exposure across the Caribbean but showed not trend across the Pacific islands (Fig. 3.2). In contrast, it showed no association with Chlorophyll-a concentration (a proxy of ocean productivity) across Caribbean sites, but both variables were positively associated across the Pacific islands (Fig. 3.2). Coral cover was also positively correlated with reef complexity across both geographical regions (Fig. 3.2), and this variable had high relative importance in all top models (Table S3.3). In both regions, reef complexity was estimated at the seascape level and does not necessarily accounts for current percentage of coral cover. Across Pacific islands, reef area and island elevation had not relationship with coral cover (Fig. 3.2). Finally, coral cover was positively associated with the average frequency of thermal stress anomalies (TSA) over ~28 years (1982-2010) in both geographical regions (Figs. 3.2 and 3.3). However, TSA had greater relative importance and had a stronger effect (greater coefficient estimates) in the Caribbean than across Pacific islands (Table S3.3, Figs. 3.2 and 3.3). In fact, the coefficient estimate for TSA was only significant in one out of two model sets for the Pacific (Fig. 3.2b).

We found no evidence of positive interaction between TSA frequency and the biomass of herbivorous fishes on coral cover across Caribbean sites (Figs. 3.2a and 3.3a), or between TSA and piscivores biomass across Pacific islands. This last interaction term was not selected in the top models for the Pacific and we excluded it from the summary table (Table S3.3, Fig. 3.3). Because the negative correlation between piscivores and TSA ( $r_s = -0.55$ ) across the Caribbean,

and between herbivores and TSA ( $r_s = -0.59$ ) across the Pacific, we could not model these variables together in the GLMMs. However, by plotting the relationships between coral cover on TSA frequency and herbivore and piscivores biomass, we found no support for the hypothesis that the response of contemporary coral cover to recent thermal stress has been modulated by contemporary fish abundance (herbivorous and piscivorous fish biomass) across geographical regions (Fig. 3.3). Nonetheless, current coral cover was positively associated with the biomass of piscivorous fishes in the Caribbean (Figs. 3.2a and 3.3a). Piscivores biomass, however, increased with reef complexity ( $r_s = 0.60$ ) (Fig. S3.2) and may be driving the association with corals. In contrast, coral cover showed no relationship with piscivorous fishes across Pacific islands (Figs 3.2b and 3.3b) or with the biomass of herbivorous fishes across both geographical regions (Figs. 3.2 and 3.3). In fact, herbivorous fishes had zero relative importance on coral cover across Pacific islands and did not make the top models (Table S3.3; Figs 3.2b and 3.3b). Finally, coral cover was also unrelated to the biomass of fish secondary consumers (i.e., invertivores and omnivores) and planktivores across both geographical regions (Fig. 3.2).

We found no relationship between contemporary coral and macroalgae cover across both geographical regions (Fig. 3.2). However, the cover of crustose coralline algae (CCA) was positively related to coral cover across Caribbean sites, but showed no association across the Pacific islands (Fig. 3.2). Turf cover was negatively related to coral cover across Caribbean sites. But we considered this association to be non-significant because the relative importance of this variable in the model set was 0.76 (Table S3.3) and the significance ( $p$ -value = 0.0488) from the GLMMs model averaging was too close to 0.05. Although we found no direct link between fish biomass (especially herbivorous fishes) and coral cover, we evaluated next well-established

hypotheses of functional and ecological relationship between herbivorous fishes and CCA and macroalgae cover across geographical regions.

### ***Models description for CCA***

CCA cover was negatively related to humans/reef across the Caribbean (Fig. 3.2a), however we found no association across Pacific islands where this covariate did not make the top models (Table S3.3, Fig. 3.2b). Among the environmental variables, wave exposure had no effect on CCA cover in either region (Fig. 3.2). CCA cover was negatively related to Chlorophyll-a concentration in two out of three model sets across the Caribbean (Table S3.3, Fig. 3.2a), but we found a weak non-significant positive association across the Pacific islands (Fig. 3.2b). Overall, reef complexity showed no effect on CCA cover across both geographical regions (Fig. 3.2), but one of two models sets across the Caribbean showed a positive association (Table S3.3, Fig. 3.2a). Finally, TSA frequency showed no effect on CCA cover across both geographical regions (Fig. 3.2). Although one of two model sets showed a weak negative association between CCA and TSA in the Pacific (Fig. 3.2b), this predictor had also low relative importance (0.54) (Table S3.3). Across the Pacific islands, CCA cover was not related to available reef area but decreased with island elevation (Fig. 3.2b).

The interaction between herbivore biomass and TSA frequency was negatively associated with CCA cover across Caribbean sites (Fig. 3.2a) but this relationship was not significant across Pacific islands (Fig. 3.2b). However, CCA cover was not directly related to herbivorous fish biomass across the Caribbean (Fig. 3.2a) but both were positively correlated across the Pacific islands (Fig. 3.2b). The relationship of other fish functional groups and CCA cover was variable. Piscivores did not make the top models across the Caribbean (Tables S3, Fig. 3.2a) but showed a

slight positive association with CCA cover across Pacific islands (Fig. 3.2a). Secondary consumers showed a negative relationship with CCA cover across the Caribbean (Fig. 3.2a) which was not strong across the Pacific (Fig. 3.2b). Planktivores showed no relationship with CCA cover in both regions (Fig. 3.2). Both turf algae and macroalgae cover had a negative effect on CCA cover across the Caribbean (Fig. 3.2a), but macroalgae was not related to CCA across the Pacific and turf was not analyzed in this last region (Fig. 3.2b).

### ***Model descriptions for macroalgae***

Macroalgae cover decreased as reef complexity, piscivore, and herbivore biomass increased, and was also negatively correlated with turf algae cover across the Caribbean (Fig. 3.2a). As turf algae was positively associated with herbivorous fish biomass ( $r_s = 0.52$ ) (Fig. S3.2a), these two covariates were modeled separately (Table S3.3). In contrast, macroalgae cover only increased with ocean productivity and slightly with wave exposure across the Caribbean (Fig. 3.2a). Finally, macroalgae cover showed no response to humans/reef and was not associated to the biomass of fish secondary consumers or planktivores across the region (Fig. 3.2a). Across the Pacific islands, macroalgae cover decreased with ocean productivity, reef complexity and island elevation (Fig. 3.2b). But in contrast to the Caribbean, it showed a positive association with the density of humans per reef area and with TSA frequency (Fig. 3.2b). Macroalgae cover showed no relationship with wave exposure, reef area or with the biomass of any fish functional groups, including herbivores across Pacific islands (Fig. 3.2b).

To further analyze the relationship between macroalgae cover and herbivorous fish biomass we run general linear regression models accounting for protection and remote vs. populated status across the Caribbean and Pacific islands, respectively (Fig. 3.4). We found that

macroalgae cover decreased as herbivorous fish biomass increased within protected areas ( $F = 5.79$ ,  $df = 13$ ,  $p = 0.0318$ ,  $R^2 = 0.31$ ) as well as outside marine reserves ( $F = 17.78$ ,  $df = 21$ ,  $p = 0.00038$ ,  $R^2 = 0.46$ ) across the Caribbean (Fig. 3.4). In contrast, macroalgae cover was not related to herbivore biomass within remote islands ( $F = 4.507$ ,  $df = 19$ ,  $p = 0.0471$ ,  $R^2 = 0.19$ ) but decreased as herbivore biomass increased within populated islands ( $F = 8.126$ ,  $df = 13$ ,  $p = 0.0136$ ,  $R^2 = 0.38$ ) across the Pacific (Fig. 3.4).

## **Discussion**

Coral reefs of the Caribbean and the Pacific not only differ greatly in species composition, functional diversity and redundancy, grazing pressure, and ecological resilience (Roff and Mumby 2012), but also in environmental conditions (Chollett et al. 2012, Gove et al. 2013). However, by analyzing major functional groups, similar patterns that are based on ecological processes emerge despite the disparity between these biogeographical regions.

Coral cover was positively associated with the average frequency of thermal stress anomalies across both geographical regions. This is not because temperature anomalies are positively affecting reef corals. There is unequivocal and extensive evidence that coral cover have drastically declined globally and regionally over the past decades due in part to warming events and other stressors (Bruno and Selig 2007, Hoegh-Guldberg et al. 2007, Eakin et al. 2010, Selig et al. 2012). Contemporary coral cover is now relatively low with regional averages of ~15-25% (Bruno and Selig 2007, Schutte et al. 2010, De'ath et al. 2012). However, frequent thermal disturbance may have already eliminated sensitive individuals, promoting other species that are more resistant to additional disturbance (see Chapter 4). At large-scales, reefs that recently (~30 years) experienced higher frequency of thermal stress anomalies may have lost



significantly less total coral cover or have recovered faster than reefs where thermal anomalies are sporadic (Thompson and Woesik 2009, Guest et al. 2012). This may respond to adaptation or acclimatization to repeated thermal anomalies by increasing the thermal tolerance threshold of some dominant coral species that drive community responses (Maynard et al. 2008); or to increased relative abundance of few weedy coral species that can successfully colonize new available substrate due to fast reproduction, high turnover, and high tolerance to disturbances (see Chapter 4).

Our results do not support the hypothesis that current fish biomass, especially herbivorous fishes, have a cascading effect on contemporary coral cover across geographical scales, such that reefs with greater fish abundance may have lost less coral cover over the years after thermal stress events. Thus, reefs with higher coral cover that have experienced and are probably more resistant to thermal stress anomalies were not associated with more herbivorous fish abundance. The evidence that increasing grazing pressure by herbivores facilitate coral resilience after bleaching events is based on exclusion experiments (Hughes et al. 2007) or on small-scale field studies that showed higher coral recovery and recruitment within a marine reserve (Mumby et al. 2007a, Mumby and Harborne 2010). However, several studies have shown that coral recovery after thermal disturbances can take many years to develop even within marine reserves (Selig and Bruno 2010), and that post disturbance protected and fished sites may reach very similar coral cover (Darling et al. 2010). For example, Stockwell et al. (2009) found no evidence of coral recovery after macroalgae decline followed an increase of total herbivores in Philippine's not-take marine reserves after 12 years of protection. Similarly, Kenya's marine protected areas (i.e., unfished reefs) showed no better or faster coral recovery when compared with fished sites after 20 years of the 1998 massive bleaching event (Darling et al. 2013).

Our results highlight that increasing herbivorous fish biomass does not necessarily promote coral resilience after warming events across broad geographical scales. However, herbivorous fishes play a crucial role in promoting coral recovery in the long term (Mumby et al. 2007a, Hughes et al. 2007). But the temporal scales of this recovery may be reef specific, depends on initial coral cover (Selig et al. 2012), and on several factors unrelated with grazing pressure (Graham et al. 2011). There is strong evidence that increasing grazing intensity, although beneficial to control macroalgae and increase CCA cover that facilitate coral recruitment (Hughes et al. 2007, Mumby and Harborne 2010), may not be sufficient to promote coral recovery after thermal stress, especially on reefs where coral cover is relatively low (Huntington et al. 2011, Toth et al. 2014). The complexities of coral community dynamics and greater generation times of corals compared with fish and algae probably mask any influence of grazing by herbivorous fishes on coral cover across large spatial scales (Newman et al. 2006, Mumby et al. 2007a). Coral recovery may directly depend on the capacity of the remaining coral assemblage to reproduce, successfully recruit and growth (Connell 1997, Graham et al. 2011), and may not respond quickly to a decline of reef macroalgae. Indeed, coral and macroalgae cover were not related across broad geographical scales in the Caribbean or Pacific islands which is supported by other studies (Roff and Mumby 2012). This also supports previous results from global meta-analysis that found little evidence of phase shifts from coral to macroalgal dominance on coral reefs (Bruno et al. 2009). Other factors such as rates of recruitment, nutrient loading, sedimentation, and diseases history, are important variables that affect coral survival and recovery (Hughes et al. 2003, Pandolfi et al. 2003, Graham et al. 2013, Mumby et al. 2014) and should be considered in studies across large geographical scales

Herbivorous fishes were differentially associated with CCA and macroalgae cover across both geographical regions. For example, as herbivorous fishes increased across the Caribbean, macroalgae cover decreased and turf algae and CCA increased. At the same time, CCA cover was negatively affected by macroalgae and turf algae. However, across Pacific islands, increased herbivores was associated with higher CCA cover but macroalgae cover only decreased across populated islands. Our results support the well-established ecological relationships that increasing herbivorous fish biomass suppresses macroalgae abundance across large geographical scales in both the Caribbean (Williams and Polunin 2001, Newman et al. 2006, Jackson et al. 2014) and the Pacific (Sandin et al. 2008). This pattern emerges regardless of several confounding factors, (e.g., protection status, human impacts, reef complexity, etc) and the disparity in the resilience of coral reefs between these two geographical regions (Roff and Mumby 2012). These results also support previous small scales empirical and modelling studies that demonstrate that changes in herbivorous fish biomass influence benthic communities via reduction of fleshy macroalgae (Mumby et al. 2006), increasing turf cover and promoting CCA growth (Mumby et al. 2007b). Our study highlights that these relationship can be detected when analyzing all functional groups of herbivorous fishes combined (e.g., parrotfish, surgeonfish, chubs) across regional scales (Williams and Polunin 2001, Roff and Mumby 2012, Jackson et al. 2014).

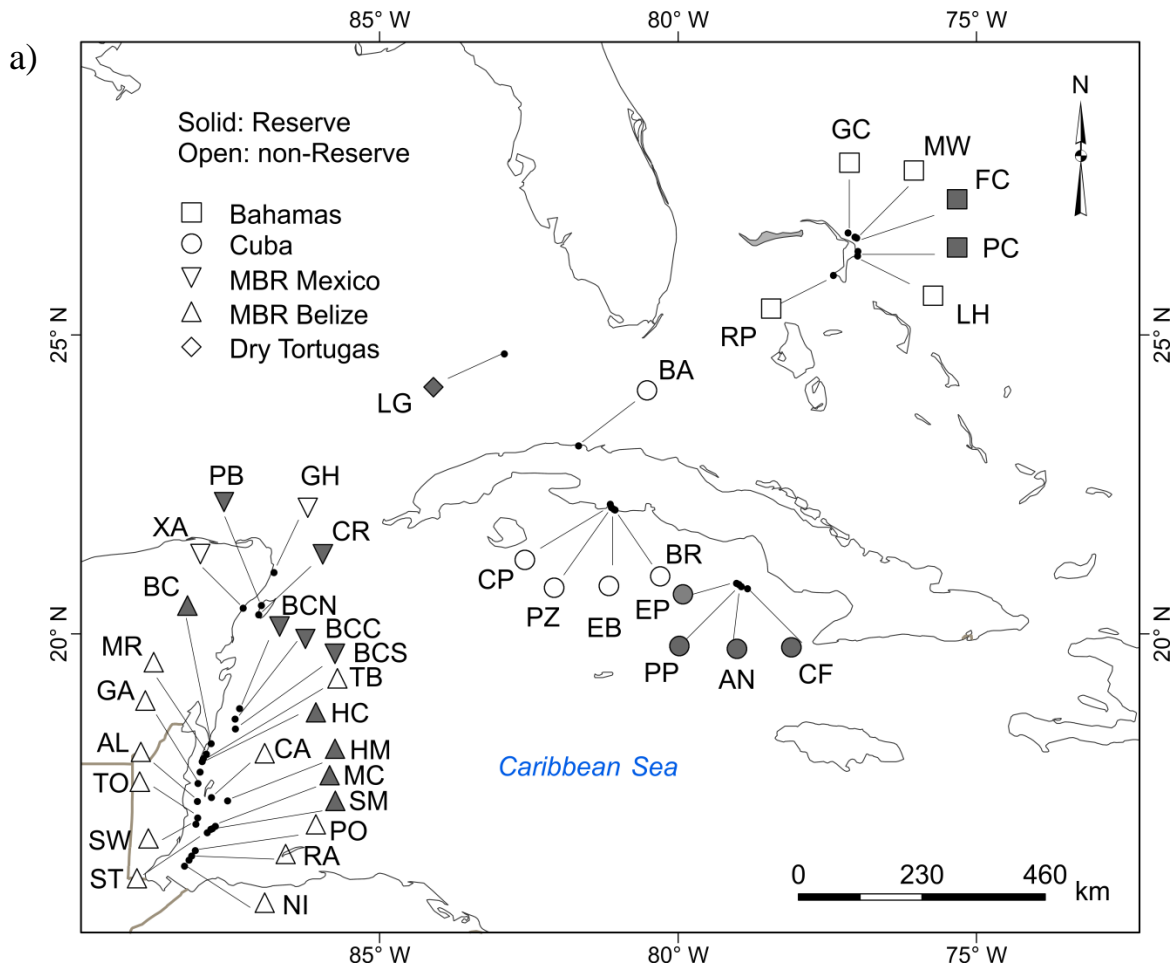
Although in our study total herbivore biomass values ( $14-80 \text{ gm}^{-2}$ ) were similar as those found across Pacific islands (Fig S3.3). Previous and more than a decade old study across the Caribbean (Williams and Polunin 2001) showed much lower total herbivorous fish biomass ( $\sim 3-17 \text{ gm}^{-2}$ ). But these discrepancies may be simply related to different surveyed sites or methods. Nonetheless, the average macroalgae cover across the Caribbean ( $\sim 39\%$ ) was two-time higher

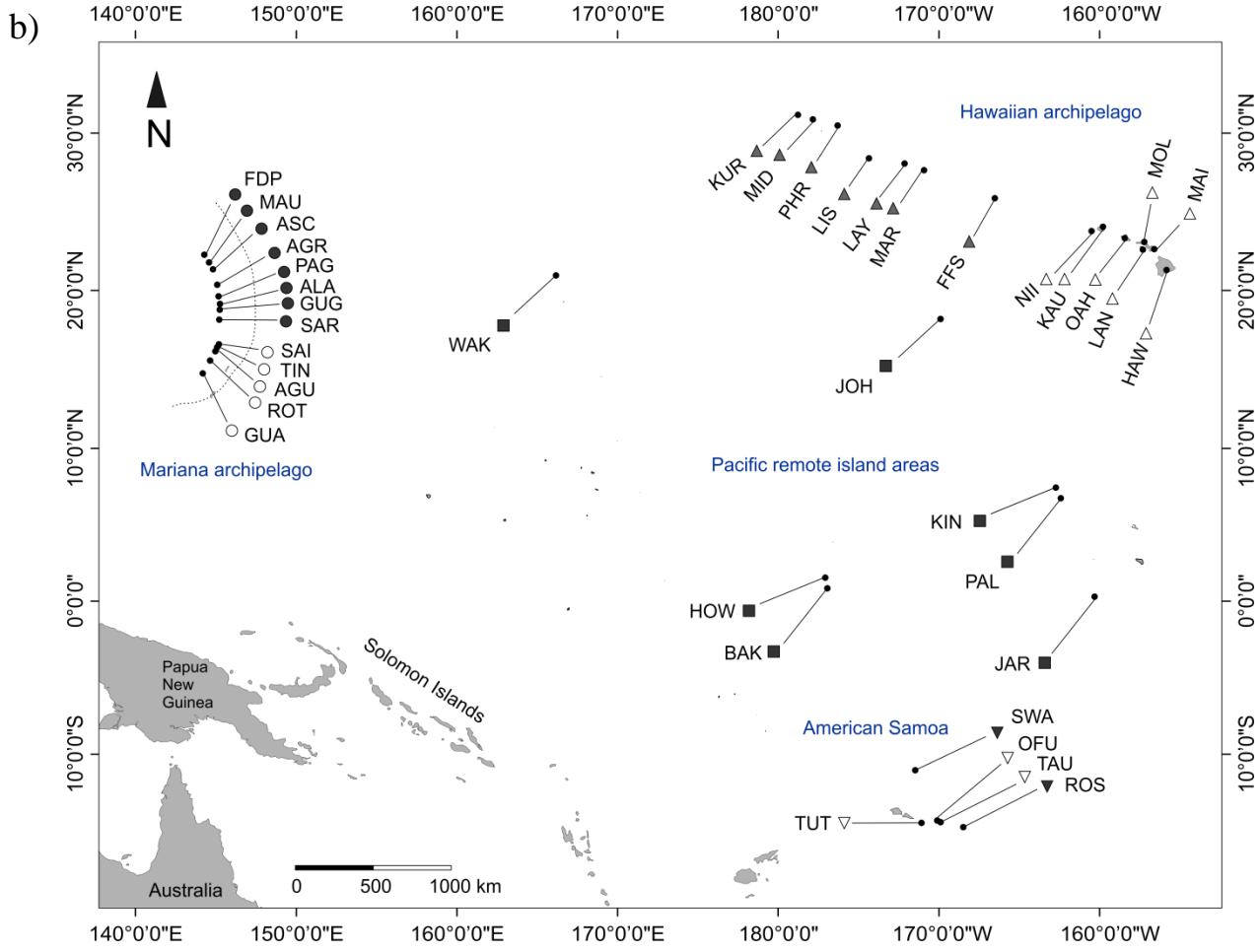
than across the Pacific (~20%). There are several non-exclusive hypotheses that may explain these differences. First, higher diversity and greater functional redundancy of herbivorous fishes may keep algae abundance at lower levels in the Pacific in comparison with the Caribbean (Bellwood et al. 2003, Burkepile and Hay 2008, Roff and Mumby 2012). Second, the functional loss of the dominant sea urchin (*Diadema antillarum*) in the Caribbean may have kept algae biomass relatively high in the region (Mumby et al. 2007b). Finally, analysis of several exclusion experiments across both regions indicate faster rates of macroalgae growth and higher rates of algae recruitment in the Caribbean than in the Pacific (Roff and Mumby 2012).

Reef complexity was an important variable positively associated with coral cover across both geographical regions, and may play a crucial role in the long term recovery of corals. Because contemporary coral cover was relatively low across both geographical areas (mean of ~15-16%) ranging from ~2% to 37%, it is likely that current reef complexity respond to architectural structure from the past (Alvarez-Filip et al. 2009). That is, remnant coral cover was higher at reefs with greater tridimensional structure which may have supported higher coral abundance decades ago. For example, higher reef structural complexity was related to large dead stand colonies of reef-builder corals such as *Orbicella spp.* and *Acropora palmata* in the Caribbean (Alvarez-Filip et al. 2011), but contemporary coral cover of these species are relatively low across the region (Chapter 4). Additionally, higher reef complexity support a more functional diverse and abundant reef fish assemblage (Bellwood et al. 2003, Rogers et al. 2014) by modifying predator-prey interactions (Hixon and Beets 1993) and providing refuge and habitat (Graham 2014) . Thus, reef complexity may facilitate greater grazing pressure by herbivores that affect macroalgae abundance. In fact, we found that macroalgae cover was negatively related to reef structural complexity.

In conclusions, we found no support for the hypothesis that higher fish abundance, especially herbivorous fish biomass, was associated with higher coral cover across geographical regions. Although reef areas with higher frequency of thermal stress anomalies showed higher coral cover, we found no evidence that herbivorous fishes have facilitated this relationship or provided more resilience to corals. Spatial patterns of coral cover at geographical scales were associated with a myriad of factors, and the relationship of herbivores-algae-cover was complex. Herbivorous fish biomass, however, was negatively associated with macroalgae cover and positively associated with crustose coralline cover across large spatial scale. Thus, herbivores play a crucial role in controlling algae abundance and provide adequate conditions for coral recovery (Hughes et al. 2007). But coral recovery may ultimately depend on the remnant coral community to successfully reproduce and growth which can take many years to achieve (Selig et al. 2012).

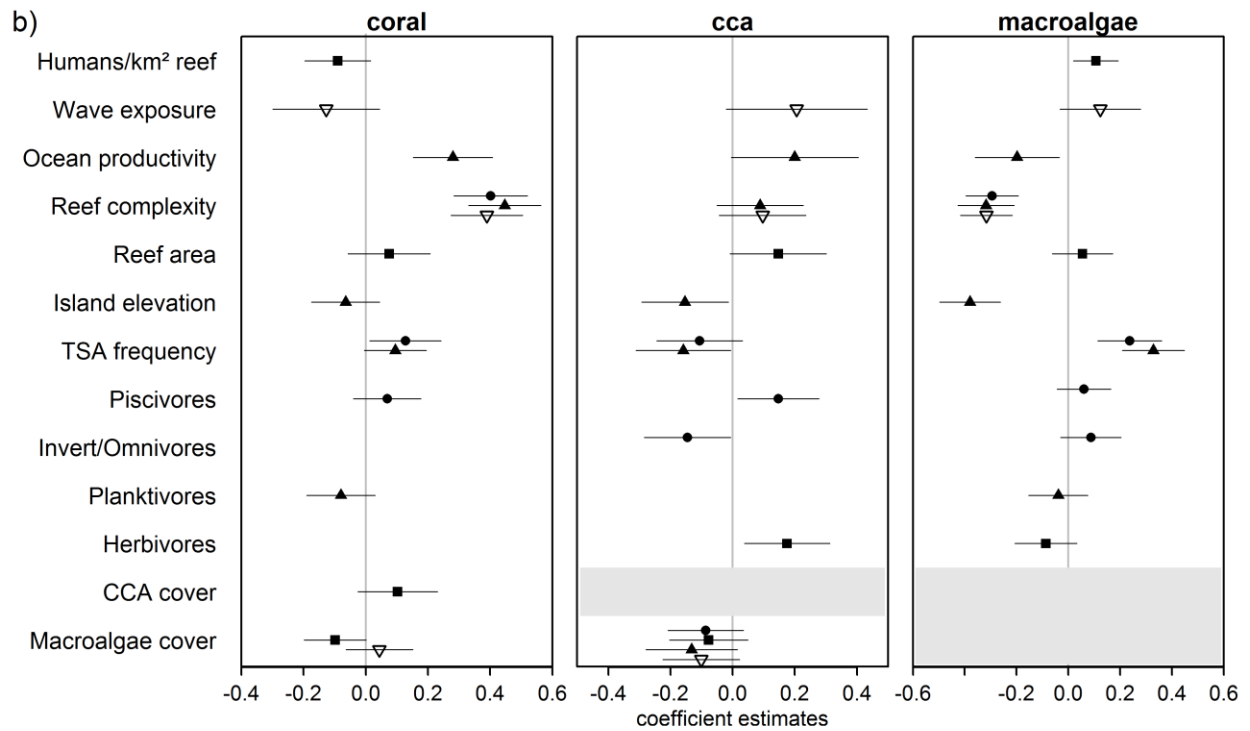
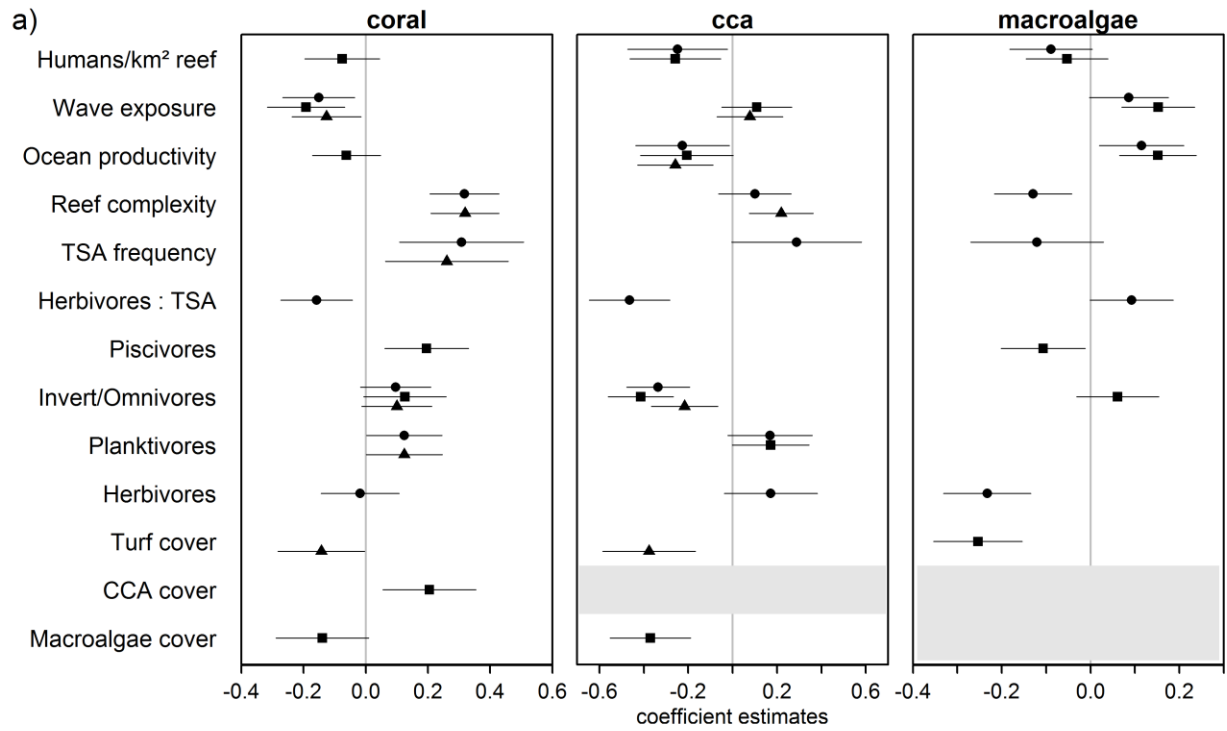
**Figure 3.1 Location of reef sites across the Western and Central Caribbean (a), and US Pacific islands (b) analyzed in this study.** Solid symbols are reefs within marine protected areas (Caribbean) or within remote islands (Pacific). Empty symbols are reefs with no protection (Caribbean) or within populated islands (Pacific). For sites and island codes see Table S3.1 for Caribbean and Table S3.2 for Pacific. MBR is Mesoamerican Barrier Reef.



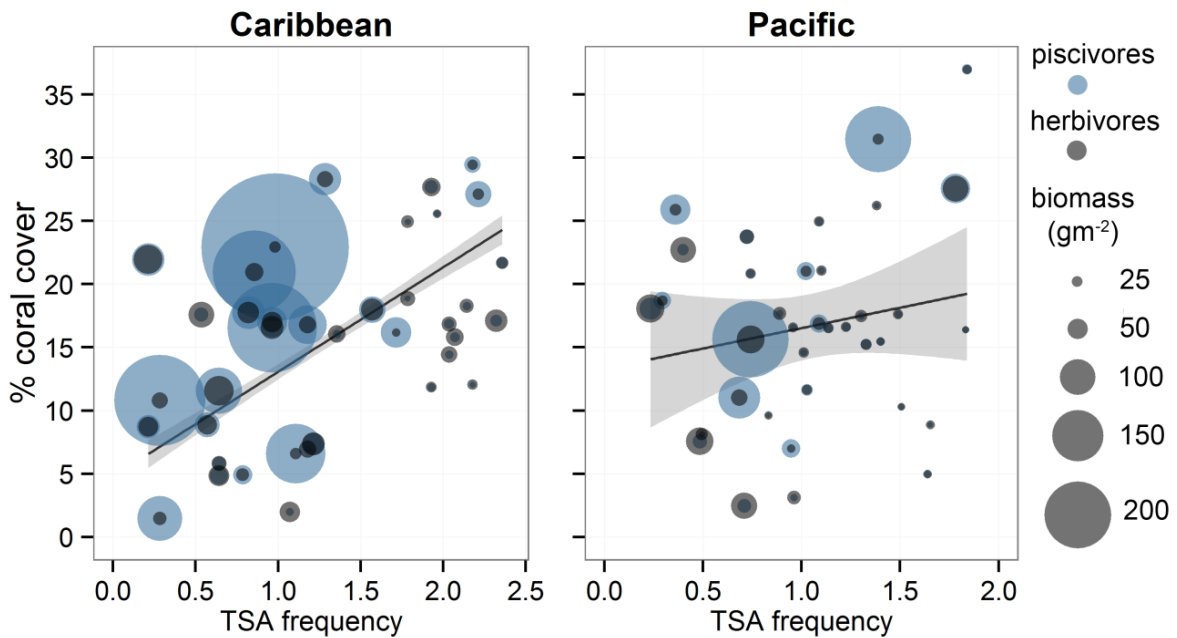


**Figure 3.2 Model-averaged coefficients from the top generalized linear mixed-effect models (GLMMs;  $\Delta AICc < 2$ ; Table S3.2) of variables associated with percentage cover of coral, crustose coralline algae (CCA), and macroalgae across 38 fore-reefs in the Caribbean (a) and 36 Pacific islands (b).** Symbol points are mean values bounded by 95% confidence intervals. Different symbols are different model sets that accounts for collinearity among variable (see Table S3.2 for details). Positive and negative values (that do not overlap the vertical line) indicate significant positive and negative associations, respectively. Hypothesized interactions are indicated by a colon between variables (e.g., Herbivores : TSA). TSA is thermal stress anomalies over ~30 years. Grey areas are variables not included as predictors in the model for that response variable.

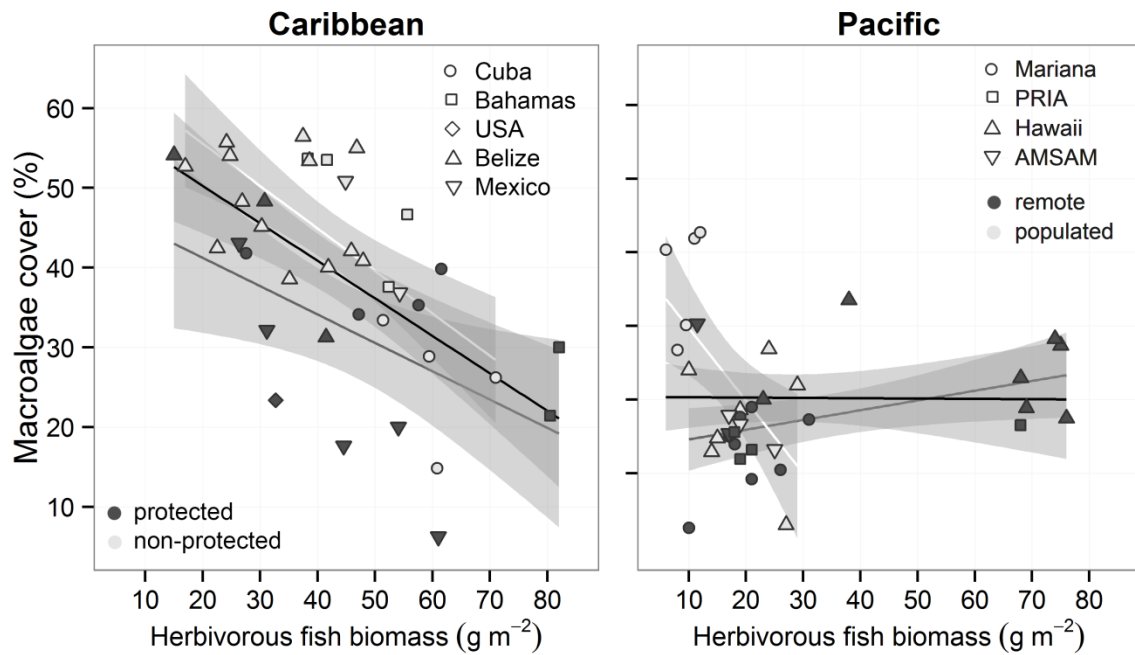




**Figure 3.3 Relationship among contemporary percentage of coral cover, TSA frequency, and the biomass of piscivorous and herbivorous fishes across 38 fore reefs in the Caribbean and 36 US Pacific islands.** Bubble size is proportional to the average fish biomass ( $\text{g m}^{-2}$ ) per site or island. Black line (bounded by 95% confidence interval) is the fitting prediction from the GLMMs model-averaging of percentage coral cover on TSA frequency accounting for all covariates in the models (Table S3.3). Note that average values were calculated at the site level in the Caribbean, while at island level in the Pacific.



**Figure 3.4 Relationship between the average of macroalgae cover (%) and total herbivorous fish biomass (gm-2) across 38 fore reefs in the Caribbean and 36 US Pacific islands.** Lines (bounded by 95% confidence interval) are fitting predictions of macroalgae cover on herbivores biomass accounting for several variables in the GLMMs. Black line is the fitting for all sites, grey line for protected/remote sites, and white lines are for non-protected/populated sites. Note that the slope is significant for protected, non-protected and all sites in the Caribbean, while in the US Pacific island the relationship is only significant within populated islands.



## References

- Allgeier, J. E., C. A. Layman, P. J. Mumby, and A. D. Rosemond. 2014. Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Global Change Biology*:n/a–n/a.
- Alvarez-Filip, L., N. K. Dulvy, I. M. Côté, A. R. Watkinson, and J. A. Gill. 2011. Coral identity underpins architectural complexity on Caribbean reefs. *Ecological Applications* 21:2223–2231.
- Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Côté, and A. R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences* 276:3019–3025.
- Ault, J. S., S. G. Smith, J. A. Bohnsack, J. Luo, D. E. Harper, and D. B. McClellan. 2006. Building sustainable fisheries in Florida's coral reef ecosystem: positive signs in the Dry Tortugas. *Bulletin of Marine Science* 78:633–654.
- Babcock, R. C., N. T. Shears, A. C. Alcala, N. S. Barrett, G. J. Edgar, K. D. Lafferty, T. R. McClanahan, and G. R. Russ. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences* 107:18256–18261.
- Bak, R. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands Journal of Sea Research* 10:285–337.
- Bellwood, D. R., A. S. Hoey, and J. H. Choat. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* 6:281–285.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Bellwood, D. R., T. P. Hughes, and A. S. Hoey. 2006. Sleeping Functional Group Drives Coral-Reef Recovery. *Current Biology* 16:2434–2439.
- Billé, R., R. Kelly, A. Biastoch, E. Harrould-Kolieb, D. Herr, F. Joos, K. Kroeker, D. Laffoley, A. Oschlies, and J.-P. Gattuso. 2013. Taking Action Against Ocean Acidification: A Review of Management and Policy Options. *Environmental Management* 52:761–779.
- Birrell, C. L., L. McCook, B. L. Willis, and G. Diaz-Pulido. 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Pages 25–63 *Oceanography and Marine Biology: An Annual Review*. R.N. Gibson, R.J.A Atkinson, J.D.M. Gordon, Taylor & Francis, London, U.K.

- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.
- Bruno, J. F., L. E. Petes, C. Drew Harvell, and A. Hettinger. 2003. Nutrient enrichment can increase the severity of coral diseases. *Ecology Letters* 6:1056–1061.
- Bruno, J. F., W. F. Precht, P. S. Vroom, and R. B. Aronson. 2014. Coral reef baselines: How much macroalgae is natural? *Marine Pollution Bulletin*.
- Bruno, J. F., and E. R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 2:e711.
- Bruno, J. F., H. Sweatman, W. F. Precht, E. R. Selig, and V. G. W. Schutte. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484.
- Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences* 105:16201–16206.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. 2nd edition. Springer New York.
- Carleton, J. H., and T. J. Done. 1995. Quantitative video sampling of coral reef benthos: large-scale application. *Coral Reefs* 14:35–46.
- Cheal, A. J., M. A. MacNeil, E. Cripps, M. J. Emslie, M. Jonker, B. Schaffelke, and H. Sweatman. 2010. Coral–macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29:1005–1015.
- Chollett, I., P. J. Mumby, F. E. Müller-Karger, and C. Hu. 2012. Physical environments of the Caribbean Sea. *Limnology and Oceanography* 57:1233–1244.
- Connell, J. H. 1997. Disturbance and recovery of coral assemblages. *Coral Reefs* 16:S101–S113.
- Côté, I. M., and E. S. Darling. 2010. Rethinking Ecosystem Resilience in the Face of Climate Change. *PLoS Biology* 8:e1000438.
- Côté, I. M., I. Mosqueira, and J. D. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish Biology* 59:178–189.
- Darling, E. S., T. R. McClanahan, and I. M. Côté. 2010. Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. *Conservation Letters* 3:122–130.

- Darling, E. S., T. R. McClanahan, and I. M. Côté. 2013. Life histories predict coral community disassembly under multiple stressors. *Global Change Biology* 19:1930–1940.
- De'ath, G., K. E. Fabricius, H. Sweatman, and M. Puotinen. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences* 109:17995–17999.
- Diaz-Pulido, G., S. Harii, L. McCook, and O. Hoegh-Guldberg. 2010. The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs* 29:203–208.
- Dove, S. G., D. I. Kline, O. Pantos, F. E. Angly, G. W. Tyson, and O. Hoegh-Guldberg. 2013. Future reef decalcification under a business-as-usual CO<sub>2</sub> emission scenario. *Proceedings of the National Academy of Sciences* 110:15342–15347.
- Dutt, V., and C. Gonzalez. 2012. Human control of climate change. *Climatic Change* 111:497–518.
- Edgar, G. J., R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, N. S. Barrett, M. A. Becerro, A. T. F. Bernard, J. Berkhout, C. D. Buxton, S. J. Campbell, A. T. Cooper, M. Davey, S. C. Edgar, G. Försterra, D. E. Galván, A. J. Irigoyen, D. J. Kushner, R. Moura, P. E. Parnell, N. T. Shears, G. Soler, E. M. A. Strain, and R. J. Thomson. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature*.
- Froese, R., and D. Pauly. 2013. FishBase. <http://www.fishbase.org>.
- Gaines, S. D., C. White, M. H. Carr, and S. R. Palumbi. 2010. Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Sciences* 107:18286–18293.
- Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301:958–960.
- Gove, J. M., G. J. Williams, M. A. McManus, S. F. Heron, S. A. Sandin, O. J. Vetter, and D. G. Foley. 2013. Quantifying climatological ranges and anomalies for Pacific coral reef ecosystems. *PloS one* 8:e61974.
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815.
- Graham, N. A., D. R. Bellwood, J. E. Cinner, T. P. Hughes, A. V. Norström, and M. Nyström. 2013. Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment* 11:541–548.
- Graham, N. A. J. 2014. Habitat Complexity: Coral Structural Loss Leads to Fisheries Declines. *Current Biology* 24:R359–R361.

- Graham, N. A. J., T. R. McClanahan, M. A. MacNeil, S. K. Wilson, N. V. C. Polunin, S. Jennings, P. Chabanet, S. Clark, M. D. Spalding, Y. Letourneur, L. Bigot, R. Galzin, M. C. Öhman, K. C. Garpe, A. J. Edwards, and C. R. C. Sheppard. 2008. Climate Warming, Marine Protected Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems. *PLoS ONE* 3:e3039.
- Graham, N. a. J., K. L. Nash, and J. T. Kool. 2011. Coral reef recovery dynamics in a changing world. *Coral Reefs* 30:283–294.
- Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24:699–711.
- Guest, J. R., A. H. Baird, J. A. Maynard, E. Muttaqin, A. J. Edwards, S. J. Campbell, K. Yewdall, Y. A. Affendi, and L. M. Chou. 2012. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE* 7:e33353.
- Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. *Ecology Letters* 5:361–366.
- Harborne, A. R., P. J. Mumby, C. V. Kappel, C. P. Dahlgren, F. Micheli, K. E. Holmes, J. N. Sanchirico, K. Broad, I. A. Elliott, and D. R. Brumbaugh. 2008. Reserve effects and natural variation in coral reef communities. *Journal of Applied Ecology* 45:1010–1018.
- Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77–101.
- Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin, R. Iglesias-Prieto, N. Muthiga, R. H. Bradbury, A. Dubi, and M. E. Hatziolos. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nyström, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933.
- Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschanivskyj, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. *Current Biology* 17:360–365.
- Huntington, B. E., M. Karnauskas, and D. Lirman. 2011. Corals fail to recover at a Caribbean marine reserve despite ten years of reserve designation. *Coral Reefs* 30:1077–1085.
- IPCC. 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.*

- Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jackson, J. B. C., M. K. Donovan, K. L. Cramer, and Lam. 2014. Status and Trends of Caribbean Coral Reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.
- Jones, G. P., M. I. McCormick, M. Srinivasan, and J. V. Eagle. 2004. Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United States of America* 101:8251–8253.
- Karnauskas, M., B. E. Huntington, E. A. Babcock, and D. Lirman. 2011. Pre-existing spatial patterns in fish abundances influence species-specific responses in a Caribbean marine reserve. *Marine Ecology Progress Series* 432:235–246.
- Keller, B. D., D. F. Gleason, E. McLeod, C. M. Woodley, S. Aïramé, B. D. Causey, A. M. Friedlander, R. Grober-Dunsmore, J. E. Johnson, S. L. Miller, and R. S. Steneck. 2009. Climate Change, Coral Reef Ecosystems, and Management Options for Marine Protected Areas. *Environmental Management* 44:1069–1088.
- Kenyon, J. C., R. E. Brainard, R. K. Hoeke, F. A. Parrish, and C. B. Wilkinson. 2006. Towed-diver surveys, a method for mesoscale spatial assessment of benthic reef habitat: a case study at Midway Atoll in the Hawaiian Archipelago. *Coastal Management* 34:339–349.
- Knowlton, N., and J. B. C. Jackson. 2008. Shifting Baselines, Local Impacts, and Global Change on Coral Reefs. *PLoS Biol* 6:e54.
- Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. S. Beach. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series* 323:107–117.
- Lang, J. C., K. W. Marks, P. A. Kramer, P. Richards Kramer, and R. N. Ginsburg. 2010. AGRRA Protocols version 5.4 Atlantic and Gulf Rapid Reef Assessment Program. University of Miami, Florida.
- Lessafre, E., D. Rizopoulos, and R. Tsonaka. 2007. The logistic-transform for bounded outcome scores. *Biostatistics* 8:72–85.
- Lester, S., B. Halpern, K. Grorud-Colvert, J. Lubchenco, B. Ruttenberg, S. Gaines, S. Aïramé, and R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series* 384:33–46.
- Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves 1. *Ecological applications* 13:3–7.
- Maynard, J., K. Anthony, P. Marshall, and I. Masiri. 2008. Major bleaching events can lead to increased thermal tolerance in corals. *Marine Biology* 155:173–182.



- McCauley, D. J., K. A. McLean, J. Bauer, H. S. Young, and F. Micheli. 2012. Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations. *Ecological Applications* 22:385–392.
- McClanahan, T. R. 2008. Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. *Oecologia* 155:169–177.
- McClanahan, T. R., J. E. Cinner, J. Maina, N. A. J. Graham, T. M. Daw, S. M. Stead, A. Wamukota, K. Brown, M. Ateweberhan, V. Venus, and N. V. C. Polunin. 2008. Conservation action in a changing climate. *Conservation Letters* 1:53–59.
- McCook, Jompa, and Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400–417–417.
- McCune, B., J. B. Grace, and D. L. Urban. 2002. *Analysis of Ecological Communities*. MjM Software Design, Glenden Beach, Oregon, USA.
- McLeod, E., R. Salm, A. Green, and J. Almany. 2009. Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment* 7:362–370.
- Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, J. N. Sanchirico, K. Buch, S. Box, R. W. Stoffle, and A. B. Gill. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101.
- Mumby, P. J., and A. R. Harborne. 2010. Marine Reserves Enhance the Recovery of Corals on Caribbean Reefs. *PLoS ONE* 5:e8657.
- Mumby, P. J., A. R. Harborne, J. Williams, C. V. Kappel, D. R. Brumbaugh, F. Micheli, K. E. Holmes, C. P. Dahlgren, C. B. Paris, and P. G. Blackwell. 2007a. Trophic cascade facilitates coral recruitment in a marine reserve. *Proceedings of the National Academy of Sciences* 104:8362–8367.
- Mumby, P. J., A. Hastings, and H. J. Edwards. 2007b. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98–101.
- Mumby, P. J., N. H. Wolff, Y.-M. Bozec, I. Chollett, and P. Halloran. 2014. Operationalizing the Resilience of Coral Reefs in an Era of Climate Change. *Conservation Letters* 7:176–187.
- Nadon, M. O., J. K. Baum, I. D. Williams, J. M. Mcpherson, B. J. Zgliczynski, B. L. Richards, R. E. Schroeder, and R. E. Brainard. 2012. Re-creating missing population baselines for Pacific reef sharks. *Conservation Biology* 26:493–503.
- Newman, M. J. H., G. A. Paredes, E. Sala, and J. B. C. Jackson. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters* 9:1216–1227.

- Oksanen, J., F. G. Blanchet, R. Kindt, M. J. Oksanen, and M. Suggests. 2013. Package “vegan.” Community ecology package Version 2:0–0.
- O’Leary, J. K., D. C. Potts, J. C. Braga, and T. R. McClanahan. 2012. Indirect consequences of fishing: reduction of coralline algae suppresses juvenile coral abundance. *Coral Reefs* 31:547–559.
- Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958.
- Polunin, N. V. C., and C. M. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* 100:177–183.
- Rasher, D. B., and M. E. Hay. 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. *Proceedings of the National Academy of Sciences* 107:9683–9688.
- Rau, G. H., E. L. McLeod, and O. Hoegh-Guldberg. 2012. The need for new ocean conservation strategies in a high-carbon dioxide world. *Nature Climate Change* 2:720–724.
- R Core Team. 2013. R: A Language and Environment for Statistical Computing, Vienna, Austria. V. 3.03. <http://www.R-project.org>.
- Roff, G., and P. J. Mumby. 2012. Global disparity in the resilience of coral reefs. *Trends in Ecology & Evolution* 27:404–413.
- Rogers, A., J. L. Blanchard, and P. J. Mumby. 2014. Vulnerability of Coral Reef Fisheries to a Loss of Structural Complexity. *Current Biology*.
- Sala, E., E. Ballesteros, P. Dendrinis, A. Di Franco, F. Ferretti, D. Foley, S. Frascchetti, A. Friedlander, J. Garrabou, H. Güçlüsoy, P. Guidetti, B. S. Halpern, B. Hereu, A. A. Karamanlidis, Z. Kizilkaya, E. Macpherson, L. Mangialajo, S. Mariani, F. Micheli, A. Pais, K. Riser, A. A. Rosenberg, M. Sales, K. A. Selkoe, R. Starr, F. Tomas, and M. Zabala. 2012. The structure of mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. *PLoS ONE* 7:e32742.
- Sandin, S. A., J. E. Smith, E. E. DeMartini, E. A. Dinsdale, S. D. Donner, A. M. Friedlander, T. Konotchick, M. Malay, J. E. Maragos, D. Obura, O. Pantos, G. Paulay, M. Richie, F. Rohwer, R. E. Schroeder, S. Walsh, J. B. C. Jackson, N. Knowlton, and E. Sala. 2008. Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE* 3:e1548.
- Sandin, S. A., and I. Williams. 2010. Trophic Classifications of Reef Fishes from the Tropical US Pacific (Version 1.0). Technical Report.

- Schils, T., P. S. Vroom, and A. D. Tribollet. 2013. Geographical partitioning of marine macrophyte assemblages in the tropical Pacific: a result of local and regional diversity processes. *Journal of Biogeography* 40:1266–1277.
- Schutte, V. G. W., E. R. Selig, and J. F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Mar Ecol Prog Ser* 402:115–122.
- Selig, E. R., and J. F. Bruno. 2010. A Global Analysis of the Effectiveness of Marine Protected Areas in Preventing Coral Loss. *PLoS ONE* 5:e9278.
- Selig, E. R., K. S. Casey, and J. F. Bruno. 2012. Temperature-driven coral decline: the role of marine protected areas. *Global Change Biology* 18:1561–1570.
- Stockwell, B., C. R. L. Jadloc, R. A. Abesamis, A. C. Alcala, and G. R. Russ. 2009. Trophic and benthic responses to no-take marine reserve protection in the Philippines. *Marine Ecology, Progress Series* 389:1–15.
- Thompson, D. M., and R. van Woesik. 2009. Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. *Proceedings of the Royal Society B: Biological Sciences* 276:2893–2901.
- Toth, L. T., R. van Woesik, T. J. T. Murdoch, S. R. Smith, J. C. Ogden, W. F. Precht, and R. B. Aronson. 2014. Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. *Coral Reefs*:1–13.
- Victor, D. G. 2008. *The collapse of the Kyoto Protocol and the struggle to slow global warming*. Princeton University Press.
- Vroom, P. S. 2011. Coral Dominance: A Dangerous Ecosystem Misnomer? *Journal of Marine Biology* 2011.
- Wiedenmann, J., C. D'Angelo, E. G. Smith, A. N. Hunt, F.-E. Legiret, A. D. Postle, and E. P. Achterberg. 2013. Nutrient enrichment can increase the susceptibility of reef corals to bleaching. *Nature Climate Change* 3:160–164.
- Williams, I. D., B. L. Richards, S. A. Sandin, J. K. Baum, R. E. Schroeder, M. O. Nadon, B. Zgliczynski, P. Craig, J. L. McIlwain, and R. E. Brainard. 2011. Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western pacific. *Journal of Marine Biology* 2011.
- Williams, and Polunin. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19:358–366–366.
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer.

## CHAPTER 4

### Ocean warming shifts coral community composition<sup>1</sup>

#### Abstract

Rising ocean temperatures threaten coral reef ecosystems with more frequent and severe bleaching events that can cause widespread mortality and decline of reef-building corals. However, the response of coral communities to warming seems to vary spatially across multiple scales depending on the thermal history of reef areas. Here we investigate whether ~30 years of thermal history can partially explain patterns in current coral community composition throughout the Caribbean. We found that contemporary coral cover was positively related to the frequency of recent thermal stress anomalies due to a shift in coral community composition towards smaller, stress-tolerant and weedy species. Our findings suggest that coral communities that have experienced more frequent thermal anomalies may be composed of more disturbance-tolerant species or genotypes. While the re-assortment of coral taxa due to environmental filtering in response to warming may result in communities that can cope with thermal stress, these communities likely have less structural complexity and coral diversity that may compromise ecosystem functioning. Our study reinforces the role of climate change in causing changes in composition and function rather than outright ecosystem loss.

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**Keywords:** Coral reefs, ecological strategies, thermal stress anomalies, selection pressure, bleaching, global warming, thermal tolerance

## **Introduction**

Greenhouse gas emissions are warming the atmosphere and oceans, causing disruptions to ecosystems and the services they provide to humanity (Hoegh-Guldberg et al. 2007, Hoegh-Guldberg and Bruno 2010, Burrows et al. 2011, IPCC 2013). The ecological responses of climate change are well documented and include changes in the phenology and physiology of organisms, altered species interactions, and shifts in range distributions (Walther et al. 2002, Hoegh-Guldberg and Bruno 2010, Burrows et al. 2011, Graham et al. 2014a). There is also growing evidence that climate change is leading to shifts in composition, structure, and functioning of natural systems as opposed to ecosystem collapse (Walther et al. 2002, Precht and Aronson 2004, Hobbs et al. 2009, Burrows et al. 2011, Graham et al. 2014a, Dornelas et al. 2014). However, the reorganization of species assemblages by global warming into novel or emerging ecosystems, and the goods or services that altered ecosystems can continue to support, remains poorly understood (Williams and Jackson 2007, Hobbs et al. 2009, Burrows et al. 2011, Graham et al. 2014a).

Several mechanisms can underlie changes in community composition in response to rapid warming. Some populations may be able to cope with increasing temperatures by dispersing to new more hospitable areas, introducing new species to existing communities, i.e., species range shifts (Greenstein and Pandolfi 2008, Burrows et al. 2011, 2014). Other populations, with slower dispersion rates, may have to acclimatize to new environmental conditions in their home range or

adapt by natural selection through the survival of resilient individuals or genotypes (Walther et al. 2002, Williams and Jackson 2007, Edmunds and Gates 2008). Still other populations will be locally extirpated as the climate changes too quickly for adaptation or acclimatization to keep pace (Edmunds and Gates 2008, Burrows et al. 2011, Hoegh-Guldberg 2012). Thus, new ecological communities can emerge from hybrids of former ones or completely novel assemblages through species immigration and/or extinctions driven by changes in local and regional environmental conditions (Burrows et al. 2014). For example, rapid warming in the Southern Ocean can allow shell-braking crabs and fishes to return to the Antarctic Peninsula, strengthening the top-down control in a region that has been free of predators since the Eocene ~41 million years ago (Aronson et al. 2009).

Global warming will be the dominant driver of change in the world's oceans over the coming decades (Hoegh-Guldberg et al. 2011, Graham et al. 2014a, McClanahan et al. 2014). Coral reef ecosystems are especially vulnerable, in part due to the narrow thermal range of their foundational species, Scleractinian corals (Hoegh-Guldberg 1999, Hoegh-Guldberg and Bruno 2010). Sensitive to elevated sea temperatures, corals can exhibit extensive bleaching (i.e., the loss of their endosymbiotic algae and/or their photosynthetic pigment) with consequent partial or whole-colony mortality (Glynn 1993, Hoegh-Guldberg et al. 2007). Mass bleaching events, combined with chronic exposure to local stressors such as overfishing, pollution, and diseases, have contributed to the regional and global decline of hard corals over the past decades (Hoegh-Guldberg 1999, Gardner et al. 2003, Pandolfi et al. 2003, Bruno and Selig 2007).

Counterintuitively, long-term exposure to these stressors can also remove less resistant and resilient genotypes and increase the ability of the system to cope with new stresses (Côté and Darling 2010, Graham et al. 2014a, McClanahan et al. 2014). For example, widespread mortality

due to bleaching not only results in coral decline (Hoegh-Guldberg 1999, Bruno and Selig 2007), but may promote differential mortality that changes coral genotypic and species composition (Loya et al. 2001, Carpenter et al. 2008, Van Woesik et al. 2011) by selecting for ‘winning’ genotypes and species that are tolerant to thermal stress (Maynard et al. 2008, Thompson and Woesik 2009, Van Woesik et al. 2011, Graham et al. 2014a, Palumbi et al. 2014). Thus, while coral assemblages have experienced substantial functional losses with thermal disturbance, post-stress communities may be better suited to survive future environmental conditions (Graham et al. 2014a, McClanahan et al. 2014).

Thermal stress anomalies vary spatially in intensity and frequency resulting in regional variability in the exposure of coral reefs to ocean warming (Thompson and Woesik 2009, Selig et al. 2010, Guest et al. 2012). Certain geographic regions experience thermal anomalies more often than others (Selig et al. 2010). For example, reefs of Central America, the Persian Gulf, and the Central Pacific display higher average frequency and magnitude of thermal stress anomalies than reefs of the Florida Keys, the Bahamas, or the Hawaiian Islands (Selig et al. 2010). Regional differences in bleaching responses by corals are likely related to the thermal history of each reef, which may result in different communities of thermally-tolerant species or genotypes across oceanographic regions (Maynard et al. 2008, Thompson and Woesik 2009, Guest et al. 2012). Evidence suggests that some reefs with historically dominant branching and plating competitive corals have been replaced by more resistant and opportunistic species (Aronson et al. 2004, Green et al. 2008, Van Woesik et al. 2011, Darling et al. 2013). For example, 20-years of coral community disassembly on Kenyan coral reefs identified the loss of the competitive life history and the replacement with an altered assemblage of stress-tolerant and weedy ‘survivor’ life histories (Darling et al. 2013). In the Caribbean, a decline in total coral

cover over the last 30 years has led to an increase in the relative dominance of fast-growing opportunistic “weedy” species, e.g., *Porites* spp. and *Agaricia* spp., with small-size colonies and high turnover rates (Aronson et al. 2004, Green et al. 2008, Alvarez-Filip et al. 2011). These shifts in coral assemblage composition have resulted in rapid losses of reef calcification and rugosity that threaten continued architectural complexity and ecosystem functionality (Alvarez-Filip et al. 2013, Bozec et al. 2014). These critical community shifts are associated with differential mortality due to bleaching events, disease outbreaks, and other local-scale stressors (Aronson et al. 2004, Green et al. 2008). While most studies have focused on documenting and forecasting coral reef deterioration (Gardner et al. 2003, Pandolfi et al. 2003, Bruno and Selig 2007, Carpenter et al. 2008, Hoegh-Guldberg et al. 2011), the potential role of ocean warming in shifting coral community composition towards more disturbance-tolerant species have been predicted (Loya et al. 2001, Maynard et al. 2008, Thompson and Woesik 2009, Van Woesik et al. 2011, Darling et al. 2012) but seldom tested across broad regional spatial scales (Precht and Aronson 2004, Greenstein and Pandolfi 2008, Graham et al. 2014b).

Here, we test the hypothesis that contemporary coral community structure (i.e., coral cover patterns and relative composition of major coral taxa) has been influenced by recent thermal history. We examine: (i) the degree to which local thermal stress anomalies are related to changes in contemporary coral cover (and presumably loss), and (ii) whether coral assemblages have shifted towards species potentially more tolerant to temperature anomalies. That is, we asked whether reef areas that experience high-frequency of thermal anomalies act as environmental filters, selecting for traits that results in compositional shifts towards thermally resistant coral species or genotypes (Thompson and Woesik 2009, Darling et al. 2012) and away from the historical composition and structure of Caribbean reefs (Aronson et al. 2004).



## **Materials and Methods**

### ***Study sites and coral surveys***

Surveys were performed at 39 sites in five countries throughout the Western and Central Caribbean in slope and spur-and-groove fore-reef habitats ~10-15m deep and formerly dominated by *Orbicella* corals (Table S4.1). Percent cover data of benthic communities (i.e., coral by species and algae by functional groups) were measured at each site using point intercepts in 6-8 transect lines (10 m long) (Lang et al. 2010) and/or in 6-8 video transects (50 m long) (Carleton and Done 1995) along the slope or spur-and-groove habitats. Point intercept transects (PITs) were used at the Belize sites, while both PITs and video transects were used at the rest of the sites. To estimate percentage cover, 100 points per transect were used in PITs (Lang et al. 2010), while ~600 points were extracted from each video transect (Carleton and Done 1995). Both methods provided similar accuracy and results in estimating benthic cover categories in our study (Supplementary Methods). To minimize seasonal variability in algal composition we conducted all surveys during the summer months of May to July 2010-2012.

### ***Thermal stress anomalies and other covariates***

We created a 29-year dataset (1982-2010) of annual frequency of weekly Thermal Stress Anomalies (Selig et al. 2006) (TSA) for each surveyed reefs using the National Oceanic and Atmospheric Administration's (NOAA) National Oceanographic Data Center (NODC) Coral Reef Temperature Anomaly Database (CoRTAD) Version 4.0 (Casey et al. 2010, Selig et al. 2010) (Fig. 4.1). Temperature anomalies for this database were calculated from the Pathfinder Version 5.2 data temperature with a spatial resolution of ~4 km grid cells (Casey et al. 2010,

Selig et al. 2010) and with a quality flag of four or better (Kilpatrick et al. 2001). TSAs area defined as deviations of one-week where sea surface temperature (SST) was 1°C or greater than the mean maximum climatological week or the long term average warmest week from 1982 to 2010 (Selig et al. 2010). This threshold is generally accepted for environmental conditions that may cause bleaching and coral mortality (Glynn 1993). We calculated the long-term (29 years) average and standard deviation of annual-frequency TSA (weeks/year) for the grid cell that corresponded to each study site to be used as fixed predictor in linear mixed effect models (Fig. 4.1).

Additionally, we measured a set of anthropogenic, physical, and biotic parameters that are known to affect coral assemblages and could modulate their response to temperature (Table 4.1). Anthropogenic-related parameters included number of humans per squared kilometer of reef and area of cultivated land within 50 km of each reef. Physical variables were mean oceanic primary productivity, wave exposure, and landscape reef complexity. Biotic variables included percentage cover of benthic macroalgae, crustose coralline algae (CCA) and turf algae, and the biomass of two functional fish groups; herbivores and piscivores. For a detailed description, measurement, and justification of each variable refer to Table 4.1 and supplementary methods.

### ***Data analysis***

We used percent coral cover as response variable because is an important metric of coral reef health that respond directly to temperature stress through bleaching and mortality (Glynn 1993). To analyze spatial differences in coral community structure, species of scleractinian corals were grouped in three life-history strategy categories (Darling et al. 2013) (e.g., competitive, stress-tolerant, and weedy, Table S4.2) as defined by Darling et al. (Darling et al.

2012) and based on a global analysis of species traits. Two Caribbean coral species (*Orbicella faveolata* and *Orbicella franksi*), that were originally classified as generalists (Darling et al. 2012), were reclassified as stress-tolerant which is consistent with the classification of their congeneric species *Orbicella annularis* (Bégin et al. 2014).

We used generalized linear mixed effect models (GLMMs) and applied a logistic (logit) transformation to the percent coral cover data (total corals and by life-history-strategy groups) where the logit was treated as normally distributed (Lessafre et al. 2007). Competitive corals (e.g., *Acropora* sp. and *Dendrogyra cylindrus*, Table S4.2) were analyzed with a binomial distribution (0-absence and 1-presence) as percentage cover of these species in our study sites was relatively low, and included an excess of zeroes and over-dispersed distribution ( $0.4 \pm 1.9$  %, mean  $\pm$  standard deviation, out of 39 study sites). To account for potential spatial autocorrelation we used a random intercept model where transect were allowed to vary within sites and survey year. Thus, coral cover ( $Y$ ) at transect  $k$  of site  $i$  and year  $j$  was described as the proportional cover ( $\pi_{ijk}$ ) out of the number of points surveyed in each transect in that site and year ( $n_{ijk}$ ). The logistic GLMM that describes  $Y_{ijk}$  was as follows,

$$Y_{ijk} \sim B(n_{ijk}, \pi_{ijk}),$$

with mean  $E(Y_{ijk})$  and variance  $\text{var}(Y_{ijk})$  where,

$$E(Y_{ijk}) = \pi_{ijk} \times n_{ijk} \text{ and } \text{var}(Y_{ijk}) = n_{ijk} \times \pi_{ijk} \times (1 - \pi_{ijk}).$$

The logit transformation of percentage coral cover was predicted by,

$$\begin{aligned} \text{logit}(\pi_{ijk}) = & \beta_0 + \beta_1 \times \text{TSA}_{ijk} + \beta_2 \times \text{Human/km}^2\text{Reef}_{ijk} + \beta_3 \times \text{CultivatedLand}_{ijk} \\ & + \beta_4 \times \text{ReefComplexity}_{ijk} + \beta_5 \times \text{Productivity}_{ijk} + \beta_6 \times \text{WaveExposure}_{ijk} \\ & + \beta_7 \times \text{Herbivore}_{ijk} + \beta_8 \times \text{Piscivore}_{ijk} + \beta_9 \times \text{Macroalgae}_{ijk} + \beta_{10} \times \text{CCA}_{ijk} + \beta_{11} \times \text{Turf}_{ijk} + a_{ij} \\ & a_{ij} \sim N(0, \sigma_a^2), \end{aligned}$$

where  $\beta_0$  is the intercept,  $\beta_{1...11}$  are coefficient estimates of the linear regression for each of the explanatory variables, and  $a_{ij}$  is the random intercept (sites nested in survey years), assumed to be normally distributed with mean zero and variance  $\sigma_a^2$ . Fish were comprised of herbivore and piscivore biomass and algae cover was divided in three functional groups (macroalgae, CCA and turf). Collinearity among explanatory variables was assessed using a Spearman rank correlation matrix and scatterplots with loess smoothing curves of span 0.5 (Fig. S4.1).

We modeled all potential combinations of explanatory variables to explain total coral cover and the three coral life histories, including interactions among fish biomass, humans per reef, and reef complexity. We used a model averaging approach for model selection based on Akaike's Information criterion corrected for small samples ( $AIC_c$ , where  $\Delta AIC_c < 3$ ) (Burnham and Anderson 2002). Two explanatory variables, *turf* and *area of cultivated land*, were sufficiently correlated ( $|r_s| > 0.5$ ) with *macroalgae* and *human population / reef*, respectively, to compromise model results (Graham 2003), thus we eliminated them from all models. To assess the extent of any remaining collinearity in the final models we calculated the variance inflation factors (VIFs) of the variables and eliminate those cofactors which values were  $>2$  (Graham 2003).

Model validation to assess heterogeneity and normality of the residuals was performed by examining the error distribution of top models ( $\Delta AIC_c < 3$ ) in the plot of normalized residuals against fitted and explanatory values, and used the normal scores of standardized residuals deviance, respectively (Zuur et al. 2009). Additionally, spline spatial correlograms were plotted to corroborate that the final model residuals were independent and not spatially autocorrelated (Zuur et al. 2009). Finally, we run a non-metric multi-dimensional scaling (NMDS) ordination analysis to explore patterns of coral community composition across reef sites. We fitted a smooth

surface using penalize splines of TSA values on the ordination results to analyze the relationship with coral species. All analyses were performed in R v.3.03 (R Core Team 2013) using the packages *lme4* v.0.99-2 for GLMMs, *MuMIn* v.1.9.13 for model averaging, *ncf* v.1.1-5 for spatial autocorrelation, and *vegan* v.2.0-1.0 for the ordination analysis.

## Results

Annual thermal-stress anomalies (TSA) increased at 22 out of 39 sites (~56%) over a 29-year period (1982-2010) across the Central and Western Caribbean (Fig. 4.1; Table S4.3 and Fig. S4.2). The long-term average ( $\pm$  standard deviation) of TSA frequency across all sites over this period was  $1.34 \pm 0.71$  anomaly weeks/year. The annual TSA frequency increased significantly at most reefs of the Mesoamerican barrier in Belize and Mexico while this trend was less pronounced for reef sites in Cuba, the Bahamas, and the Florida keys (Fig. 4.1; Fig. S4.2). Mean annual TSA frequency also varied significantly among sub-regions ( $F = 280.7$ ,  $df = 4$ ,  $p < 2.2e-16$ ) (Fig. 4.1; Fig. S4.3). The lowest long-term anomalies were found in Dry Tortugas, FL ( $0.28 \pm 0.00$  weeks/year) and Abaco, Bahamas ( $0.42 \pm 0.20$  weeks/year) and the highest values were found in Belize ( $1.94 \pm 0.94$  weeks/year) (Fig S4.3).

Current coral cover was positively and significantly associated with long-term TSA frequency across the study sites (Fig. S4.4). A simple exploratory linear regression model showed that annual average TSA frequency alone explained ~ 25 % of the variability in average of current coral cover across 39 reef sites ( $F=12.069$ ,  $df = 38$ ,  $R^2 = 0.246$ ,  $p = 0.0013$ ; Fig. S4.4). Coral cover ranged from  $1.5 \pm 1.2$  % (mean  $\pm$  standard deviation) at Dry Tortugas, FL (site: LG) to  $29.5 \pm 13.2$  % at Pompion, Belize (site: PO) (Fig. S4.4). The site with the lowest TSA

frequency was Little Harbor in Abaco, Bahamas ( $0.21 \pm 0.55$  weeks/year; LH) and the reef with the highest frequency was Ranguana, Belize ( $2.36 \pm 2.59$  weeks/year; RA) (Fig 4.1; Fig. S4.4).

The possible combinations of all explanatory variables for all response variables produced 6 to 28 models of 4 to 10 parameters (including fixed and random effects) with model weights between 0.02 and 0.33 for all coral groups considering  $\Delta AIC < 3$  (Table 4.2). TSA frequency was identified as the most important variable (i.e.,  $w_i = 1.00$ ) for all corals response variables, except the competitive life history ( $w_i = 0.11$ ). Macroalgae cover was important in models of stress-tolerant, weedy, and all corals ( $w_i = 1.00$ ), but was less important for competitive life histories ( $w_i = 0.05$ , Table 4.2). Reef landscape complexity showed higher relative importance ( $w_i > 0.71$ ) in all top models, while wave exposure had the highest importance for total coral cover ( $w_i = 0.68$ ) (Table 4.2). Piscivore and herbivore fish biomass had relative high importance ( $w_i = 0.77$  and  $w_i = 1.00$ ) for competitive and weedy corals, respectively. The rest of the explanatory variables had lower ( $w_i < 0.56$ ) relative importance for any other coral group (Table 4.2).

Competitive coral species were only slightly and positively associated with reef landscape complexity among all explanatory factors (Fig. 4.2). Reef complexity was also good predictor of weedy and total coral cover but had no strong effect on stress-tolerant corals (Fig. 4.2). Algae cover was negatively associated with weedy and stress-tolerant coral species which was reflected in total coral cover, but had no effect on competitive corals (Fig. 4.2). Piscivore and herbivore biomass, CCA cover, ocean productivity, wave exposure, and humans/reef had no measurable effect on most coral life-history strategies (Fig. 4.2). However, herbivore biomass was weakly negatively related to the cover of weedy coral species (Fig. 4.2).

Long term TSA frequency had the strongest and most positive effect on coral cover among all explanatory variables (Figs. 4.2 and 4.3). Weedy species (e.g., *Porites* spp., *Agaricia* spp.) showed a positive and strong response to TSA, followed by stress-tolerant (e.g., *Siderastrea siderea*, *Orbicella* spp.) (Figs. 4.2 and 4.3). Competitive corals (e.g., *Acropora* spp. and *Dendrogyra cylindrus*) displayed no trend with respect to long term average TSA frequency (Figs. 4.2 and 4.3). Percent cover of these competitive species was extremely low and patchy across the study sites (mean  $\pm$  standard deviation,  $0.32 \pm 1.28$  %). In fact, the averaged coefficient estimates for every explanatory variable that explain competitive corals showed wider confidence intervals than the rest of the coral groups (Fig. 4.2).

The ordination analysis supported the results of the predictive models (Fig. 4.4). After fitting the TSA data onto the ordination, this factor explained 39% of the variability observed in coral community composition across sites ( $r^2 = 0.390$ ,  $p = 0.0007$  based on 1000 permutations) (Fig. 4.4). Higher cover percentage of certain species were associated with higher TSA values (Fig. 4.4) that drove the relationship at life-history levels (Fig. 4.3). Weedy corals such as *Agaricia agaricites*, *Porites astreoides*, *Porites porites* and *Agaricia tenuifolia*, and stress-tolerant species such as *Siderastrea siderea*, *Orbicella* spp. complex and *Montastrea annularis* were more abundant on sites with higher TSA frequencies (Fig. 4.4).

## **Discussion**

We took advantage of variation among regions and sites in the thermal stress regime to infer effects of warming on coral cover and species composition across the Caribbean. Contemporary coral cover was positively associated with the frequency of thermal-stress anomalies across the region (Figs. 4.2 and 4.3). This is not because ocean warming

(operationally measured as temperature anomalies) is not affecting reef corals. There is extensive evidence at global, regional, and local scales that temperature anomalies promote coral mortality and reduce coral cover (Glynn 1993, Bruno et al. 2001, Hughes et al. 2003, Hoegh-Guldberg et al. 2007, Baker et al. 2008, Selig et al. 2012) especially in the Caribbean (Williams and Bunkley-Williams 1988, Lang et al. 1992, Winter et al. 1998, Wilkinson and Souter 2008, Eakin et al. 2010). However, warming and other stressors have been affecting reefs for decades and coral cover is now relatively low (generally regional averages range from 15-25% (Bruno and Selig 2007, Bruno et al. 2009, Schutte et al. 2010, De'ath et al. 2012), but see (Ateweberhan et al. 2011)) that additional disturbance and environmental stress is having smaller and increasingly undetectable effects on total coral cover. In other words, there is much less coral to lose now than in the 1980s. Selig et al. (2012) found a positive association between TSA frequency and annual coral cover loss globally, however, this effect was dependent on initial coral cover. Reefs with relative high coral cover are generally dominated by competitive taxa that are very sensitive to anomalously high temperatures (Bruno et al. 2001) and many other stressors (Bruno et al. 2007, Darling et al. 2013). Thus, coral communities that are often disturbed and that have lost sensitive species are more resistant to future disturbance, and change in total coral cover would no longer be a useful metric to assess the general impact of a disturbance like a temperature anomaly. In contrast, reef areas with lower anomaly frequencies may be more vulnerable when they experience an acute thermal stress event (Côté and Darling 2010).

Our results suggest that ocean warming is selecting for weedy and stress-tolerant species that can survive short-term temperature anomalies or are able to rapidly colonize disturbed reefs after mass bleaching events. The cover of weedy species (e.g., *Porites* spp., *Agaricia* spp.) was most strongly positively related to the frequency of high temperature anomalies, followed by



stress-tolerant species (e.g., *Orbicella* spp., *Siderastrea siderea*). The extremely low cover (<1% across sites) of once dominant competitive corals (e.g., *Acropora* spp.) was not related to temperature anomalies (Figs. 4.2 and 4.3). This is not surprising because the primary cause of the decline of Caribbean acroporids was the regional white band epizootic that largely preceded temperature anomalies related to greenhouse gas emissions (Aronson and Precht 2001, 2006, Barton and Casey 2005, Schutte et al. 2010, Williams and Miller 2012). Similar shifts towards weedy and stress-tolerant life histories (although not in response to ocean warming *per se*) have been documented in other areas of the Caribbean (Aronson et al. 2004, Green et al. 2008, Alvarez-Filip et al. 2013), Kenya (Darling et al. 2013), and Australia's Great Barrier Reef (Graham et al. 2014b).

There are at least two non-mutually exclusive explanations for the observed dominance of weedy and stress-tolerant coral taxa in highly disturbed environments, such as those with more frequent TSAs. First, they could be less sensitive to thermal stress. Temperature anomalies can increase thermal tolerance in coral species or genotypes (Loya et al. 2001, Edmunds and Gates 2008, Thompson and Woesik 2009, Van Woesik et al. 2011, Oliver and Palumbi 2011). Increased thermal tolerance is assumed to occur through a variety of mechanisms including phenotypic plasticity (i.e., acclimatization) or adaptation of the coral host or their endosymbionts (Baker et al. 2004, Edmunds and Gates 2008, Hoegh-Guldberg 2012, Palumbi et al. 2014). Second, various life history traits could enable them to recover from acute disturbances. For example, weedy species can rapidly recolonize unoccupied substrate after disturbances such as temperature anomalies (Darling et al. 2013) and diseases outbreaks (Aronson et al. 2004). This ability is after all what defines a weedy life history (Grime 1977). Most weedy coral species (e.g., *Agaricia* spp. and *Porites* spp.) are brooders (i.e., internal fertilization with production of

few larvae) that reach maturity early at smaller colony size and reproduce year around via sexual and asexual reproduction (Darling et al. 2012). Even at low colony densities, brooders can still produce larvae that can settle on available space after mortality of their benthic competitors (Green et al. 2008). Thus, weedy corals could benefit from ocean warming despite their physiological sensitivity to thermal stress because they can rapidly colonize disturbed environments. This is made possible by the patchy nature of temperature anomalies across the region (Fig. 4.1)(Selig et al. 2010).

Most stress-tolerant corals have massive, submassive, or encrusting growth forms with thick tissue that are proposed to have higher colony mass-transfer efficiencies under thermal stress and bleaching (Loya et al. 2001). Slower growth rates, larger colony size, and larger corallites may also allow stress-tolerant corals to persevere frequent stressful events of bleaching and recover from partial colony mortality (Darling et al. 2012, 2013). Although most stress-tolerant species are broadcast spawners (i.e., external fertilization with high fecundity), they are vulnerable to reproductive failure at low colony densities (Edmunds and Elahi 2007). A combination of traits that are tolerant to environmental disturbances may allow these corals to survive acute bleaching events and persevere over the long term.

The shift towards smaller opportunistic weedy coral species (Fig. 4.4) due to warming and other disturbances can reduce structural complexity, reef accretion, and thus functional integrity of the reef (Alvarez-Filip et al. 2013). Interestingly, we found a positive relationship between landscape-scale structural complexity and coral cover, especially for competitive and weedy coral species (Fig. 4.2). While competitive branching corals can increase structural complexity (Alvarez-Filip et al. 2011) we speculate that weedy corals may not contribute positively to reef structure (Alvarez-Filip et al. 2013). Much of this structural complexity was

created by dead stands of large *Acropora palmata* (competitive) and *Orbicella faveolata* (stress-tolerant), even though live cover of these species was as low as 0.12% and 1.74 %, respectively. It is likely that reefs with higher structural complexity, historically had higher live coral, thus current complexity values are to a large degree a remnant of past composition and cover (Alvarez-Filip et al. 2011). Additionally, greater reef complexity created by the skeletons of dead corals may provide more settlement habitat for coral recruits, particularly for opportunistic weedy species with little competition from formerly dominant coral taxa (Green et al. 2008, Alvarez-Filip et al. 2013). However, this relic feature of reefs of the past is ephemeral as biological and physical processes may eventually (in a matter of decades) erode these skeletons, flatten the reef surface, and remove any remaining structure of provided by long-dead corals.

Relative or absolute increase of weedy coral species does not ensure persistence of reef functionality since community calcification and reef accretion will decrease or cease (Alvarez-Filip et al. 2013). Because they grow more slowly and form smaller colonies with greater turnover rates, weedy coral taxa contribute far less to reef accretion and habitat complexity than large stress-tolerant and competitive corals (Alvarez-Filip et al. 2013, Bozec et al. 2014). As the current cover of large-colonies of reef-building corals such as *Acropora* spp. and *Orbicella* spp. continue to decline due to diseases, bleaching, and reproductive failure (Edmunds and Elahi 2007, Williams and Miller 2012), non-reef building weedy species such as *Porites* spp. and *Agaricia* spp. are increasing proportionally in abundance (Aronson et al. 2004, Green et al. 2008, Alvarez-Filip et al. 2013). These new assemblages will provide less structural complexity (Alvarez-Filip et al. 2013, McClanahan et al. 2014), the framework that coral reefs are built on, and that provide critical habitat to support a diverse and productive ecosystem for fishes and other reef inhabitants. Similarly, the loss of foundation species, as a result of climate change and

anthropogenic disturbance, are being observed in other ecosystems like tropical forests with profound consequences for fluxes of energy and nutrient, food webs, and biodiversity (Ellison et al. 2005).

The magnitude and frequency of warm temperature anomalies will continue to increase with business as usual carbon emissions scenarios (IPCC 2013). This could potentially strengthen shifts in coral species composition and ecosystem functioning (Thompson and Woesik 2009, Van Woesik et al. 2011). Our results suggest that coral communities that experience greater thermal stress will become dominated by smaller weedy species with high population turnover (Aronson et al. 2004, Green et al. 2008, Graham et al. 2014a) and stress-tolerant species of massive or encrusting growth forms with slower rates of calcification (Hoegh-Guldberg et al. 2007, Graham et al. 2014a, McClanahan et al. 2014). These communities will likely contribute less to carbonate accretion and architectural complexity, which compromise overall ecosystem structure and functioning (Alvarez-Filip et al. 2013, Graham et al. 2014b). While strong environmental filtering from thermal anomalies may favor a coral assemblage dominated by few more thermally resistant individuals (Maynard et al. 2008, Thompson and Woesik 2009, Van Woesik et al. 2011), even the most thermally tolerant taxa may reach physiological limits (Hoegh-Guldberg et al. 2007, Graham et al. 2014a) with projected 4°C increases of planetary warming (IPCC 2013). Over the short-term, bleaching events on reefs with stressful thermal histories may become less severe and frequent if coral assemblages are able to tolerate new environmental conditions (Thompson and Woesik 2009, Guest et al. 2012, Graham et al. 2014a). However, it is unclear when future limits of thermal tolerance will be reached (Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011). We document growing evidence of high variability in species responses to climate change and that responses of dominant species will

likely drive community patterns (Aronson et al. 2004, Darling et al. 2013, Alvarez-Filip et al. 2013). Instead of ecosystem collapse, a rapidly changing environment may slowly erode ecosystem composition and function. Efforts to identify climate refugia and global actions to control greenhouse gas emissions are our best hope to support functioning coral reefs into the future.

## References

- Alvarez-Filip, L., J. P. Carricart-Ganivet, G. Horta-Puga, and R. Iglesias-Prieto. 2013. Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Scientific Reports* 3.
- Alvarez-Filip, L., N. K. Dulvy, I. M. Côté, A. R. Watkinson, and J. A. Gill. 2011. Coral identity underpins architectural complexity on Caribbean reefs. *Ecological Applications* 21:2223–2231.
- Aronson, R. B., I. G. Macintyre, C. M. Wapnick, and M. W. O’Neill. 2004. Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology* 85:1876–1891.
- Aronson, R. B., R. M. Moody, L. C. Ivany, D. B. Blake, J. E. Werner, and A. Glass. 2009. Climate change and trophic response of the antarctic bottom fauna. *PLoS ONE* 4:e4385.
- Aronson, R. B., and W. F. Precht. 2001. White-band disease and the changing face of Caribbean coral reefs. Pages 25–38 *in* J. W. Porter, editor. *The ecology and etiology of newly emerging marine diseases*. Springer Netherlands.
- Aronson, R. B., and W. F. Precht. 2006. Conservation, precaution, and Caribbean reefs. *Coral Reefs* 25:441–450.
- Ateweberhan, M., T. R. McClanahan, N. A. J. Graham, and C. R. C. Sheppard. 2011. Episodic heterogeneous decline and recovery of coral cover in the Indian Ocean. *Coral Reefs* 30:739–752.
- Baker, A. C., P. W. Glynn, and B. Riegl. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science* 80:435–471.
- Baker, A. C., C. J. Starger, T. R. McClanahan, and P. W. Glynn. 2004. Coral reefs: Corals’ adaptive response to climate change. *Nature* 430:741–741.
- Barton, A. D., and K. S. Casey. 2005. Climatological context for large-scale coral bleaching. *Coral Reefs* 24:536–554.
- Bégin, C., E. S. Darling, T. A. Oliver, and I. M. Côté. 2014. Impacts of multiple stressors on Caribbean coral reefs: Community shifts and coral species vulnerability. *Coral Reefs in review*.
- Bozec, Y.-M., L. Alvarez-Filip, and P. J. Mumby. 2014. The dynamics of architectural complexity on coral reefs under climate change. *Global Change Biology*:n/a–n/a.
- Bruno, J. F., and E. R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 2:e711.

- Bruno, J. F., E. R. Selig, K. S. Casey, C. A. Page, B. L. Willis, C. D. Harvell, H. Sweatman, and A. M. Melendy. 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology* 5:e124.
- Bruno, J. F., C. E. Siddon, J. D. Witman, P. L. Colin, and M. A. Toscano. 2001. El Niño related coral bleaching in Palau, Western Caroline Islands. *Coral Reefs* 20:127–136.
- Bruno, J. F., H. Sweatman, W. F. Precht, E. R. Selig, and V. G. W. Schutte. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. 2nd edition. Springer New York.
- Burrows, M. T., D. S. Schoeman, L. B. Buckley, P. Moore, E. S. Poloczanska, K. M. Brander, C. Brown, J. F. Bruno, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, W. Kiessling, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. B. Schwing, W. J. Sydeman, and A. J. Richardson. 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334:652–655.
- Burrows, M. T., D. S. Schoeman, A. J. Richardson, J. G. Molinos, A. Hoffmann, L. B. Buckley, P. J. Moore, C. J. Brown, J. F. Bruno, C. M. Duarte, B. S. Halpern, O. Hoegh-Guldberg, C. V. Kappel, W. Kiessling, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, W. J. Sydeman, S. Ferrier, K. J. Williams, and E. S. Poloczanska. 2014. Geographical limits to species-range shifts are suggested by climate velocity. *Nature* 507:492–495.
- Carleton, J. H., and T. J. Done. 1995. Quantitative video sampling of coral reef benthos: large-scale application. *Coral Reefs* 14:35–46.
- Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortés, J. C. Delbeek, L. DeVantier, G. J. Edgar, A. J. Edwards, D. Fenner, H. M. Guzmán, B. W. Hoeksema, G. Hodgson, O. Johan, W. Y. Licuanan, S. R. Livingstone, E. R. Lovell, J. A. Moore, D. O. Obura, D. Ochavillo, B. A. Polidoro, W. F. Precht, M. C. Quibilan, C. Reboton, Z. T. Richards, A. D. Rogers, J. Sanciangco, A. Sheppard, C. Sheppard, J. Smith, S. Stuart, E. Turak, J. E. N. Veron, C. Wallace, E. Weil, and E. Wood. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321:560–563.
- Casey, K. S., T. B. Brandon, P. Cornillon, and R. Evans. 2010. The past, present, and future of the AVHRR pathfinder SST program. Pages 273–287 in V. Barale, J. F. R. Gower, and L. Alberotanza, editors. *Oceanography from Space*. Springer Netherlands, Dordrecht.
- Chollett, I., P. J. Mumby, F. E. Müller-Karger, and C. Hu. 2012. Physical environments of the Caribbean Sea. *Limnology and Oceanography* 57:1233–1244.
- Côté, I. M., and E. S. Darling. 2010. Rethinking Ecosystem Resilience in the Face of Climate Change. *PLoS Biology* 8:e1000438.

- Darling, E. S., L. Alvarez-Filip, T. A. Oliver, T. R. McClanahan, and I. M. Côté. 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters* 15:1378–1386.
- Darling, E. S., T. R. McClanahan, and I. M. Côté. 2013. Life histories predict coral community disassembly under multiple stressors. *Global Change Biology* 19:1930–1940.
- De'ath, G., K. E. Fabricius, H. Sweatman, and M. Puotinen. 2012. From the Cover: The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences* 109:17995–17999.
- Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344:296–299.
- Eakin, C. M., J. A. Morgan, S. F. Heron, T. B. Smith, G. Liu, L. Alvarez-Filip, B. Baca, E. Bartels, C. Bastidas, C. Bouchon, M. Brandt, A. W. Bruckner, L. Bunkley-Williams, A. Cameron, B. D. Causey, M. Chiappone, T. R. L. Christensen, M. J. C. Crabbe, O. Day, E. de la Guardia, G. Díaz-Pulido, D. DiResta, D. L. Gil-Agudelo, D. S. Gilliam, R. N. Ginsburg, S. Gore, H. M. Guzmán, J. C. Hendee, E. A. Hernández-Delgado, E. Husain, C. F. G. Jeffrey, R. J. Jones, E. Jordán-Dahlgren, L. S. Kaufman, D. I. Kline, P. A. Kramer, J. C. Lang, D. Lirman, J. Mallela, C. Manfrino, J.-P. Maréchal, K. Marks, J. Mihaly, W. J. Miller, E. M. Mueller, E. M. Muller, C. A. Orozco Toro, H. A. Oxenford, D. Ponce-Taylor, N. Quinn, K. B. Ritchie, S. Rodríguez, A. R. Ramírez, S. Romano, J. F. Samhuri, J. A. Sánchez, G. P. Schmahl, B. V. Shank, W. J. Skirving, S. C. C. Steiner, E. Villamizar, S. M. Walsh, C. Walter, E. Weil, E. H. Williams, K. W. Roberson, and Y. Yusuf. 2010. Caribbean Corals in Crisis: Record Thermal Stress, Bleaching, and Mortality in 2005. *PLoS ONE* 5:e13969.
- Edmunds, P. J., and R. Elahi. 2007. The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecological Monographs* 77:3–18.
- Edmunds, P. J., and R. D. Gates. 2008. Acclimatization in tropical reef corals. *Marine Ecology Progress Series* 361:307–310.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppe, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–486.
- Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301:958–960.
- Glynn, P. W. 1993. Coral reef bleaching: ecological perspectives. *Coral Reefs* 12:1–17.



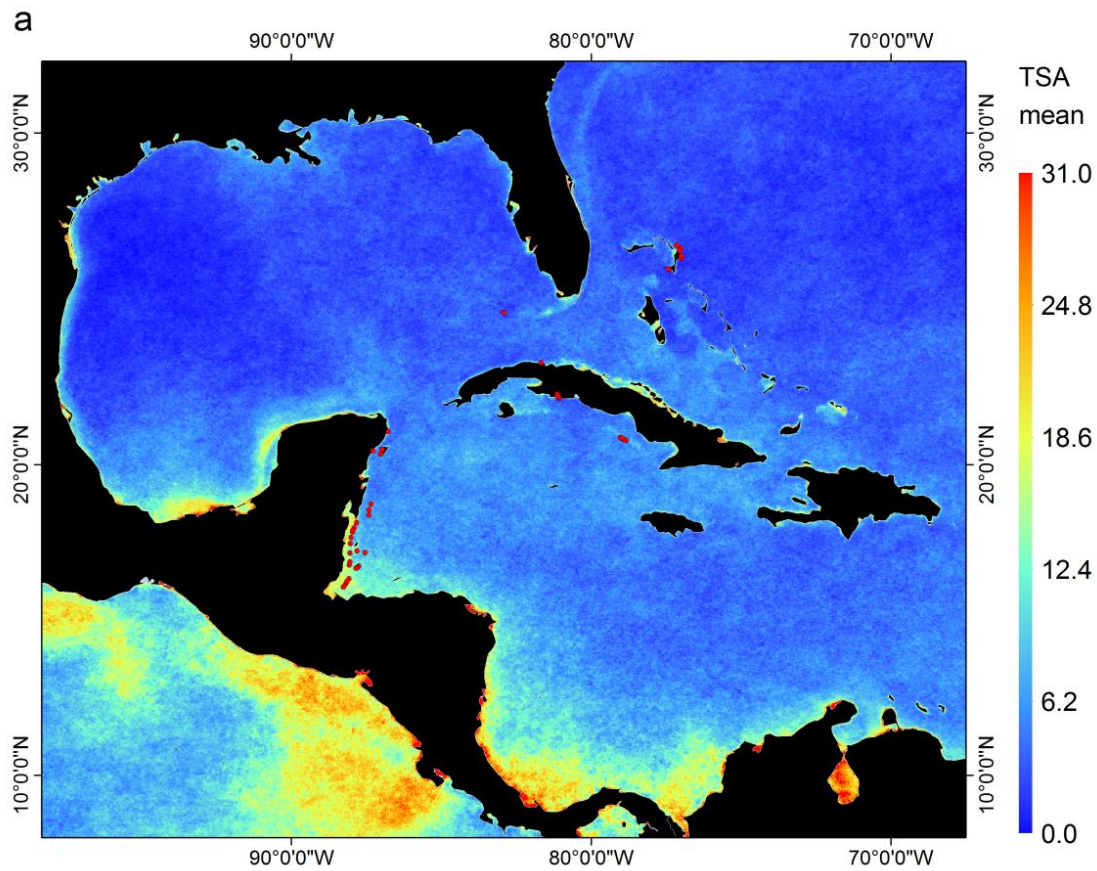
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815.
- Graham, N. A., J. E. Cinner, A. V. Norström, and M. Nyström. 2014a. Coral reefs as novel ecosystems: embracing new futures. *Current Opinion in Environmental Sustainability* 7:9–14.
- Graham, N. A. J., K. M. Chong-Seng, C. Huchery, F. A. Januchowski-Hartley, and K. L. Nash. 2014b. Coral Reef Community Composition in the Context of Disturbance History on the Great Barrier Reef, Australia. *PLoS ONE* 9:e101204.
- Green, D., P. Edmunds, and R. Carpenter. 2008. Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Marine Ecology Progress Series* 359:1–10.
- Greenstein, B. J., and J. M. Pandolfi. 2008. Escaping the heat: range shifts of reef coral taxa in coastal Western Australia. *Global Change Biology* 14:513–528.
- Grime, J. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Guest, J. R., A. H. Baird, J. A. Maynard, E. Muttaqin, A. J. Edwards, S. J. Campbell, K. Yewdall, Y. A. Affendi, and L. M. Chou. 2012. Contrasting Patterns of Coral Bleaching Susceptibility in 2010 Suggest an Adaptive Response to Thermal Stress. *PLoS ONE* 7:e33353.
- Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24:599–605.
- Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50:839–866.
- Hoegh-Guldberg, O. 2012. The adaptation of coral reefs to climate change: Is the Red Queen being outpaced? *Scientia Marina* 76:403–408.
- Hoegh-Guldberg, O., and J. F. Bruno. 2010. The impact of climate change on the world's marine ecosystems. *Science* 328:1523–1528.
- Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin, R. Iglesias-Prieto, N. Muthiga, R. H. Bradbury, A. Dubi, and M. E. Hatzitolos. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- Hoegh-Guldberg, O., J. C. Ortiz, and S. Dove. 2011. The future of coral reefs. *Science* 334:1494–1495.
- Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nystrom, S.

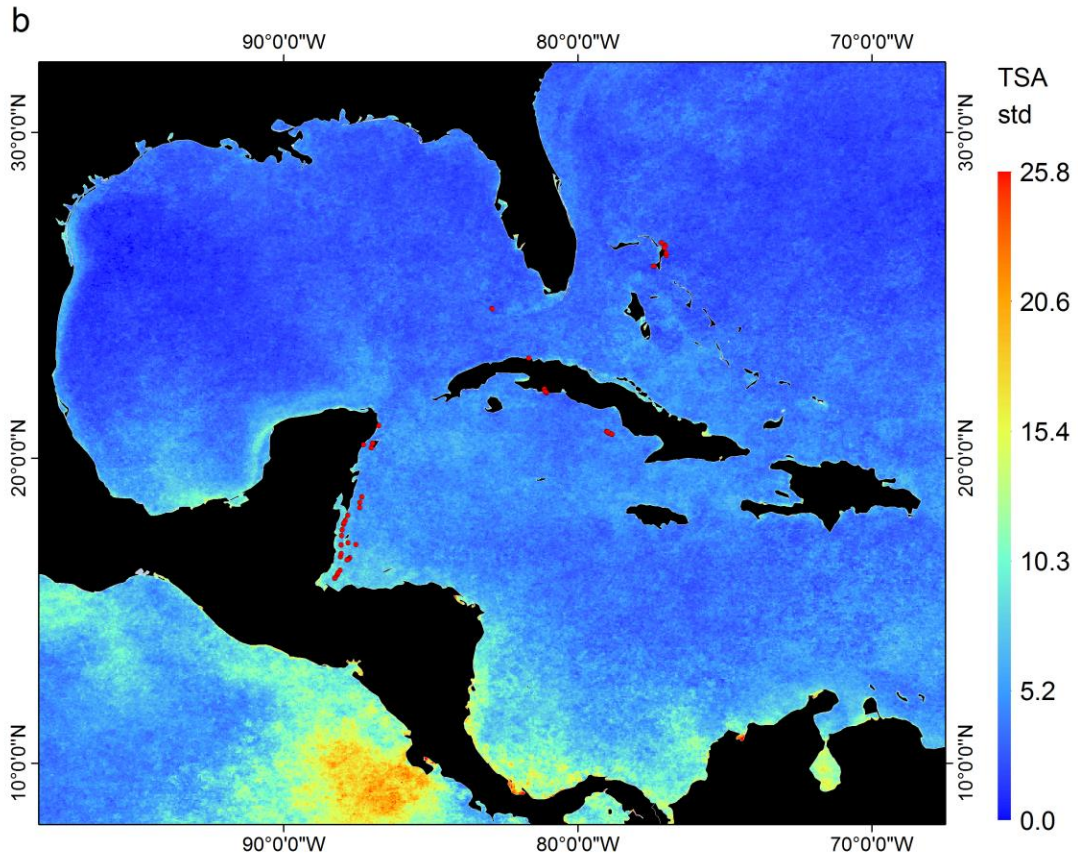
- R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933.
- IPCC. 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Kilpatrick, K. A., G. P. Podestá, and R. Evans. 2001. Overview of the NOAA/NASA advanced very high resolution radiometer Pathfinder algorithm for sea surface temperature and associated matchup database. *Journal of Geophysical Research: Oceans* 106:9179–9197.
- Lang, J. C., H. R. Lasker, E. H. Gladfelter, P. Hallock, W. C. Japp, F. J. Losada, and R. G. Muller. 1992. Spatial and temporal variability during periods of “recovery” after mass bleaching on Western Atlantic coral reefs. *American Zoologist* 32:696–706.
- Lang, J. C., K. W. Marks, P. A. Kramer, P. Richards Kramer, and R. N. Ginsburg. 2010. *AGRRA Protocols version 5.4 Atlantic and Gulf Rapid Reef Assessment Program.* University of Miami, Florida.
- Lessafre, E., D. Rizopoulos, and R. Tsonaka. 2007. The logistic-transform for bounded outcome scores. *Biostatistics* 8:72–85.
- Loya, Sakai, Yamazato, Nakano, Sambali, and Van Woesik. 2001. Coral bleaching: the winners and the losers. *Ecology Letters* 4:122–131.
- Maynard, J., K. Anthony, P. Marshall, and I. Masiri. 2008. Major bleaching events can lead to increased thermal tolerance in corals. *Marine Biology* 155:173–182.
- McClanahan, T. R., N. A. Graham, and E. S. Darling. 2014. Coral reefs in a crystal ball: predicting the future from the vulnerability of corals and reef fishes to multiple stressors. *Current Opinion in Environmental Sustainability* 7:59–64.
- Oliver, T. A., and S. R. Palumbi. 2011. Many corals host thermally resistant symbionts in high-temperature habitat. *Coral Reefs* 30:241–250.
- Palumbi, S. R., D. J. Barshis, N. Traylor-Knowles, and R. A. Bay. 2014. Mechanisms of reef coral resistance to future climate change. *Science*:1251336.
- Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958.
- Pandolfi, J. M., S. R. Connolly, D. J. Marshall, and A. L. Cohen. 2011. Projecting coral reef futures under global warming and ocean acidification. *Science* 333:418–422.

- Precht, W. F., and R. B. Aronson. 2004. Climate flickers and range shifts of reef corals. *Frontiers in Ecology and the Environment* 2:307–314.
- R Core Team. 2013. *R: A Language and Environment for Statistical Computing*, Vienna, Austria. V. 3.03. <http://www.R-project.org>.
- Schutte, V. G. W., E. R. Selig, and J. F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Mar Ecol Prog Ser* 402:115–122.
- Selig, E. R., K. S. Casey, and J. F. Bruno. 2010. New insights into global patterns of ocean temperature anomalies: implications for coral reef health and management: Global variability in temperature anomalies on coral reefs. *Global Ecology and Biogeography* 19:397–411.
- Selig, E. R., K. S. Casey, and J. F. Bruno. 2012. Temperature-driven coral decline: the role of marine protected areas. *Global Change Biology* 18:1561–1570.
- Selig, E. R., C. Drew Harvell, J. F. Bruno, B. L. Willis, C. A. Page, K. S. Casey, and H. Sweatman. 2006. Analyzing the Relationship Between Ocean Temperature Anomalies and Coral Disease Outbreaks at Broad Spatial Scales. Pages 111–128 *Coral Reefs and Climate Change: Science and Management*. American Geophysical Union.
- Thompson, D. M., and R. van Woesik. 2009. Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. *Proceedings of the Royal Society B: Biological Sciences* 276:2893–2901.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Wilkinson, C., and D. Souter. 2008. Status of Caribbean coral reefs after bleaching and hurricanes in 2005. Global Coral Reef Monitoring Network, and Reef and Rainforest Research Centre.
- Williams, D. E., and M. W. Miller. 2012. Attributing mortality among drivers of population decline in *Acropora palmata* in the Florida Keys (USA). *Coral Reefs* 31:369–382.
- Williams, E. H., and L. Bunkley-Williams. 1988. Bleaching of Caribbean reef symbionts in 1987-1988. Pages 313–318 *Proceedings of the 6th International Coral Reef Symposium*. Australia.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.
- Winter, A., R. S. Appeldoorn, A. Bruckner, E. H. J. Williams, and C. Goenaga. 1998. Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea). *Coral Reefs* 17:377–382.

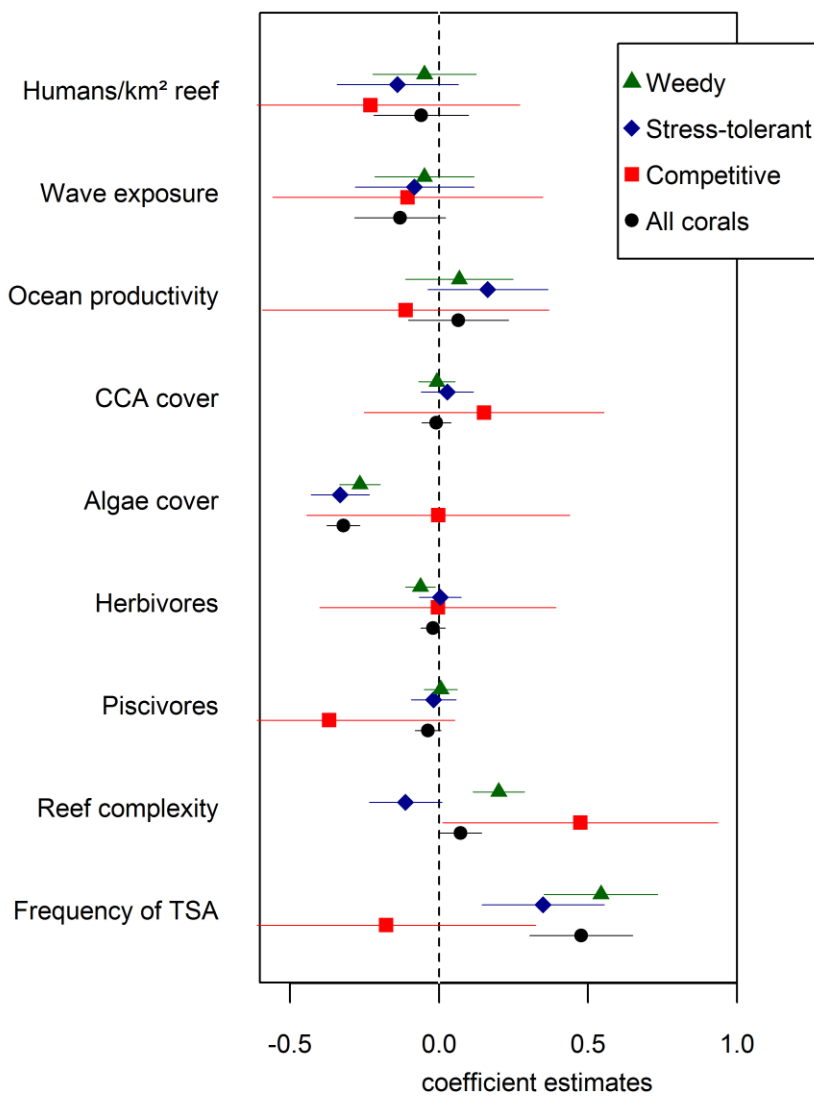
- Van Woesik, R., K. Sakai, A. Ganase, and Y. Loya. 2011. Revisiting the winners and the losers a decade after coral bleaching. *Mar Ecol Prog Ser* 434:67–76.
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer.

**Figure 4.1 Long-term mean and standard deviation of frequency of thermal stress-anomalies for the Western and Central Caribbean.** Long-term mean frequency of TSA (a) and standard deviation (b) over 29 years (1982-2010) for the Western and Central Caribbean. Red dots are surveyed reefs where coral cover was measured. For sites coordinates refer to Supplementary Table S4.1.

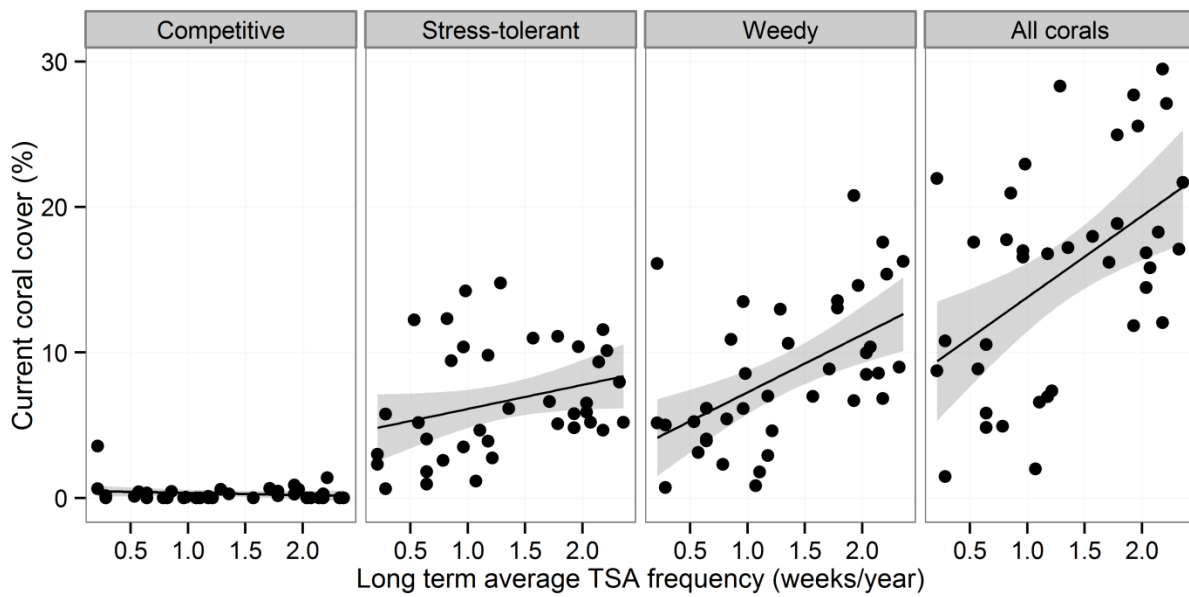




**Figure 4.2 Model-averaged coefficients from the top generalized mixed-effect models of current coral cover.** Estimates coefficient from model averages ( $\Delta AIC < 3$ ; Table 4.2) of current of total coral cover and cover of four life-history-strategy groups responding to annual frequency of TSA (thermal-stress anomalies) and other covariates (Table 4.1). Symbols are mean values bounded by 95% confidence intervals (CI). Positive or negative values where CI does not cross the vertical zero line show a significant effect on coral cover.

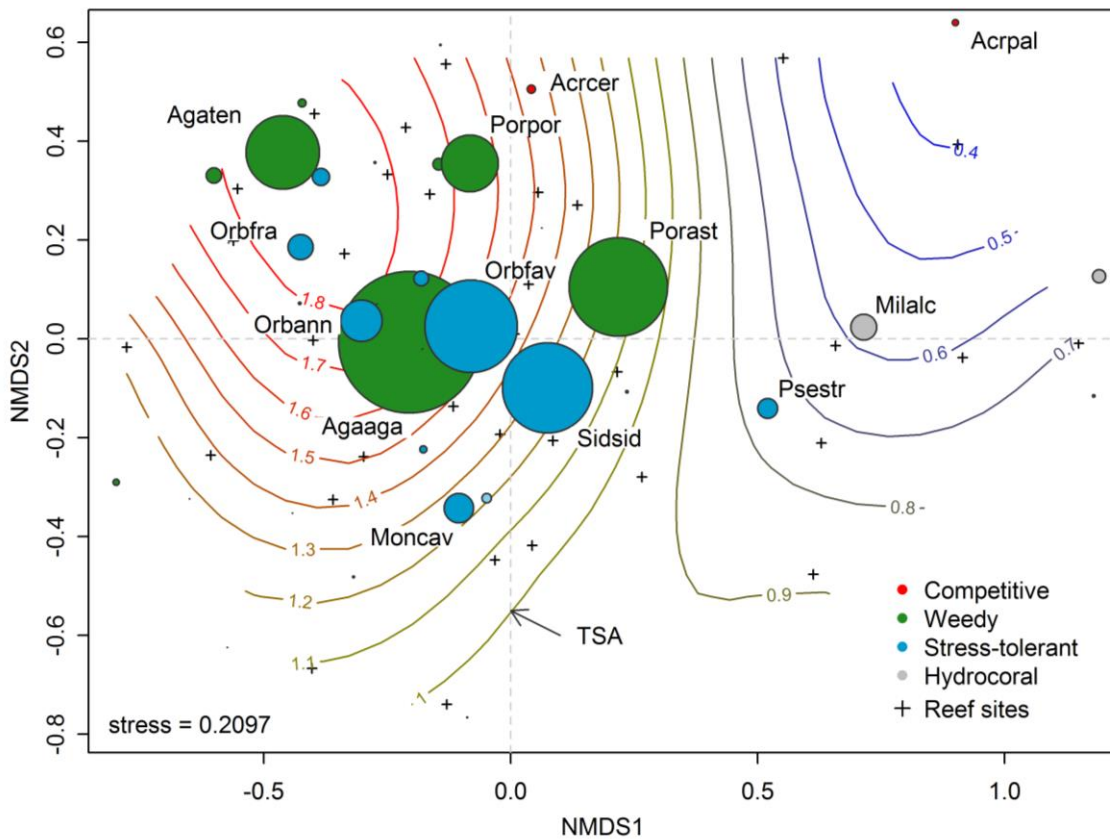


**Figure 4.3 Relationship between current coral cover of life-history strategies and average frequency of annual thermal stress anomalies.** Thermal stress anomalies as deviations of one-week where sea surface temperature (SST) was 1°C or greater than the mean maximum climatological week or the long term average warmest week from 1982 to 2010 (Selig et al. 2010). Black dots are current average of coral cover for each of the study sites. Black line is the predicted response from models bounded by 95% confidence intervals.





**Figure 4.4 Non-metric multidimensional scaling ordination of coral species abundance on the frequency of thermal stress anomalies.** Scleractinian coral species are divided in three life-history strategies separated from hydrocorals. Circle size is proportional to the average of absolute cover of each species across sites. Average frequency of thermal stress anomalies (TSA) are isolines with numbers (weeks/year). Only the most abundant species are labeled. For species codes refer to Table S4.2.



**Table 4.1 Description of variables used as predictors in the generalized linear mixed-effect models (GLMMs).** Each variable is known to potentially influence current coral cover across the study sites. \*See supplementary methods for a detailed description of each variable and reasoning for usage.

<b>Variable name</b>	<b>Range</b>	<b>Units</b>	<b>Source</b>
<i>Anthropogenic</i>			
Humans per reef area	0.4-4314.1	#/km <sup>2</sup> reef	World Gridded Population*
Cultivated land within 50 km	0-3917	km <sup>2</sup>	Global Land Cover 2010*
<i>Physical</i>			
Thermals stress anomalies (TSA)	0.2-2.4	frequency	CorTAD v.4*
Net primary productivity	203-1610	mg C m <sup>-2</sup>	Aqua MODIS*
Wave exposure (log)	3.9-7.9	J m <sup>-3</sup>	Caribbean wave exposure*
Reef structural complexity	1.5-5	#	In situ estimations*
<i>Biotic</i>			
Macroalgae cover	6.2-71.2	%	In situ measurements/video
Crustose coralline algae cover	0-17.2	%	In situ measurements/video
Turf algae cover	1.3-55.7	%	In situ measurements/video
Herbivore fish biomass	14.1-210.1	g m <sup>-2</sup>	In situ measurements*
Piscivore fish biomass	3.6-441.0	g m <sup>-2</sup>	In situ measurements*

**Table 4.2 Relative importance of explanatory variables from the top GLMMs of logit transformed percentage cover from competitive, stress-tolerant, weedy, and all corals species.** Relative importance is the sum of the weights of all models that contain that particular variable. Top models were chosen for  $\Delta AIC_c < 3$ , where  $\Delta AIC_c$  is the difference in  $AIC_c$  values between model  $i$  and the best model considered. Weights is the probability of model  $i$  being the best of the set. Range of the model summary parameters (df, logLik,  $AIC_c$ ) are shown for each coral group.

	<b>Competitive</b>	<b>Stress-tolerant</b>	<b>Weedy</b>	<b>All corals</b>
Frequency of TSA	0.11	1.00	1.00	1.00
Algae cover	0.05	1.00	1.00	1.00
Reef complexity	1.00	0.72	1.00	0.91
Wave exposure	0.13	0.19	0.14	0.68
Piscivore biomass	0.77	0.13	0.12	0.67
Herbivore biomass	0.05	0.10	1.00	0.23
Humans/km <sup>2</sup> reef	0.29	0.41	0.14	0.16
Ocean productivity	0.13	0.55	0.15	0.13
CCA cover	0.16	0.16	0.12	0.08
Degree of freedom	4-7	5-9	7-8	6-10
logLik	(-125.6, -127.7)	(-1021.8, -1025.7)	(-1218.3, -1218.5)	(-1344.7, -1348.7)
$AIC_c$	(262.4-265.4)	(2059.9, 2062.7)	(2451.4, 2453.1)	(2707.1, 2709.9)
$\Delta AIC_c$ ( $\Delta AIC < 3$ )	0.0-2.99	0.0-2.89	0.0-2.04	0.0-2.92
Weights	0.03-0.15	0.02-0.08	0.12-0.33	0.03-0.13
Number of top models	17	28	6	19

**APPENDIX 1: SUPPLEMENTARY MATERIAL FOR CHAPTER 1**

**Table S1.1 Study sites, site codes, regions and, protection level.** Habitat type, S&G: Spur and Grove; Protection level, NTZ: No-take zone, MPA: marine protected area. Date of survey is month and year(s).

Site name	Site code	Habitat type	Depth (m)	Date of survey	Latitude	Longitude	Protection level	MR year
Mesoamerican Barrier, Mexico								
Cancún	GH	S & G	12	Jul 12	21.02544	-86.7713	none	
Cozumel North	PB	S & G	10	Jul 12	20.47188	-86.9815	NTZ	1996
Akumal	XA	S & G	15	Jul 12	20.42689	-87.2860	none	
Cozumel South	CR	S & G	15	Jul 12	20.31961	-87.0266	NTZ	1996
Chinchorro North	BCN	S & G	15	Jul 12	18.74867	-87.3476	MPA	1996
Chinchorro Central	BCC	S & G	15	Jul 12	18.57457	-87.4198	MPA	1996
Chinchorro South	BCS	S & G	15	Jul 12	18.41008	-87.4169	MPA	1966
Mesoamerican Barrier, Belize								
Bacalar Chico	BC	S & G	12-15	May 10/12	18.16282	-87.82222	NTZ	1996
Mexico Rocks	MR	S & G	12-15	May 10/12	17.98782	-87.90382	none	
Tackle Box	TB	S & G	12-15	May 10/12	17.91056	-87.95083	none	
Hol Chan	HC	S & G	12-15	May 10/12	17.86343	-87.97238	NTZ	1987
Gallows	GA	S & G	12-15	May 10/12	17.49592	-88.04255	none	
Calabash Caye	CA	S & G	12-15	May 10/12	17.26147	-87.81970	none	
Half Moon Caye	HM	S & G	12-15	May 10/12	17.20560	-87.54679	NTZ	1982
Alligator Caye	AL	S & G	12-15	May 10/12	17.19660	-88.05115	none	
Tobacco Caye	TO	S & G	12-15	May 10/12	16.91911	-88.04757	none	
South Water Caye	SW	S & G	12-15	May 10/12	16.81346	-88.07756	MPA	1996
Middle Caye	MC	S & G	12-15	May 10/12	16.73703	-87.80536	MPA	1993
South Middle Caye	SM	S & G	12-15	May 10/12	16.72875	-87.82867	MPA	1993
Pampion Caye	PO	S & G	12-15	May 10/12	16.37310	-88.08913	none	
Ranguana Caye	RA	S & G	12-15	May 10/12	16.28501	-88.15031	none	
Southwest Caye	ST	S & G	12-15	May 10/12	16.11247	-88.27107	none	
Nicholas Caye	NI	S & G	12-15	May 10/12	16.11230	-88.25586	MPA	2003
Dry Tortugas, USA	LG	S & G	12	Jun 12	24.68508	-82.91050	NTZ	1992
Bay of Pigs, Cuba								
Cueva Peces	CP	Slope	10-12	Jun 10/12	22.16627	-81.13827	none	
Punta Perdiz	PZ	Slope	10-12	Jun 10/12	22.11003	-81.11626	none	
Ebano	EB	Slope	10-12	Jun 10	22.07914	-81.07599	none	
Brinco	BR	Slope	10-12	Jun 12	22.06939	-81.05588	none	
Bacunayagua, Cuba	BC	Slope	10-12	Jun 12	23.14653	-81.66664	none	
Jardines de la Reina, Cuba								
El Peruano	EP	Slope	10-12	Jun 11	20.84411	-79.02166	NTZ	1996
Pipin	PP	S & G	12-15	Jun 11	20.82586	-78.98026	NTZ	1996
Anclita	AN	Slope	10-12	Jun 11	20.78697	-78.94317	NTZ	1996
Cueva Pulpo	CF	Slope	10-12	Jun 11	20.75266	-78.83634	NTZ	1996
Abaco, Bahamas								
Guana Cay	GC	S & G	10-12	Jul 11/12	26.70967	-77.15408	none	
Fowls Cay	FC	Slope	10	Jul 11/12	26.63717	-77.03848	NTZ	2009
Man o' War	MW	S & G	10-12	Jul 11/12	26.62122	-77.00550	none	
Pelican Cay	PC	Slope	10	Jul 11/12	26.39783	-76.98850	NTZ	1972
Little Harbor	LH	S & G	10-12	Jul 11/12	26.32390	-76.99160	none	
Rocky Point	RP	Slope	10-12	Jul 11/12	25.99661	-77.40092	Remote	

**Table S1.2 Fish trophic guilds, species taxonomic information, and allometric parameters used to calculate biomass.**

<b>Trophic Group</b>	<b>Family</b>	<b>Common Name</b>	<b>Species Name</b>	<b>a</b>	<b>b</b>
Apex predator	Carangidae	Greater Amberjack	<i>Seriola dumerili</i>	0.0325	2.870
Apex predator	Carangidae	Almaco Jack	<i>Seriola rivoliana</i>	0.0122	2.957
Apex predator	Carcharhinidae	Silky Shark	<i>Carcharhinus falsiformis</i>	0.0101	3.060
Apex predator	Carcharhinidae	Blacktip Shark	<i>Carcharhinus limbatus</i>	0.0061	3.010
Apex predator	Carcharhinidae	Reef Shark	<i>Carcharhinus perezii</i>	0.0271	3.000
Apex predator	Carcharhinidae	Lemon shark	<i>Negaprion brevirostris</i>	0.0053	3.160
Apex predator	Elopidae	Tarpon	<i>Megalops atlanticus</i>	0.0120	2.984
Apex predator	Lutjanidae	Cubera Snapper	<i>Lutjanus cyanopterus</i>	0.0152	3.060
Apex predator	Muraenidae	Green Moray	<i>Gymnothorax funebris</i>	0.0041	2.856
Apex predator	Rhincodontidae	Nurse Shark	<i>Ginglymostoma cirratum</i>	0.0105	2.892
Apex predator	Scombridae	Cero	<i>Scomberomorus regalis</i>	0.0202	2.800
Apex predator	Serranidae	Black Grouper	<i>Mycteroperca bonaci</i>	0.0082	3.140
Apex predator	Serranidae	Yellowmouth Grouper	<i>Mycteroperca interstitialis</i>	0.0141	3.000
Apex predator	Serranidae	Tiger Grouper	<i>Mycteroperca tigris</i>	0.0094	3.120
Apex predator	Serranidae	Yellowfin Grouper	<i>Mycteroperca venenosa</i>	0.0122	3.000
Apex predator	Sphyraenidae	Great Barracuda	<i>Sphyraena barracuda</i>	0.0070	2.972
Pisc/Invertivore	Aulostomidae	Trumpetfish	<i>Aulostomus maculatus</i>	0.0040	2.866
Pisc/Invertivore	Belontiidae	Houndfish	<i>Tylosurus crocodilus</i>	0.0008	3.205
Pisc/Invertivore	Bothidae	Peacock Flounder	<i>Bothus lunatus</i>	0.0098	3.189
Pisc/Invertivore	Carangidae	Bar Jack	<i>Carangoides ruber</i>	0.0180	2.990
Pisc/Invertivore	Carangidae	Blue Runner	<i>Caranx crysos</i>	0.0318	2.949
Pisc/Invertivore	Carangidae	Crevalle Jack	<i>Caranx hippos</i>	0.0329	2.855
Pisc/Invertivore	Carangidae	Horse Eye Jack	<i>Caranx latus</i>	0.0186	2.856
Pisc/Invertivore	Carangidae	Palomet	<i>Trachinotus goodei</i>	0.0204	3.000
Pisc/Invertivore	Carangidae	Yellow Jack	<i>Caranx bartholomaei</i>	0.0259	2.908
Pisc/Invertivore	Centropomidae	Common Snook	<i>Centropomus undecimalis</i>	0.0104	2.910
Pisc/Invertivore	Dasyatidae	Southern Stingray	<i>Dasyatis americana</i>	0.0739	2.810
Pisc/Invertivore	Haemulidae	Sailors Choice	<i>Haemulon parra</i>	0.0199	2.993
Pisc/Invertivore	Haemulidae	White Grunt	<i>Haemulon plumieri</i>	0.0259	3.000
Pisc/Invertivore	Lutjanidae	Mutton Snapper	<i>Lutjanus analis</i>	0.0146	3.034
Pisc/Invertivore	Lutjanidae	Schoolmaster	<i>Lutjanus apodus</i>	0.0189	3.000
Pisc/Invertivore	Lutjanidae	Gray Snapper	<i>Lutjanus griseus</i>	0.0240	2.910
Pisc/Invertivore	Lutjanidae	Dog Snapper	<i>Lutjanus jocu</i>	0.0198	2.960
Pisc/Invertivore	Lutjanidae	Mahogany Snapper	<i>Lutjanus mahogoni</i>	0.0428	2.719
Pisc/Invertivore	Lutjanidae	Lane Snapper	<i>Lutjanus synagris</i>	0.0216	2.917
Pisc/Invertivore	Lutjanidae	Yellowtail Snapper	<i>Ocyurus chrysurus</i>	0.0314	2.793
Pisc/Invertivore	Scombridae	King Mackerel	<i>Scomberomorus caballa</i>	0.0091	2.960
Pisc/Invertivore	Scorpinidae	Lionfish	<i>Pterois volitans</i>	0.0050	3.291
Pisc/Invertivore	Serranidae	Graysby	<i>Cephalopholis cruentata</i>	0.0121	3.082
Pisc/Invertivore	Serranidae	Coney	<i>Cephalopholis fulva</i>	0.0188	2.973
Pisc/Invertivore	Serranidae	Rock Hind	<i>Epinephelus adscensionis</i>	0.0125	3.224
Pisc/Invertivore	Serranidae	Red Hind	<i>Epinephelus guttatus</i>	0.0084	3.100
Pisc/Invertivore	Serranidae	Jewfish	<i>Epinephelus itajara</i>	0.0131	3.056
Pisc/Invertivore	Serranidae	Red Grouper	<i>Epinephelus morio</i>	0.0162	2.990
Pisc/Invertivore	Serranidae	Nassau Grouper	<i>Epinephelus striatus</i>	0.0065	3.229
Pisc/Invertivore	Serranidae	Greater Soapfish	<i>Rypticus saponaceus</i>	0.0010	1.000
Pisc/Invertivore	Serranidae	Shy Hamlet	<i>Hypoplectrus guttavarius</i>	0.0090	3.040
Pisc/Invertivore	Serranidae	Indigo Hamlet	<i>Hypoplectrus indigo</i>	0.0110	3.182

Pisc/Invertivore	Serranidae	Black Hamlet	<i>Hypoplectrus nigricans</i>	0.0110	3.182
Pisc/Invertivore	Serranidae	Barred Hamlet	<i>Hypoplectrus puella</i>	0.0090	3.040
Pisc/Invertivore	Serranidae	Butter Hamlet	<i>Hypoplectrus unicolor</i>	0.0090	3.040
Pisc/Invertivore	Sphyraenidae	Southern Sennet	<i>Sphyraena picudilla</i>	0.0067	2.942
Macroinvertivore	Balistidae	Queen Triggerfish	<i>Balistes vetula</i>	0.0354	2.900
Macroinvertivore	Balistidae	Ocean Triggerfish	<i>Canthidermis sufflamen</i>	0.0217	3.000
Macroinvertivore	Carangidae	Permit	<i>Trachinotus falcatus</i>	0.0301	2.958
Macroinvertivore	Echeneidae	Sharksucker	<i>Echeneis naucrates</i>	0.0010	3.290
Macroinvertivore	Ephippidae	Atlantic Spadefish	<i>Chaetodipterus faber</i>	0.0530	2.952
Macroinvertivore	Gerreidae	Yellowfin Mojarra	<i>Gerres cinereus</i>	0.0184	3.084
Macroinvertivore	Haemulidae	Black Margate	<i>Anisotremus surinamensis</i>	0.0233	3.010
Macroinvertivore	Haemulidae	Porkfish	<i>Anisotremus virginicus</i>	0.0148	3.167
Macroinvertivore	Haemulidae	White Margate	<i>Haemulon album</i>	0.0144	3.070
Macroinvertivore	Haemulidae	Tomtate	<i>Haemulon aurolineatum</i>	0.0120	3.100
Macroinvertivore	Haemulidae	Caesar Grunt	<i>Haemulon carbonarium</i>	0.0147	3.056
Macroinvertivore	Haemulidae	Smallmouth Grunt	<i>Haemulon chrysargyreum</i>	0.0106	3.047
Macroinvertivore	Haemulidae	French Grunt	<i>Haemulon flavolineatum</i>	0.0232	3.000
Macroinvertivore	Haemulidae	Spanish Grunt	<i>Haemulon macrostomum</i>	0.0176	3.060
Macroinvertivore	Haemulidae	Cottonwick	<i>Haemulon melanurum</i>	0.0226	2.953
Macroinvertivore	Haemulidae	Bluestriped Grunt	<i>Haemulon sciurus</i>	0.0194	2.999
Macroinvertivore	Haemulidae	Striped Grunt	<i>Haemulon striatum</i>	0.0175	3.099
Macroinvertivore	Holocentridae	Squirrelfish	<i>Holocentrus adscensionis</i>	0.0216	3.000
Macroinvertivore	Holocentridae	Longspine Squirrelfish	<i>Holocentrus rufus</i>	0.0170	3.000
Macroinvertivore	Holocentridae	Blackbar Soldierfish	<i>Myripristis jacobus</i>	0.1110	2.720
Macroinvertivore	Holocentridae	Longjaw Squirrelfish	<i>Neoniphon marianus</i>	0.0215	3.000
Macroinvertivore	Labridae	Spanish Hogfish	<i>Bodianus rufus</i>	0.0145	3.053
Macroinvertivore	Labridae	Slippery Dick	<i>Halichoeres bivittatus</i>	0.0105	3.093
Macroinvertivore	Labridae	Yellowhead Wrasse	<i>Halichoeres garnoti</i>	0.0052	3.375
Macroinvertivore	Labridae	Clown Wrasse	<i>Halichoeres maculipinna</i>	0.0028	3.693
Macroinvertivore	Labridae	Rainbow Wrasse	<i>Halichoeres pictus</i>	0.0052	3.375
Macroinvertivore	Labridae	Puddingwife	<i>Halichoeres radiatus</i>	0.0131	3.038
Macroinvertivore	Labridae	Hogfish	<i>Lachnolaimus maximus</i>	0.0237	2.950
Macroinvertivore	Labridae	Bluehead	<i>Thalassoma bifasciatum</i>	0.0101	3.040
Macroinvertivore	Malacanthidae	Sand Tilefish	<i>Malacanthus plumieri</i>	0.0001	2.680
Macroinvertivore	Myliobatidae	Spotted Eagle Ray	<i>Aetobatus narinari</i>	0.0059	3.130
Macroinvertivore	Ostracidae	Honeycomb Cowfish	<i>Acanthostracion polygonius</i>	0.0178	3.083
Macroinvertivore	Pomacanthidae	Blue Angelfish	<i>Holacanthus bermudensis</i>	0.0319	2.899
Macroinvertivore	Pomacanthidae	Queen Angelfish	<i>Holacanthus ciliaris</i>	0.0337	2.900
Macroinvertivore	Priacanthidae	Glasseye Snapper	<i>Heteropriacanthus cruentatus</i>	0.0188	3.000
Macroinvertivore	Serranidae	Harlequin Bass	<i>Serranus tigrinus</i>	0.0145	3.048
Macroinvertivore	Sparidae	Saucereye Porgy	<i>Calamus calamus</i>	0.0125	3.180
Macroinvertivore	Sparidae	Sheepshead Porgy	<i>Calamus penna</i>	0.0764	2.666
Macroinvertivore	Tetraodontidae	Bandtail Puffer	<i>Sphoeroides spengleri</i>	0.0235	3.050
Microinvertivore	Chaetodontidae	Foureye Butterflyfish	<i>Chaetodon capistratus</i>	0.0220	3.190
Microinvertivore	Chaetodontidae	Spotfin Butterflyfish	<i>Chaetodon ocellatus</i>	0.0318	2.984
Microinvertivore	Chaetodontidae	Banded Butterflyfish	<i>Chaetodon striatus</i>	0.0220	3.140
Microinvertivore	Gobiidae	Neon Goby	<i>Elacatinus oceanops</i>	0.0080	3.137
Microinvertivore	Grammatidae	Fairy Basslet	<i>Gramma loreto</i>	0.0001	1.111
Microinvertivore	Grammatidae	Blackcap Basslet	<i>Gramma melacara</i>	0.0001	1.111
Microinvertivore	Monacanthidae	Whitespotted Filefish	<i>Cantherhines macrocerus</i>	0.0561	2.653
Microinvertivore	Mullidae	Yellow Goatfish	<i>Mulloidichthys martinicus</i>	0.0110	3.092
Microinvertivore	Mullidae	Spotted Goatfish	<i>Pseudupeneus maculatus</i>	0.0150	3.157
Microinvertivore	Sciaenidae	Jackknife Fish	<i>Equetus lanceolatus</i>	0.0011	3.844
Microinvertivore	Sciaenidae	Spotted Drum	<i>Equetus punctatus</i>	0.0153	3.062
Planktivore	Labridae	Creole Wrasse	<i>Clepticus parrae</i>	0.0145	3.053

Planktivore	Pomacentridae	Blue Chromis	<i>Chromis cyanea</i>	0.0188	3.000
Planktivore	Pomacentridae	Brown Chromis	<i>Chromis multilineata</i>	0.0262	2.753
Large Omnivore	Balistidae	Black Durgon	<i>Melichthys niger</i>	0.0217	3.000
Large Omnivore	Pomacanthidae	Rock Beauty	<i>Holacanthus tricolor</i>	0.0203	3.126
Large Omnivore	Pomacanthidae	Gray Angelfish	<i>Pomacanthus arcuatus</i>	0.0203	3.126
Large Omnivore	Pomacanthidae	French Angelfish	<i>Pomacanthus paru</i>	0.0203	3.126
Small Omnivore	Monacanthidae	Scrawled Filefish	<i>Aluterus scriptus</i>	0.0022	3.000
Small Omnivore	Monacanthidae	Orangespotted Filefish	<i>Cantherhines pullus</i>	0.0684	2.563
Small Omnivore	Pomacentridae	Sergeant Major	<i>Abudefduf saxatilis</i>	0.0227	3.142
Small Omnivore	Pomacentridae	Dusky Damsel fish	<i>Stegastes adustus</i>	0.0384	3.010
Small Omnivore	Pomacentridae	Beaugregory	<i>Stegastes leucostictus</i>	0.0303	2.887
Small Omnivore	Pomacentridae	Threespot Damsel fish	<i>Stegastes planifrons</i>	0.0379	2.857
Small Omnivore	Pomacentridae	Cocoa Damsel fish	<i>Stegastes variabilis</i>	0.0324	2.836
Small Omnivore	Tetraodontidae	Sharpnose Puffer	<i>Canthigaster rostrata</i>	0.0323	2.953
Herbivore	Acanthuridae	Ocean Surgeonfish	<i>Acanthurus bahianus</i>	0.0236	2.975
Herbivore	Acanthuridae	Doctorfish	<i>Acanthurus chirurgus</i>	0.0225	3.000
Herbivore	Acanthuridae	Blue Tang	<i>Acanthurus coeruleus</i>	0.0305	3.000
Herbivore	Blenniidae	Redlip Blenny	<i>Ophioblennius atlanticus</i>	0.0324	2.379
Herbivore	Kyphosidae	Bermuda Chub	<i>Kyphosus saltatrix</i>	0.0174	3.080
Herbivore	Pomacentridae	Yellowtail Damsel fish	<i>Microspathodon chrysurus</i>	0.0239	3.082
Herbivore	Pomacentridae	Longfin Damsel fish	<i>Stegastes dienaecus</i>	0.0353	2.896
Herbivore	Pomacentridae	Bicolor Damsel fish	<i>Stegastes partitus</i>	0.0182	3.152
Herbivore	Scaridae	Midnight Parrotfish	<i>Scarus coelestinus</i>	0.0153	3.062
Herbivore	Scaridae	Blue Parrotfish	<i>Scarus coeruleus</i>	0.0124	3.111
Herbivore	Scaridae	Rainbow Parrotfish	<i>Scarus guacamaia</i>	0.0155	3.063
Herbivore	Scaridae	Striped Parrotfish	<i>Scarus iserti</i>	0.0158	3.052
Herbivore	Scaridae	Princess Parrotfish	<i>Scarus taeniopterus</i>	0.0177	3.000
Herbivore	Scaridae	Queen parrotfish	<i>Scarus vetula</i>	0.0158	3.052
Herbivore	Scaridae	Greenblotch Parrotfish	<i>Sparisoma atomarium</i>	0.0122	3.028
Herbivore	Scaridae	Redband Parrotfish	<i>Sparisoma aurofrenatum</i>	0.0129	3.110
Herbivore	Scaridae	Redtail Parrotfish	<i>Sparisoma chrysopteron</i>	0.0135	3.100
Herbivore	Scaridae	Bucktooth Parrotfish	<i>Sparisoma radians</i>	0.0179	3.035
Herbivore	Scaridae	Redfin Parrotfish	<i>Sparisoma rubripinne</i>	0.0194	3.000
Herbivore	Scaridae	Stoplight Parrotfish	<i>Sparisoma viride</i>	0.0250	2.921

**Table S1.3 Summary of preliminary, anthropogenic, physical, biotic, and management-related predictors used in the analysis.** For a detailed description of each variable see Appendix 1.1.

Variable name	Range	Units	Source
<i>Anthropogenic</i>			
Coastal Development in 50km	0-26470	light pixels	Suomi NPP satellite <sup>a</sup>
Humans within 50 km	54-67140	#	World Gridded Population <sup>b</sup>
Humans of closest town	0-628300	#	Country census
Distance to population centers	1.6-115.8	km	Calculated in ArcGIS 10
Cultivated land within 50 km	0-3917	km <sup>2</sup>	Global Land Cover 2000 <sup>c</sup>
<i>Physical</i>			
Net primary productivity	203-1610	mg C m <sup>-2</sup> day <sup>-1</sup>	Aqua MODIS
Sea surface temperature (SST)	26.0-29.3	°C	AHVR Pathfinder v5.2
Minimum SST	20.8-26.5	°C	AHVR Pathfinder v5.2
Wave exposure (log)	3.9-7.9	J m <sup>-3</sup>	(Chollett et al. 2012)
Depth	10-16	meters	In situ measurements
Reef structural complexity	1.5-5	#	In situ estimations
Distance to deep water	0.03-32.9	km	NOAA bathymetry charts
Distance to tide channels	0.4-6.0	km	Calculated in ArcGIS 10
Distance to mangrove	0.34-31.9	km	Calculated in ArcGIS 10
Reef area within 5 km	0.1-25.9	km <sup>2</sup>	Global Coral Reef 2010 <sup>d</sup>
Reef area within 10 km	0.4-43.1	km <sup>2</sup>	Global Coral Reef 2010
<i>Biotic</i>			
Mangrove perimeter in 5 km	0-175.6	km	Global Mangrove 2011 <sup>e</sup>
Mangrove perimeter in 10 km	0-406.10	km	Global Mangrove 2011
Live coral cover	1.5-31.6	%	In situ measurements/video
Macroalgae cover	6.2-71.2	%	In situ measurements/video
Gorgonian cover	0-17.2	%	In situ measurements/video
Fish biomass (lower trophic)	3.5-441.0	g m <sup>-2</sup>	In situ measurements
<i>Management regime</i>			
Protection level	None, MPA, NTZ	categorical	Reef Base
Reserve size	7.8-2170	km <sup>2</sup>	Reef Base
Reserve age	3-40	years	Reef Base
Poaching level	low, high	categorical	Reef Base, Interviews

a Suomi NPP satellite global at 750 m resolution available at NASA Earth Observatory (Black Marble)

b Gridded Population of the World V.3 at 0.25 degree resolution estimated for 2010

c Global Land Cover 2000 database

d Global Distribution of Coral Reef 2010 database from Ocean Data Viewer UNEP-WCMC

e Global Distribution of Mangroves USGS 2011 database from the Ocean Data Viewer UNEP-WCMC



## **Appendix 1.1 Detailed descriptions of covariates**

### ***Human population density***

We considered three measures of human effects based on population size: 1) humans within 50 km (maximum number of people that occurred within 50-km radius of each site); 2) number of humans in the nearest population center (indicator of spatially immediate human pressure); and 3) distance to nearest population centers (indicator of long-distance effects, calculated from each site to the center of nearest population settlements). We chose 50 km as radius for the first measured variable because it is a reasonable range of anthropogenic influence on Caribbean reefs (Mora, 2008). Projection estimates of human population counts for the year 2010 were obtained from the Gridded Population of the World V.3 at 0.25 degree resolution (SEDAC, 2010) and calculated in ArcGIS v10.0.

### ***Coastal Development***

This variable quantified the use of electrical power measured as the intensity of the Earth's city lights at night within 50 km radius of each site. Power infrastructure can be used as a proxy of coastal development which is a good surrogate for fishing pressure (Sanderson et al. 2002). Light intensity was calculated as the sum of pixel values that corresponded to city and town lights within the interest area. We used the high resolution (750 m) composite map of the world assembled from data acquired by the Suomi NPP satellite global available at NASA Earth Observatory (<http://earthobservatory.nasa.gov/Features/NightLights/page3.php>). All calculations were performed in ArcGIS v10.0.

### ***Cultivated land***

We quantified the area of cultivated land that occurred within a 50 km radius of each reef site. The raster data for this variable was obtained from the Global Land Cover 2000 database (GLC 2003). Specifically, we used the regional dataset (North and Central America) that depicts the spatial distribution of 29 different land attributes for the year 2000 as calculated from satellite images at 1 km resolution. Cultivated land could be a surrogate of terrestrial run-offs with potential effects on macroalgae cover when herbivory is reduced (McCook 1999). Additionally sediment derived from agriculture may alter predator-prey interactions in coral reef fish and compromise planktivores feeding efficiency (Wenger et al. 2013). Spatial analyses were performed in ArcGIS v10.

### ***Marine Reserve size, age, and poaching level***

In this study we only considered marine reserves where fishing was not allowed, at least in theory (i.e. no-take areas). We assessed three variables that together describe some degree of protection effectiveness for reef sites inside marine reserves (Mora et al. 2006). These variables were reserve size, years since the establishment (reserve age) and poaching level. Reserve size and age can positively influence fish communities, as in general, older and larger reserves tend to accumulate relative more fish biomass than younger and smaller reserves (Côté et al. 2001, Halpern 2003, Claudet et al. 2008, Babcock et al. 2010). In contrast, poaching can directly affect fish abundance and undermine the protection efforts particularly when reserves are small (Kritzer 2004). Poaching levels inside the reserve was classified as “low” or “high” based on interviews with park managers and regular users such as dive shops (method modified from Mora et al.

2006). We assumed that poaching inevitable exist in each reserve, thus a range of low to high was established based on a 5 point scale for which 1-2 was low while 3-5 was high.

### ***Reef Area***

Reef areas within 5 km and 10 km radius of each site was calculated from the Global Distribution of Coral Reefs (2010) database as available at the Ocean Data Viewer United Nations Environment Program's World Conservation Monitoring Centre (UNEP-WCMC) (<http://data.unep-wcmc.org/datasets/13>). This database represents the global distribution of warm water coral reefs compiled mostly from the Millennium Coral Reef Mapping Project validated and un-validated maps as well as other sources acquired by UNEP-WCMC. Reef areas within the interest region were calculated in ArcGIS v10.0.

### ***Reef structural complexity***

For each transect set we visually estimated structural reef complexity on a scale of 0-5, where 0 was given to reefs with no vertical relief; 1, low and sparse relief; 2, low but widespread relief; 3, moderately complex relief; 4, very complex relief with numerous caves and fissures; and 5, reefs with exceptionally complex habitats, with numerous caves and overhangs (Polunin and Roberts 1993). This topographic measure provided an assessment of reef complexity at the seascape level which is relevant to large and medium-sized fish (Polunin and Roberts 1993, Wilson et al. 2007). To minimize estimation subjectivity among observers, at least two divers estimated reef structural complexity for each transect set and the average was calculated to be used in the models. We evaluated the accuracy of the estimations among observers by comparing

the standard deviations (SD) among transects per site and found that SDs were 0-0.7 in all cases, meaning that average estimation differences were never over 1 unit.

### ***Mangrove Perimeter***

Mangrove abundance was quantified as the perimeter covered by mangrove within 5 km and 10 km radius of each site. Estimates of Caribbean mangrove distribution were obtained from the Global Distribution of Mangroves USGS (2011) database as available at the Ocean Data Viewer UNEP-WCMC (<http://data.unep-wcmc.org/datasets/21>). This database depicts the distributions of global mangroves based on Global Land Survey data and Landsat images. Landsat images (30 m resolution) were interpreted using unsupervised and supervised digital image classification techniques. Each image was atmospherically corrected, ground truth and validated with existing maps and databases.

### ***Net primary productivity***

We calculated mean oceanic net primary productivity ( $\text{mg C m}^{-2} \text{ day}^{-1}$ ) for each site between 2002 and 2012 using remote-sensing. This was obtained from Aqua MODIS satellite monthly data combined in the vertical generalized production model (Behrenfeld and Falkowski 1997) at a spatial resolution of  $0.0833^\circ$  (Oregon State University 2013). We used the mean of the last ten years period because primary productivity is inherently variable in time and established predatory communities may respond better to long term trends in primary productivity than to survey year or monthly mean values. Calculations were performed in ArcGIS 10.0.

### ***Sea surface temperature***

We used AHVRR Pathfinder Version 5.2 (PFV5.2) satellite data obtained from the US National Oceanographic Data Center and GHRSSST (NOAA 2013). The PFV5.2 data are an updated version of the Pathfinder Version 5.0 and 5.1 collections described in Casey et al. (2010). We calculated average monthly sea surface temperature (SST, 2002-2011) for each source 4 km<sup>2</sup> grid cell that corresponded to each reef site. We also calculated mean minimum monthly SST by selecting the lowest monthly average temperature per year to compute an average across years. Mean minimum monthly SST could be a better predictor of physiological constraints of some fish predator species (Jennings et al. 2008, Nadon et al. 2012). We used mean temperature of nine years because it may represent better the temperature regimen these top consumers experience overtime. All calculations were performed in ArcGIS 10.0.

### ***Wave exposure***

The log of wind driven wave exposure ( $J m^{-3}$ ) was extracted in ArchGIS 10.0 from the wave stress map for the Caribbean basin built by Chollett *et al.* (2012) and available at (<http://www.marinespatialecologylab.org/wp-content/uploads/2010/11/PECS1.png>). This index does not include the influence of tides or swells, which are not generated by local wind, and it is an approximation of wave patterns in shallow areas (Chollett et al. 2012). Wave exposure has been a good predictor of spatial variation in reef building corals such as *Orbicella* sp. (former *Montastrea* sp.) (Chollett and Mumby 2012) and can partially explain beta diversity patterns of benthic communities (Harborne et al. 2011). Wave exposure may also directly affect the biomass and diversity of tropical reef fish (Friedlander et al. 2003) and the distribution and abundance of temperate reef fish by compromising swimming abilities (Fulton and Bellwood 2004).

Alternatively, by modifying the distribution of foundation species like corals, wave exposure could affect fish species that depend on them. The detailed description of the wave exposure calculations and assumptions can be found in Chollett & Mumby (2012).

### ***Benthic cover***

Percent cover data of benthic communities by categories (i.e. coral by species, algae by genus or functional groups, gorgonians, sponges, and other) were measured at each site using point intercepts in 6-8 transect lines (10 m long) (Lang et al. 2010) and/or in 6-8 video transects (50 m long) (Carleton and Done 1995). Point intercept transects (PITs) were used at the Belize sites, while both PITs and video transects were used at the rest of the sites. Both methods provided similar accuracy and results in estimating benthic cover categories in our study. Each benthic transect corresponded to a fish transect set. To estimate percent cover, 100 points per transect was used in PITs (Lang et al. 2010), while ~600 points were extracted from each video transect (Carleton and Done 1995). As model predictors we only used live coral, fleshy algae, and gorgonian cover as they provide physical structure that may affect small and medium size fish predators (Alvarez-Filip et al. 2011).

### **References**

See references in Appendix 1.5

**Table S1.4 Spearman's rank ( $r_s$ ) order correlation matrix for response and explanatory variables.** Bold values are correlations  $r_s > 0.50$ . Upper matrix panel are correlations within marine reserves. Lower matrix corresponds to values for all sites. Number codes are: apex predator (1), piscivore-invertivore (2), herbivore (3), omnivore (4), invertivore (5), planktivore (6), mangrove within 5 km (7), mangrove within 10 km (8), coral cover (9), algae cover (10), gorgonian cover (11), net primary productivity (12), sea surface temperature (13), minimum sea surface temperature (14), wave exposure (15), depth (16), reef structural complexity (17), distance to deep water (18), distance to channels (19), distance to mangrove (20), reef area within 5 km (21), reef area within 10 km (22), coastal development within 50 km (23), number of humans within 50 km (24), number of humans in the closest town (25), minimum distance to closest town (26), area of cultivate land within 50 km (27), reserve age (28), reserve size (29). Note that reserve age and size are only applicable to sites within reserves.

**Table S1.4**

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1		0.38	0.02	0.10	0.10	0.05	0.29	0.25	0.07	0.12	0.16	0.29	0.11	-0.12	-0.16	-0.04	0.26	-0.08	0.12	-0.33	-0.04	0.03	-0.40	-0.39	-0.36	0.39	-0.49	0.08	0.32
2	0.35		0.26	0.31	0.42	0.18	0.03	-0.03	-0.02	-0.06	0.07	0.10	-0.04	-0.06	-0.35	0.08	0.21	-0.27	0.28	-0.12	0.10	0.14	-0.24	-0.30	-0.28	0.32	-0.19	0.16	0.46
3	0.16	0.36		0.02	0.22	0.08	-0.16	-0.20	0.00	-0.46	0.07	-0.19	<b>-0.50</b>	-0.36	-0.09	-0.39	0.31	0.15	0.28	0.05	-0.40	-0.24	-0.06	-0.25	0.04	-0.12	-0.15	0.20	-0.23
4	0.07	0.24	0.18		0.29	0.33	0.06	0.00	0.06	-0.14	-0.17	-0.18	0.14	0.34	-0.41	0.35	-0.01	-0.54	0.29	-0.14	0.00	-0.10	0.22	0.17	0.11	-0.03	0.15	0.07	0.34
5	0.18	0.37	0.35	0.25		0.31	-0.16	-0.21	0.03	-0.24	0.04	-0.15	-0.14	0.18	-0.37	0.10	0.07	-0.30	0.33	0.00	0.14	0.12	-0.02	-0.08	-0.19	0.14	-0.03	-0.08	0.26
6	0.06	0.25	0.16	0.28	0.22		-0.01	-0.03	0.24	-0.07	-0.05	-0.21	0.07	0.23	-0.13	0.19	0.21	-0.30	0.15	-0.10	-0.04	-0.05	0.10	0.11	0.02	-0.08	0.11	0.01	-0.03
7	0.21	0.05	-0.03	-0.02	-0.05	-0.11		<b>0.97</b>	<b>0.52</b>	0.38	0.14	0.46	0.61	-0.27	-0.21	0.04	0.02	0.08	-0.30	-0.89	-0.32	-0.38	-0.44	-0.30	0.00	0.24	-0.32	-0.04	0.28
8	0.15	0.04	-0.01	-0.05	-0.10	-0.08	<b>0.93</b>		<b>0.53</b>	0.43	0.13	0.47	0.67	-0.28	-0.14	-0.01	-0.07	0.19	-0.47	<b>-0.79</b>	-0.35	-0.39	-0.42	-0.27	0.01	0.15	-0.27	-0.13	0.19
9	-0.09	-0.07	-0.15	0.03	-0.04	0.05	0.21	0.26		-0.02	-0.08	0.00	0.38	0.04	-0.24	0.06	0.28	-0.07	-0.25	<b>-0.58</b>	-0.18	-0.21	-0.31	-0.01	-0.12	0.08	-0.22	-0.30	-0.01
10	-0.13	-0.20	-0.29	-0.03	-0.16	-0.19	0.19	0.06	-0.10		-0.06	<b>0.50</b>	<b>0.59</b>	0.12	0.21	0.22	-0.12	0.03	<b>-0.50</b>	-0.27	0.16	0.17	-0.17	-0.10	-0.09	0.16	0.05	0.07	0.17
11	0.14	0.05	0.07	-0.02	0.08	0.04	0.08	0.00	-0.20	0.02		0.48	-0.17	-0.44	0.00	-0.22	-0.26	0.38	0.18	-0.04	0.05	0.17	<b>-0.53</b>	<b>-0.67</b>	-0.40	0.47	-0.43	0.05	0.29
12	0.04	-0.04	-0.22	0.05	-0.02	-0.07	0.04	-0.02	0.17	0.31	0.14		0.43	-0.25	0.27	0.06	-0.25	0.24	-0.17	-0.28	0.24	0.41	<b>-0.64</b>	<b>-0.71</b>	-0.46	0.66	-0.38	0.42	<b>0.55</b>
13	-0.26	-0.32	-0.37	0.04	-0.23	-0.08	-0.10	0.00	0.31	0.17	-0.23	0.29		0.38	0.06	0.44	-0.17	-0.30	-0.45	-0.47	0.17	0.08	-0.13	0.10	-0.08	0.17	0.05	-0.02	0.38
14	-0.28	-0.27	-0.35	0.11	-0.10	0.00	-0.17	-0.13	0.27	0.14	-0.26	0.18	<b>0.61</b>		-0.01	<b>0.71</b>	0.08	-0.79	0.08	0.07	0.50	0.36	0.39	<b>0.59</b>	-0.07	-0.03	0.30	-0.08	0.20
15	0.00	-0.10	0.01	-0.20	-0.10	-0.23	0.00	-0.15	-0.29	0.24	0.25	-0.17	-0.28	-0.26		-0.20	-0.26	0.36	-0.13	0.40	0.08	0.21	0.03	0.08	0.00	-0.05	0.00	0.22	-0.38
16	-0.12	-0.17	-0.35	0.15	-0.05	0.04	0.00	-0.15	0.10	0.27	-0.06	0.14	0.32	0.48	0.00		0.05	-0.65	-0.03	-0.11	0.52	0.39	0.21	0.28	-0.02	0.15	0.38	0.11	0.45
17	0.28	0.37	0.25	-0.02	0.11	0.29	0.13	0.15	0.22	-0.33	0.00	-0.19	-0.21	-0.27	-0.20	-0.15		-0.34	0.12	-0.34	-0.05	0.03	-0.22	-0.05	-0.25	0.15	-0.31	0.09	-0.10
18	0.11	-0.02	0.14	-0.18	-0.08	-0.28	0.28	0.21	-0.10	0.15	0.27	-0.02	-0.33	<b>-0.50</b>	0.49	-0.18	-0.07		-0.41	0.19	-0.38	-0.25	-0.22	-0.35	0.13	-0.18	-0.10	-0.16	-0.48
19	0.06	0.06	0.14	0.00	0.04	-0.17	0.07	0.04	-0.18	-0.02	0.16	-0.29	0.03	0.06	0.14	-0.20	-0.11	0.14		0.12	0.07	0.08	0.06	-0.14	-0.14	0.26	-0.27	0.37	0.29
20	-0.08	0.12	0.06	-0.04	0.01	0.18	-0.41	-0.35	-0.17	-0.17	-0.06	-0.28	-0.26	-0.17	0.07	-0.08	0.10	-0.28	-0.10		0.22	0.29	0.48	0.25	0.16	-0.33	0.41	0.07	-0.33
21	-0.14	-0.22	-0.37	0.00	-0.01	-0.08	-0.09	-0.26	0.08	0.33	0.10	0.42	0.28	0.48	0.05	<b>0.56</b>	-0.19	-0.14	-0.04	-0.20		<b>0.91</b>	-0.14	0.03	-0.52	<b>0.57</b>	0.06	0.01	0.46
22	-0.08	-0.09	-0.23	-0.06	0.01	-0.03	-0.11	-0.24	0.09	0.23	0.12	0.26	0.05	0.31	0.13	0.32	0.00	-0.12	0.15	-0.04	<b>0.83</b>		-0.33	-0.23	-0.68	<b>0.66</b>	-0.08	0.18	0.45
23	-0.23	-0.16	0.10	0.08	-0.01	0.08	-0.29	-0.20	-0.21	-0.10	-0.14	-0.24	-0.04	-0.07	-0.09	0.13	-0.18	0.06	-0.15	0.05	-0.11	-0.25		<b>0.79</b>	<b>0.81</b>	<b>-0.81</b>	<b>0.76</b>	0.04	-0.42
24	-0.23	-0.17	-0.09	0.07	0.00	0.08	-0.30	-0.17	0.07	-0.11	-0.39	-0.10	0.26	0.19	-0.24	0.01	-0.06	-0.41	-0.46	0.11	-0.13	-0.27	0.47		<b>0.57</b>	<b>-0.65</b>	<b>0.61</b>	-0.32	-0.42
25	-0.28	-0.25	-0.01	-0.01	-0.15	0.01	-0.04	0.09	-0.01	-0.05	-0.27	-0.17	0.16	-0.06	-0.13	0.02	-0.14	-0.02	-0.37	-0.09	-0.24	-0.41	<b>0.76</b>	<b>0.72</b>		<b>-0.86</b>	<b>0.70</b>	0.10	-0.49
26	0.05	-0.05	-0.20	0.08	0.03	0.01	-0.08	-0.18	0.13	0.08	0.28	0.45	0.43	0.39	-0.15	0.33	-0.01	-0.17	0.21	-0.40	<b>0.68</b>	<b>0.51</b>	-0.28	-0.28	-0.39		<b>-0.65</b>	0.17	<b>0.72</b>
27	-0.34	-0.13	-0.06	0.05	-0.01	0.11	-0.30	-0.11	0.07	-0.05	-0.36	-0.01	0.16	0.19	-0.35	0.08	-0.16	-0.35	<b>-0.50</b>	0.22	-0.19	-0.29	<b>0.52</b>	<b>0.62</b>	<b>0.63</b>	-0.43		0.05	-0.24
28																													0.29



**Table S1.5 Covariate selection procedure for closely related variables for each predator group based on AICc** (AIC corrected for small samples). wAIC<sub>c</sub>, AIC<sub>c</sub> weights; Pr(>|z|)

significance level from the generalized linear models; CoastDev50km, coastal development within 50 km; PopDen50km, number of humans within 50 km; PopDenclstowns, number of humans in the closest population center; CultLand50km, area of cultivated land within 50 km; DistPop, minimum distance to nearest population center; SSTmin, average monthly minimum sea surface temperature; SST, average sea surface temperature; ReefArea5km(10km), reef area within 5 and 10 km; MangrvPer5km(10km), mangrove perimeter within 5 and 10 km.

All Sites Covariate	Predators			Apex predators			Pisc-Invertivores		
	AICc	wAICc	Pr(> z )	AICc	wAICc	Pr(> z )	AICc	wAICc	Pr(> z )
<b>CoastDev50km</b>	670.4	<b>1</b>	***	767.6	<b>1</b>	***	634.5	<b>0.97</b>	***
PopDen50km	684.3	0	***	791.1	0	***	641.4	0.03	***
PopDenclstowns	710.7	0	***	819.5	0	***	661.8	0	**
CulLand50km	711.1	0	***	798.9	0	***	666.0	0	*
DistPop	725.2	0	ns	842.1	0	ns	669.3	0	ns
<b>SSTmin</b>	686.8	<b>0.96</b>	***	812.2	<b>0.93</b>	***	641.0	<b>0.68</b>	***
SST	693.4	0.04	***	817.4	0.07	***	642.0	0.38	***
<b>ReefArea5km</b>	713.7	<b>0.96</b>	***	835.8	<b>0.62</b>	*	658.9	<b>0.98</b>	***
ReefArea10km	720.3	0.04	*	836.7	0.38	*	666.2	0.02	.
<b>MangrvPer5km</b>	719.6	<b>0.79</b>	*	817.3	<b>1</b>	***	668.4	<b>0.60</b>	ns
MangrvPer10km	722.3	0.21	.	829.1	0	***	669.3	0.40	ns

Reserves (NTZ) Covariate	Predators			Apex predators			Pisc-Invertivores		
	AICc	wAICc	Pr(> z )	AICc	wAICc	Pr(> z )	AICc	wAICc	Pr(> z )
CoastDev50km	218.7	<b>0.22</b>	***	276.6	<b>0.26</b>	***	206.3	0.16	***
PopDen50km	216.2	<b>0.75</b>	***	280.3	0.04	***	203.2	<b>0.74</b>	***
CulLand50km	223.4	0.02	***	274.6	<b>0.69</b>	***	212.0	0.01	***
DistPop	225.2	0.01	***	291.1	0	***	207.5	0.09	*
PopDenclstowns	230.3	0	**	294.7	0	***	212.5	0.01	*
<b>SSTmin</b>	239.7	0.51	ns	306.4	0.20	ns	218.1	0.53	ns
SST	239.8	0.49	ns	303.6	0.80	.	218.3	0.38	ns
<b>ReefArea5km</b>	239.2	0.39	ns	306.4	0.49	ns	218.0	0.30	ns
ReefArea10km	240.1	0.61	ns	306.3	0.51	ns	216.3	0.70	ns
<b>MangrvPer5km</b>	239.5	0.60	ns	297.5	<b>0.77</b>	**	218.5	0.34	ns
MangrvPer10km	240.3	0.40	ns	299.9	0.23	*	217.2	0.66	ns

Significance codes: 0 '\*\*\*', 0.001 '\*\*', 0.01 '\*', 0.05 '.', non-significant 'ns'

**Appendix 1.2 Analysis and R code to predict total predator biomass in the absence of humans** considering all sites as no fishing areas based on the best explanatory model from Table 1.1. Note that all numerical predictors were standardized and centered before model run. Some predictors were log transformed to improve model fit.

# Top model for total predatory fish biomass

```
modelPR.final <- glmer(log(Predators+1) ~ log(CoastDev50km) + I(SSTmin^2) +
  Rugosity + Coral + Gorgonian + log(Invertivore) + log(Omnivore) +
  log(Planktivore) + log(Herbivore) + Protection.level +
  (1|Year/Region/Site.Code), na.action=na.omit,
  Data = fishcoral, family= Gaussian ("log"), nAGQ=1L)
summary (modelPR.final)
```

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]

```
Family: gaussian ( log )
Formula: Predators.log ~ log(CoastDev50km) + I(SSTmin.s^2) + Rugosity.s +
  Coral.s + Gorgonian.s + scale(Invert.log) + scale(Herbivore.log) +
  scale(Omniv.log) + scale(Planktivore.log) + (1 | Year/Region/Site.Code) +
  Protection.Level
Data: fishcoral
```

AIC	BIC	logLik	deviance	df.resid
462.3	525.1	-215.2	430.3	358

Scaled residuals:

Min	1Q	Median	3Q	Max
-2.7773	-0.5935	-0.0186	0.5598	4.0192

Random effects:

Groups	Name	Variance	Std.Dev.
Site.Code:(Region:Year)	(Intercept)	4.769e-03	0.0690604
Region:Year	(Intercept)	8.772e-07	0.0009366
Year	(Intercept)	7.373e-04	0.0271531
Residual		1.757e-01	0.4191577

Number of obs: 374, groups: Site.Code:(Region:Year), 62; Region:Year, 14; Year, 3

Fixed effects:

	Estimate	Std. Error	t value	Pr(> z )	
(Intercept)	0.847396	0.040077	21.144	< 2e-16	***
CoastDev50km.s	-0.073770	0.019775	-3.730	0.000191	***
I(SSTmin.s^2)	0.019078	0.012005	1.589	0.112022	
Rugosity.s	0.047850	0.016361	2.925	0.003448	**
Coral.s	-0.026879	0.012604	-2.133	0.032963	*
Gorgonian.s	-0.024912	0.012930	-1.927	0.054013	.
scale(Invert.log)	0.039759	0.010812	3.677	0.000236	***
scale(Herbivore.log)	0.021963	0.011721	1.874	0.060962	.
scale(Omniv.log)	0.033216	0.010522	3.157	0.001595	**
scale(Planktivore.log)	0.011406	0.011098	1.028	0.304087	
Protection.LevelMPA	-0.163262	0.053497	-3.052	0.002275	**
Protection.LevelNTZ	0.004572	0.042879	0.107	0.915090	

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

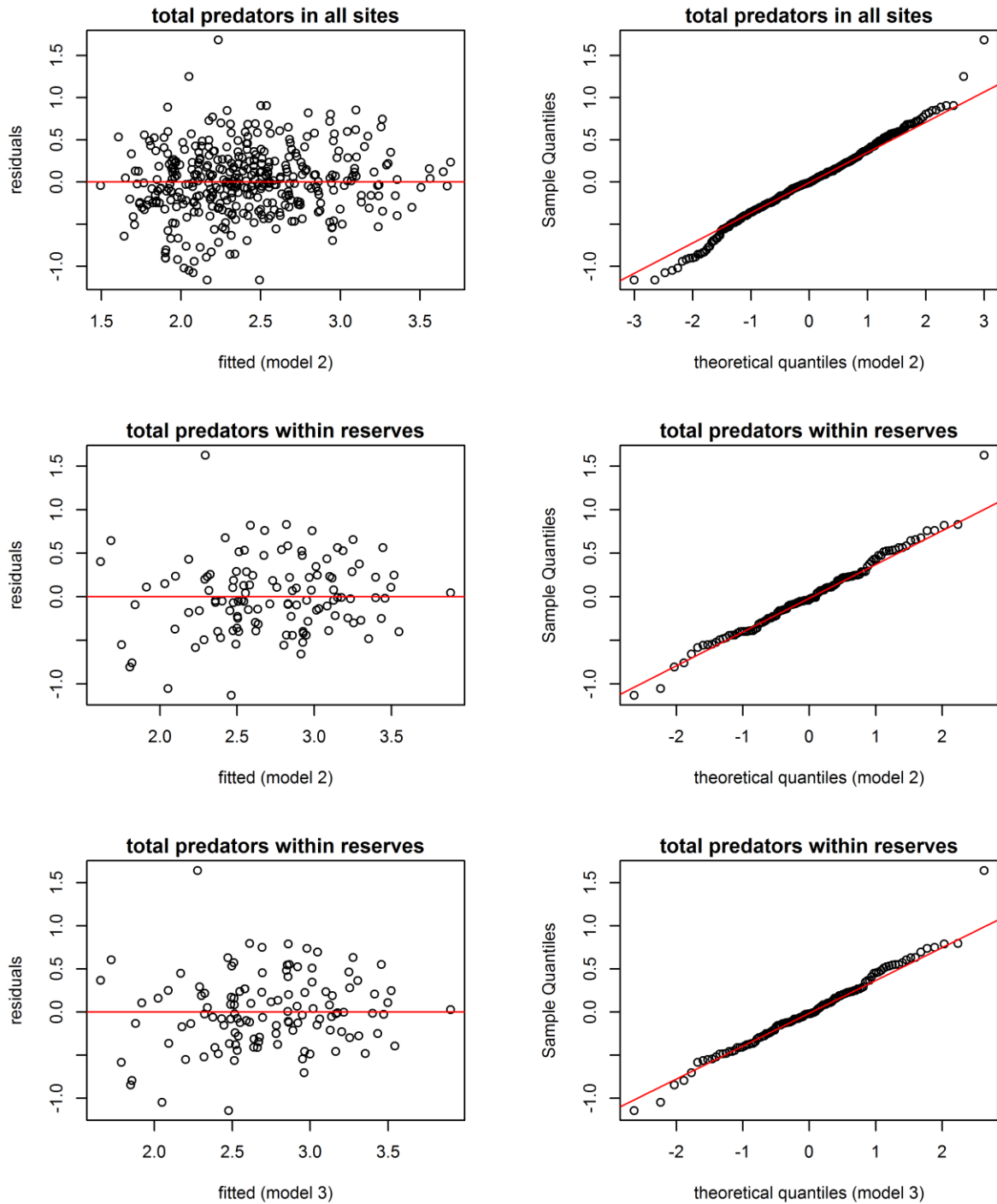
```
#Calculate prediction when coastal development is zero and all sites are NTZ
```

```
prediction <- predict(modelPR.final, newdata = data.frame(  
  LightInt50km.s = 0*fishcoral$LightInt50km.s,  
  SSTmin.s= fishcoral$SSTmin.s,  
  Rugosity.s = fishcoral$Rugosity.s,  
  Coral.s= fishcoral$Coral.s,  
  Gorgonian.s= fishcoral$Gorgonian.s,  
  Invert.log = fishcoral$Invert.log,  
  Herbivore.log = fishcoral$Herbivore.log,  
  Omniv.log= fishcoral$Omniv.log,  
  Planktivore.log = fishcoral$Planktivore.log,  
  Protection.Level = recode(fishcoral$Protection.Level, "'none'='NTZ';'MPA'='NTZ'"),  
  Site.Code = fishcoral$Site.Code,  
  Region= fishcoral$Region,  
  Year = fishcoral$Year),  
  type = "response", se.fit=TRUE, na.action = na.omit)
```

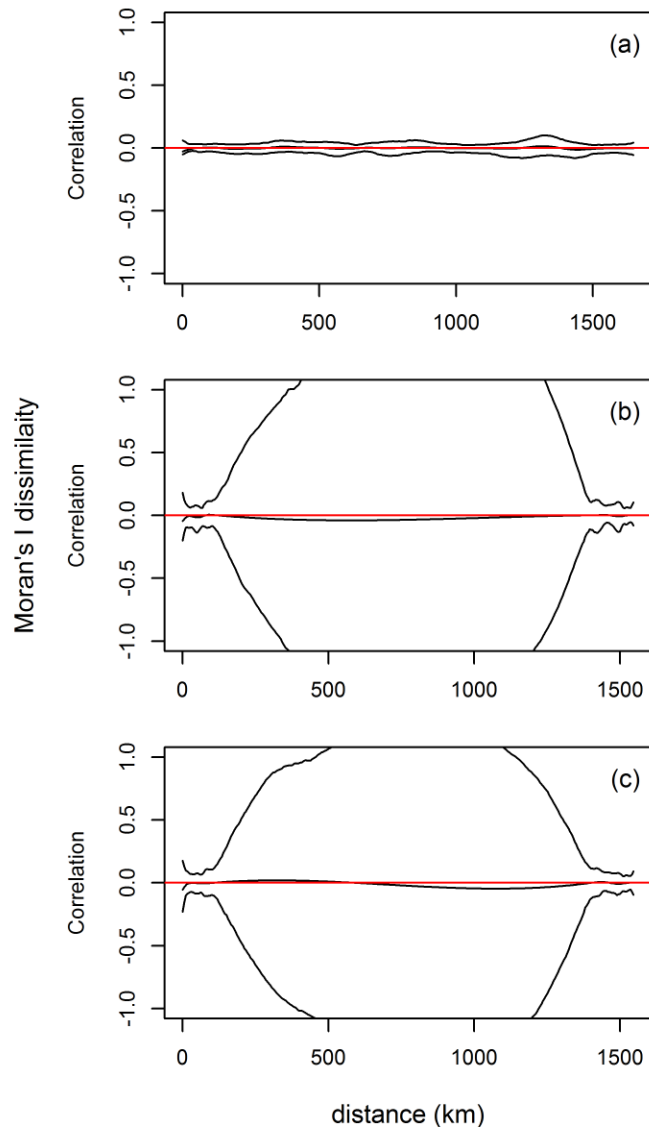
```
#Convert predicted values to biomass values since predator biomass was log10(x+1)  
transformed
```

```
fishcoral$Predicted.predators=(10^(prediction)-1)
```

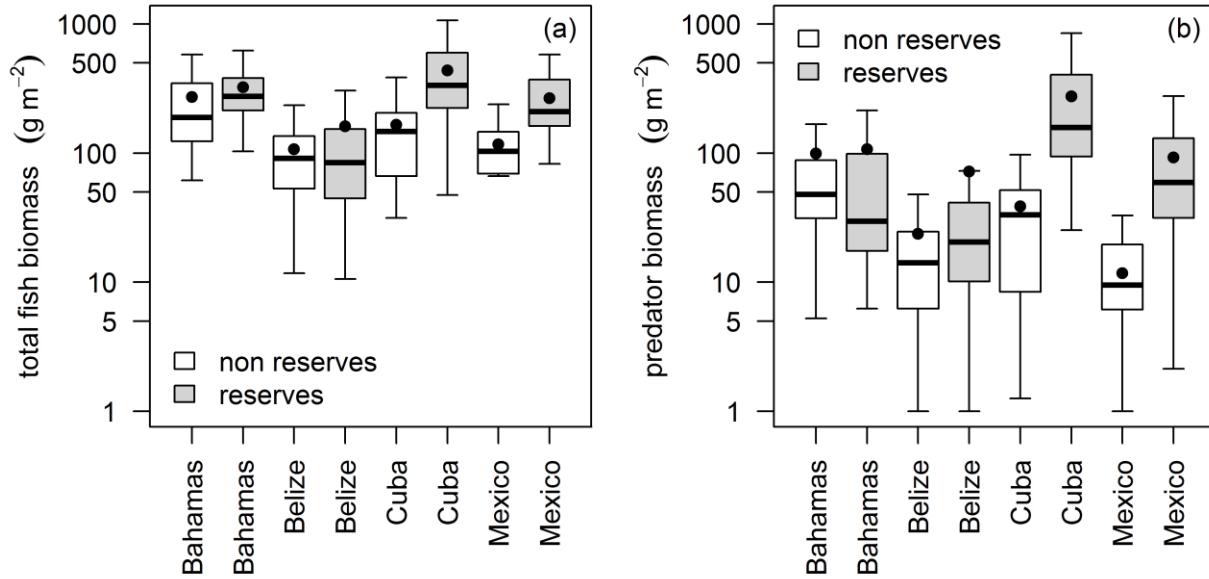
**Figure S1.1** Plots of residuals vs. fitted values (left panels) and normal scores of standardized residual deviance (right panels) for the final models (Set A and B) of total predator biomass. The plots for apex predators and piscivore-invertivores are not shown because the patterns are similar to total predators. See Table 1.1 for model details.



**Figure S1.2 Plots of the spline correlogram function against distance.** The spline correlogram is based on the residuals of the final models for total predators in all sites (a) and for two selected models within marine reserves (b and c). See Table 1.1 for models. The plots for apex predators and piscivore-invertivores show similar patterns and are not shown. A 95% pointwise confidence envelope is superimposed.

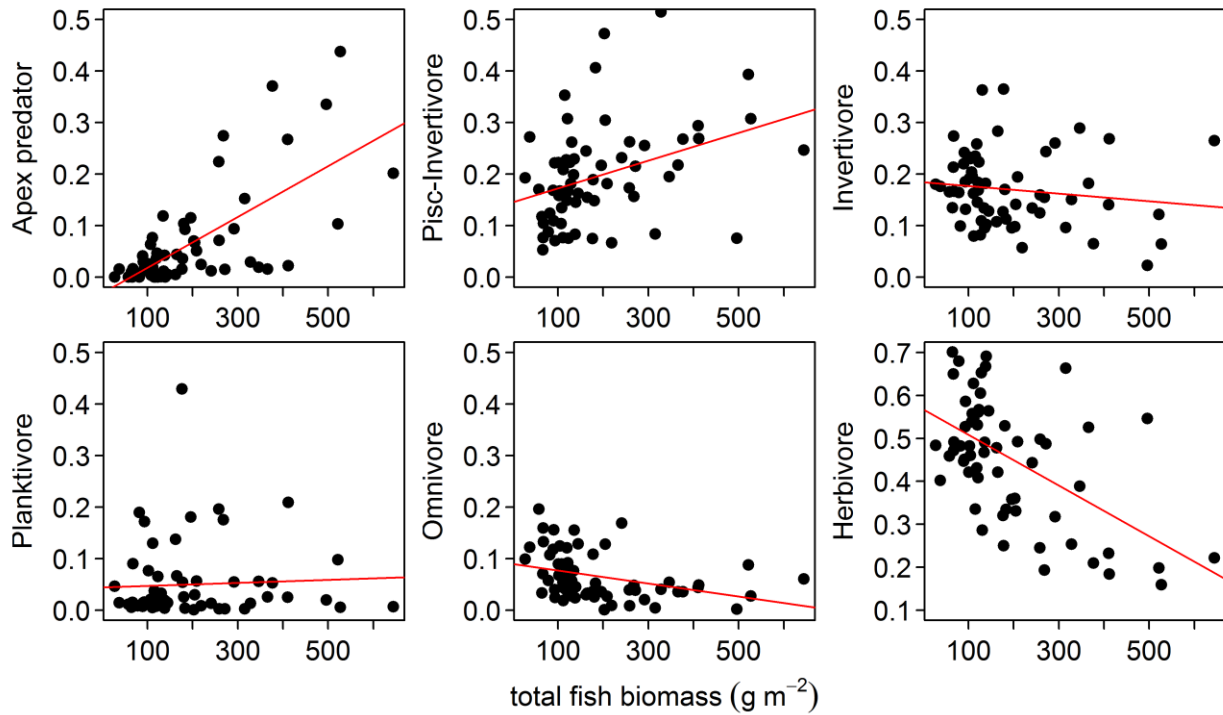


**Figure S1.3 Boxplot of total fish (a) and predator biomass (b) by country and protection level.** White boxes are non-reserve whereas grey boxes are reserves. Black points represent the pooled means by site and year of survey for each country. Dry Tortugas is excluded because does not have a non-reserve site.

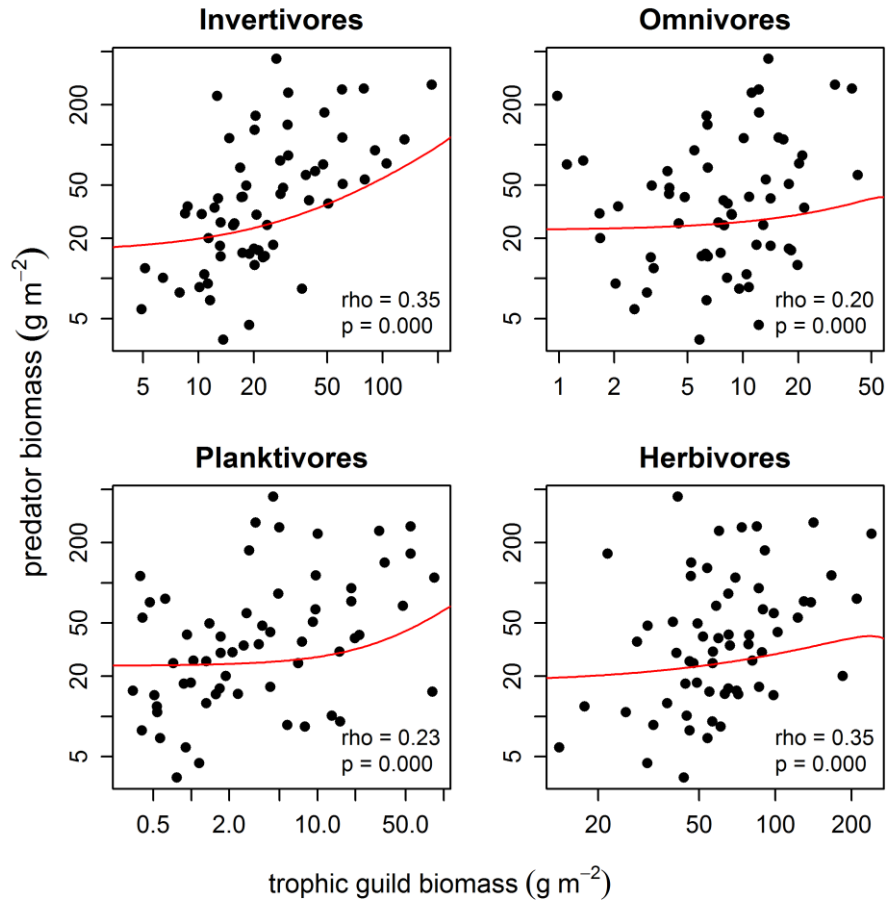


**Figure S1.4 Scatterplots of the mean proportion of trophic guilds per site and survey year.**

Red line is the best fit from a linear model. Note that higher total fish biomass is driven by higher proportion of apex predators and piscivore-invertivores, while lower total fish biomass is comprised mostly (> 0.55) of herbivores.



**Figure S1.5 Scatterplots of the mean biomass of predators (apex predator + piscivores-invertivore) and lower trophic guilds across sites. The Spearman's rank correlation coefficient (rho) and the significance probability (p) are shown. Red lines are loess smoothing curve with a span width of 3 in each panel to aid visual interpretation. Axes are in log scale.**





### Appendix 1.3 Detailed description of reef fish biomass variability

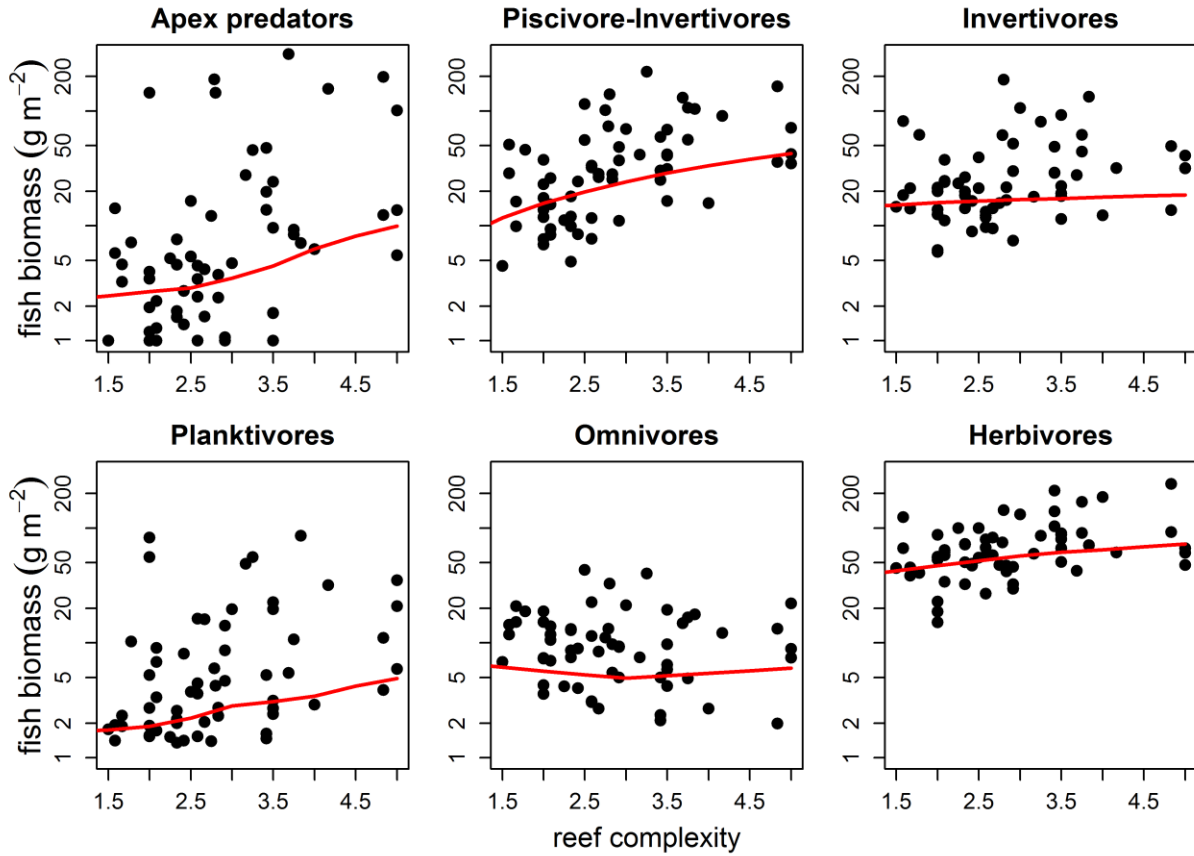
The combined average of total fish biomass in the marine reserves of Abaco, Cuba and Mexico ( $337 \pm 25 \text{ g m}^{-2}$ ) was 1.6 times higher than in the unprotected reefs of these sub-regions ( $215 \pm 20 \text{ g m}^{-2}$ ,  $p < 0.001$ ). Similarly, the combined predator biomass in reserves of Abaco, Cuba and Mexico ( $154 \pm 22 \text{ g m}^{-2}$ ) was 2.4 times greater than the combined value of their unprotected sites ( $65 \pm 10 \text{ g m}^{-2}$ ,  $p < 0.001$ ). We found no significant difference in the combined total fish or predator biomass inside and outside marine reserves of Abaco ( $p = 0.44$ ,  $p = 0.68$ , respectively), or in Belize ( $p = 0.78$ ,  $p = 0.94$ , respectively). However, reef sites inside the marine reserves of Hol Chan (HC) and Half Moon Caye (HM) had the highest fish and predator biomass within Belize (Fig. 1.2). Yet the highest total fish biomass found in Belize at HM ( $212 \pm 14 \text{ g m}^{-2}$ ) was comparable with the combined average of the unprotected sites in the rest of the sub-regions ( $\sim 215 \pm 20 \text{ g m}^{-2}$ ). The combined total fish biomass for Belize ( $118 \pm 8 \text{ g m}^{-2}$ ) was 1.8 times lower than in the unprotected sites of Abaco, Cuba and Mexico ( $p < 0.01$ , Fig. 1.2, Fig. S1.3). Finally, most sites in the marine reserves of Abaco, Cuba and Mexico had average total fish biomass  $> 200 \text{ g m}^{-2}$  and predator biomass  $> 100 \text{ g m}^{-2}$  (Fig. 1.2, Fig. S1.3).

The proportion trend of trophic groups within the fish assemblages varied across reef sites (Fig. 1.2, Fig. S1.4). The proportion of apex predators and piscivore-invertivores increased with increased total fish biomass from 0% to  $\sim 22\%$  ( $r_s = 0.67$ ,  $p < 0.001$ ) and from  $\sim 15\%$  to  $\sim 35\%$  ( $r_s = 0.58$ ,  $p < 0.001$ ), respectively (Fig. S1.4). In combination, the proportion of predators increased from  $\sim 13\%$  to  $\sim 55\%$  ( $r_s = 0.76$ ,  $p < 0.001$ ) with increased total fish biomass. Invertivores, planktivores and omnivores did not follow a clear pattern with increased total fish biomass and each group represented less than 20% of the total biomass at most sites. In contrast,

the proportional trend of herbivores decreased from ~55% to ~20% ( $r_s = -0.58$ ,  $p < 0.001$ ) with increased total fish biomass (Fig. S1.4).

The biomass of invertivores, omnivores, planktivores, and herbivores were slightly but significantly and positively correlated with total predator biomass (Fig. S1.5). This relationship was relatively stronger and less variable for invertivores and herbivores ( $r_s = 0.35$ ,  $p = 0.000$ ), but weaker and more variable for planktivores and herbivores ( $r_s = 0.20-0.23$ ,  $p \sim 0.000$ ) (Fig. S1.5).

**Figure S1.6 Relationship between reef structural complexity and fish trophic guilds.** Red lines are loess smoothing curve with a span width of 3 in each panel to aid visual interpretation. Y axis is in log scale. Reef complexity is described in Appendix 1.1.



## **Appendix 1.4 Detailed discussion of the relationships between predatory fish biomass and cofactors and their potential underlying mechanisms**

Ocean productivity had a small positive effect on apex predator biomass. Large predators have been related with quantity and quality of primary production in terrestrial ecosystems (e.g., Serengeti in Africa, Hopcraft et al. 2010). In marine ecosystems, the positive indirect effect of ocean productivity on teleost biomass has been tested theoretically (Jennings et al. 2008) and empirically (Chassot et al. 2010) at global scales, and is probably driven by bottom-up increases of prey populations (Frank et al. 2007). The observed weak connection of apex predators with ocean productivity may not be through increasing reef fish prey, as they did not respond to primary productivity (Fig. 3.3). Instead, mobile apex predators, such as reef sharks and jacks, may also be feeding upon prey directly linked with ocean productivity via plankton in adjacent oceanic waters (McCauley et al. 2012).

Reef complexity was one of the most important predictors of fish predator biomass. This variable has a strong positive influence on the relative abundance, species richness, and local distribution of small and medium-sized fishes (e.g., 10-30 cm TL) (Wilson et al. 2007, Graham and Nash 2013). As reef complexity increases, refuges become more available to avoid predation and competition (Hixon and Beets 1993). In contrast, less clear is the relationship between landscape reef complexity and the density of large-bodied reef fish (Richards et al. 2012) or reef sharks (Nadon et al. 2012). Large transient predators that actively chase their prey may avoid highly complex environments that reduce hunting efficiency (Hixon and Beets 1993). Conversely, sites with higher structural complexity may attract relative large resident and transient predators that take advantage of greater prey availability (McCauley et al. 2012). Reef tridimensional structure complexity is nonetheless crucial to enhance predatory fish biomass and

may be further compromised by the Caribbean-wide reduction of architectural complexity (Alvarez-Filip et al. 2009).

Several physical and biotic cofactors, such as “ocean temperature”, “coral cover”, “gorgonian abundance”, and herbivore and planktivore biomass did not have a significant effect on predator biomass; however, they improved model fit and may be important to support predator biomass within regions. Ocean temperature, for example, showed a weak “unimodal” response on the biomass of piscivore-invertivores. Non-linear relationship between the diversity of pelagic fish predators and temperature has been observed at a global scale (Worm et al. 2005). However, a clear response to temperature by an entire trophic level may be difficult to detect as the response to temperature gradients is species-specific through physiological constraints that affect individual biomass (Jennings et al. 2008, Munday et al. 2008).

Mangrove was a predictor of apex predator biomass, but unexpectedly not of piscivore-invertivores. Reefs associated with mangrove habitats have been reported to support more species, and higher density and biomass of reef fishes, including greater prey biomass for piscivore predators (Nagelkerken et al. 2002, Mumby et al. 2004). Mangroves also provide protection and high-quality nursery grounds for juveniles of top predator teleosts (e.g., *Sphyraena barracuda*, Nagelkerken et al. 2002) and sharks (e.g., *Negaprion brevirostris*, Chapman et al. 2009) that later may migrate as adults to adjacent reef habitats (Mumby et al. 2004). Piscivore-invertivores in our study included several species with strong mangrove association (e.g., most *Lutjanus* spp., see Mumby et al. 2004), but other species with a weak connection with mangroves (e.g., *Lutjanus mahogoni*, see Nagelkerken et al. 2002) may dilute the average response of the trophic guild. Further research will be needed to identify those

species with tight connections with mangrove across our sites, but such endeavor was not objective in this paper.

Lower trophic levels were good predictors of total predator biomass, especially for piscivore-invertivores (Table 1.1, Fig. 1.3). We found no evidence of top-down regulation at a regional scale. In fact, the higher the biomass of lower trophic levels, the greater the biomass of predators tended to be. Predator dependence on prey, for example, is common within large reserves of terrestrial savannas and woodland ecosystems (Jhala et al. 2008, Sinclair et al. 2010). Positive associations among reef fish trophic guilds also increase as fishing pressure decreases with protection (Newman et al. 2006, Babcock et al. 2010). Since reef predators are often generalists with opportunistic feeding habits, preying upon several trophic levels including their own, predation pressure may be distributed across levels (Russ and Alcala 2003). Alternatively, subsistence fishing in the Caribbean has simultaneously targeted and depleted all trophic levels potentially overriding predator-prey interactions at regional scale (Hawkins and Roberts 2004, Paddack et al. 2009).

**Table S1.6 Estimates of current and potential average biomass ( $\pm$  standard error, se) of predatory reef fishes in the absence of humans (i.e. coastal development) while categorizing every site as a no-take zone (i.e. no fishing). The potential percent lost is shown. Sites with exceptionally high predicted predator biomass are highlighted. Site order follows Fig. 5. For site codes refer to Table S1.1.**

Sites	Protection level	Current biomass		Predicted biomass		% lost
		mean	se	mean	se	
EB	None	3.5	1.3	81.8	8.7	95.8
NI	MPA	9.5	3.0	205.2	26.8	95.4
XA	None	9.1	4.7	147.0	16.4	93.8
SM	MPA	23.2	16.0	185.7	21.6	87.5
SW	MPA	8.5	2.0	194.0	14.1	95.6
CA	None	16.4	7.9	145.0	20.0	88.7
MR	None	10.7	4.1	119.7	10.1	91.1
BC	NTZ	10.1	3.0	124.7	5.7	91.9
MC	MPA	15.0	5.2	177.3	17.4	91.5
GH	None	14.4	2.9	229.2	33.3	93.7
RA	None	27.8	8.1	196.9	22.9	85.9
AL	None	15.9	2.9	199.1	21.8	92.0
ST	None	16.6	2.8	201.1	17.9	91.7
GA	None	32.8	11.4	287.7	37.1	88.6
HC	NTZ	85.4	67.7	222.5	53.8	61.6
PC	NTZ	88.2	38.4	502.0	76.9	82.4
TO	None	19.8	3.6	199.6	20.8	90.1
CP	None	28.3	7.3	214.9	20.9	86.8
PO	None	41.9	12.7	238.0	30.3	82.4
BCS	MPA	50.9	28.4	299.2	25.0	83.0
PZ	None	35.3	10.8	290.9	41.0	87.9
TB	None	71.9	39.5	295.1	86.6	75.6
MW	None	34.2	8.7	310.3	28.2	89.0
FC	NTZ	125.9	57.2	736.0	182.3	82.9
HM	NTZ	89.7	41.8	408.2	63.0	78.0
PB	NTZ	59.2	18.3	667.3	131.8	91.1
BR	None	67.2	28.4	480.4	38.1	86.0
LH	None	63.2	10.5	520.8	51.2	87.9
GC	None	47.7	7.7	471.3	58.9	89.9
<b>CR</b>	<b>NTZ</b>	<b>83.0</b>	<b>35.8</b>	<b>890.9</b>	<b>116.8</b>	<b>90.7</b>
<b>BA</b>	<b>None</b>	<b>72.3</b>	<b>21.7</b>	<b>826.7</b>	<b>150.1</b>	<b>91.3</b>
LG	NTZ	129.0	52.2	273.6	35.3	52.8
AN	NTZ	90.8	16.2	273.1	49.6	66.7
<b>BCN</b>	<b>MPA</b>	<b>109.3</b>	<b>16.3</b>	<b>1067.4</b>	<b>169.3</b>	<b>89.8</b>
<b>RP</b>	<b>None</b>	<b>268.6</b>	<b>73.4</b>	<b>1157.8</b>	<b>200.8</b>	<b>76.8</b>
EP	NTZ	263.6	77.5	505.8	103.2	47.9
<b>BCC</b>	<b>MPA</b>	<b>174.1</b>	<b>35.4</b>	<b>1562.0</b>	<b>308.5</b>	<b>88.9</b>
PP	NTZ	244.5	58.3	402.2	60.7	39.2
CF	NTZ	441.0	139.4	474.3	92.1	7.0

## Appendix 1.5 References

- Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Côté, and A. R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences* 276:3019–3025.
- Alvarez-Filip, L., J. A. Gill, and N. K. Dulvy. 2011. Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. *Ecosphere* 2:art118.
- Babcock, R. C., N. T. Shears, A. C. Alcala, N. S. Barrett, G. J. Edgar, K. D. Lafferty, T. R. McClanahan, and G. R. Russ. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences* 107:18256–18261.
- Behrenfeld, M. J., and P. G. Falkowski. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and oceanography*:1–20.
- Carleton, J. H., and T. J. Done. 1995. Quantitative video sampling of coral reef benthos: large-scale application. *Coral Reefs* 14:35–46.
- Casey, K. S., T. B. Brandon, P. Cornillon, and R. Evans. 2010. The past, present, and future of the AVHRR pathfinder SST program. Pages 273–287 *in* V. Barale, J. F. R. Gower, and L. Alberotanza, editors. *Oceanography from Space*. Springer Netherlands, Dordrecht.
- Chapman, D., E. A. Babcock, S. H. Gruber, J. Dibattista, B. Franks, S. Kessel, T. Guttridge, E. K. Pikitch, and K. A. Feldheim. 2009. Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. *Molecular Ecology* 18:3500–3507.
- Chassot, E., S. Bonhommeau, N. K. Dulvy, F. Mélin, R. Watson, D. Gascuel, and O. Le Pape. 2010. Global marine primary production constrains fisheries catches. *Ecology Letters* 13:495–505.
- Chollett, I., and P. J. Mumby. 2012. Predicting the distribution of *Montastraea* reefs using wave exposure. *Coral Reefs* 31:493–503.
- Chollett, I., P. J. Mumby, F. E. Müller-Karger, and C. Hu. 2012. Physical environments of the Caribbean Sea. *Limnology and Oceanography* 57:1233–1244.
- Claudet, J., C. W. Osenberg, L. Benedetti-Cecchi, P. Domenici, J.-A. García-Charton, Á. Pérez-Ruzafa, F. Badalamenti, J. Bayle-Sempere, A. Brito, F. Bulleri, J.-M. Culioli, M. Dimech, J. M. Falcón, I. Guala, M. Milazzo, J. Sánchez-Meca, P. J. Somerfield, B. Stobart, F. Vandeperre, C. Valle, and S. Planes. 2008. Marine reserves: size and age do matter. *Ecology Letters* 11:481–489.



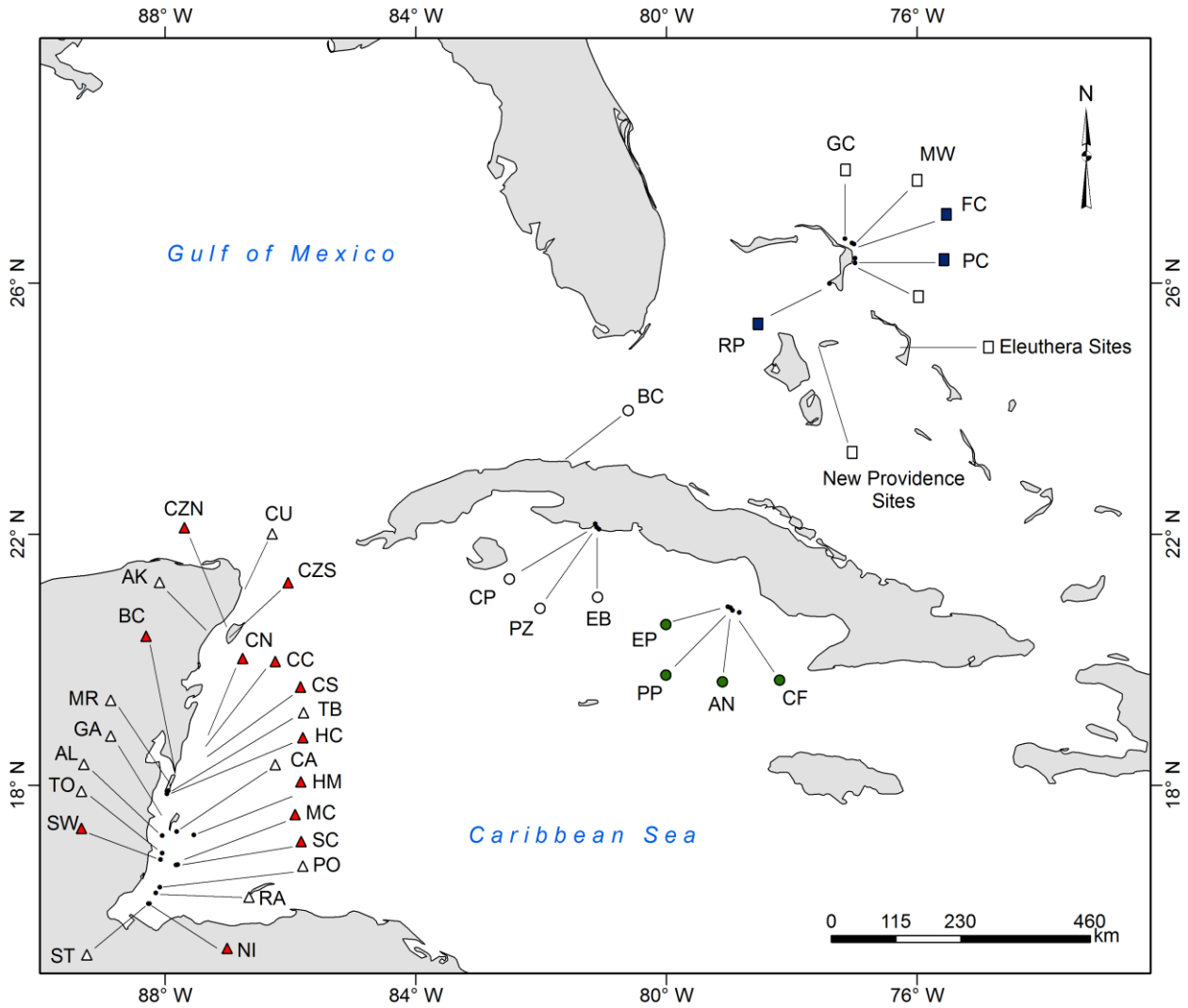
- Côté, I. M., I. Mosqueira, and J. D. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish Biology* 59:178–189.
- Frank, K. T., B. Petrie, and N. L. Shackell. 2007. The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology & Evolution* 22:236–242.
- Friedlander, A. M., E. K. Brown, P. L. Jokiel, W. R. Smith, and K. S. Rodgers. 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305.
- Fulton, C. J., and D. R. Bellwood. 2004. Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. *Marine Biology* 144:429–437.
- GLC. 2003. Global Land Cover 2000 Project.  
<http://bioval.jrc.ec.europa.eu/products/glc2000/products.php>.
- Global Distribution of Mangrove USGS. 2011. Global distribution of mangrove USGS.  
<http://data.unep-wcmc.org/datasets/21>.
- Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32:315–326.
- Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13:117–137.
- Harborne, A. R., P. J. Mumby, K. Żychaluk, J. D. Hedley, and P. G. Blackwell. 2011. Modeling the beta diversity of coral reefs. *Ecology* 87:2871–2881.
- Hawkins, J. P., and C. M. Roberts. 2004. Effects of artisanal fishing on Caribbean coral reefs. *Conservation Biology* 18:215–226.
- Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77–101.
- Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution* 25:119–128.
- Jennings, S., F. Mélin, J. L. Blanchard, R. M. Forster, N. K. Dulvy, and R. W. Wilson. 2008. Global-scale predictions of community and ecosystem properties from simple ecological theory. *Proceedings of the Royal Society B: Biological Sciences* 275:1375–1383.
- Jhala, Y. V., R. Gopal, and Q. Qureshi. 2008. Status of tigers, co-predators and prey in India. National Tiger Conservation Authority, Govt., of India, New Delhi and Wildlife Institute of India, Dehradun. TR 2011/003.

- Kritzer, J. P. 2004. Effects of noncompliance on the success of alternative designs of marine protected-area networks for conservation and fisheries management. *Conservation Biology* 18:1021–1031.
- Lang, J. C., K. W. Marks, P. A. Kramer, P. Richards Kramer, and R. N. Ginsburg. 2010. AGRRA Protocols version 5.4 Atlantic and Gulf Rapid Reef Assessment Program. University of Miami, Florida.
- McCauley, D. J., H. S. Young, R. B. Dunbar, J. A. Estes, B. X. Semmens, and F. Micheli. 2012. Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications* 22:1711–1717.
- McCook, L. J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:357–367.
- Mora, C., S. Andr  fou  t, M. J. Costello, C. Kranenburg, A. Rollo, J. Veron, K. J. Gaston, and R. A. Myers. 2006. Coral reefs and the global network of marine protected areas. *Science* 312:1750–1751.
- Mumby, P. J., A. J. Edwards, J. E. Arias-Gonz  lez, K. C. Lindeman, P. G. Blackwell, A. Gall, M. I. Gorchynska, A. R. Harborne, C. L. Pescod, H. Renken, C. C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427:533–536.
- Munday, P. L., G. P. Jones, M. S. Pratchett, and A. J. Williams. 2008. Climate change and the future for coral reef fishes. *Fish and Fisheries* 9:261–285.
- Nadon, M. O., J. K. Baum, I. D. Williams, J. M. Mcpherson, B. J. Zgliczynski, B. L. Richards, R. E. Schroeder, and R. E. Brainard. 2012. Re-creating missing population baselines for Pacific reef sharks. *Conservation Biology* 26:493–503.
- Nagelkerken, I., C. M. Roberts, G. van der Velde, M. Dorenbosch, M. C. van Riel, E. C. de la Morinire, and P. H. Nienhuis. 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.
- Newman, M. J. H., G. A. Paredes, E. Sala, and J. B. C. Jackson. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters* 9:1216–1227.
- NOAA, (National Oceanic and Atmospheric Administration). 2013. The AVHRR Pathfinder Version 5.2 dataset. <http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/>.
- Oregon State University. 2013. Ocean Productivity: Online VGPM Data. <http://orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.vgpm.m.chl.m.sst4.php>.

- Paddack, M. J., J. D. Reynolds, C. Aguilar, R. S. Appeldoorn, J. Beets, E. W. Burkett, P. M. Chittaro, K. Clarke, R. Esteves, A. C. Fonseca, G. E. Forrester, A. M. Friedlander, J. García-Sais, G. González-Sansón, L. K. B. Jordan, D. B. McClellan, M. W. Miller, P. P. Molloy, P. J. Mumby, I. Nagelkerken, M. Nemeth, R. Navas-Camacho, J. Pitt, N. V. C. Polunin, M. C. Reyes-Nivia, D. R. Robertson, A. Rodríguez-Ramírez, E. Salas, S. R. Smith, R. E. Spieler, M. A. Steele, I. D. Williams, C. L. Wormald, A. R. Watkinson, and I. M. Côté. 2009. Recent region-wide declines in Caribbean reef fish abundance. *Current Biology* 19:590–595.
- Polunin, N. V. C., and C. M. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* 100:177–183.
- Richards, B. L., I. D. Williams, O. J. Vetter, and G. J. Williams. 2012. Environmental factors affecting large-bodied coral reef fish assemblages in the mariana archipelago. *PLoS ONE* 7:e31374.
- Russ, G. R., and A. C. Alcala. 2003. Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983-2000. *Ecological Applications* 13:1553–1565.
- Sanderson, E., W., M. Jaitteh, M. Levy A., K. Redford H., A. Wannebo V., and G. Woolmer. 2002. The human footprint and the last of the Wild. *BioScience* 52:891–904.
- Sinclair, A. R. E., K. Metzger, J. S. Brashares, A. Nkwabi, G. Sharam, J. M. Fryxell, J. Terborgh, and J. A. Estes. 2010. Trophic cascades in African savanna: Serengeti as a case study. *Trophic cascades: predators, prey and the changing dynamics of nature*, Island Press, Washington, DC, USA:255–274.
- UNEP-WCMC, WorldFish Centre, WRI, and TNC. 2010. Global distribution of warm-water coral reefs, compiled from multiple sources, including the Millennium Coral Reef Mapping Project. UNEP World Conservation Monitoring Centre. Cambridge (UK). <http://data.unep-wcmc.org/datasets/13>.
- Wenger, A. S., M. I. McCormick, I. M. McLeod, and G. P. Jones. 2013. Suspended sediment alters predator–prey interactions between two coral reef fishes. *Coral Reefs* 32:369–374.
- Wilson, S., N. Graham, and N. Polunin. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology* 151:1069–1076.
- Worm, B., M. Sandow, A. Oschlies, H. K. Lotze, and R. A. Myers. 2005. Global patterns of predator diversity in the open oceans. *Science* 309:1365–1369.

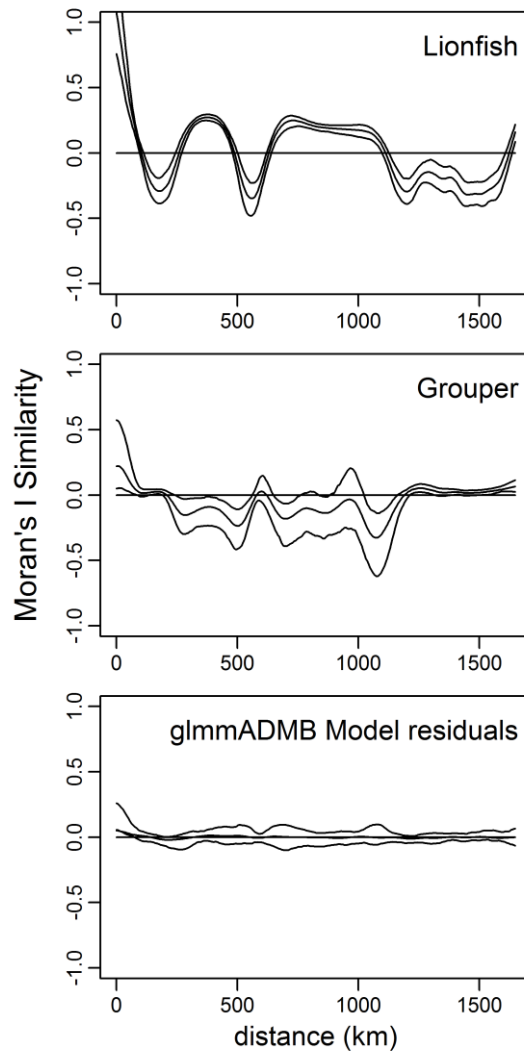
**APPENDIX 2: SUPPLEMENTARY MATERIAL FOR CHAPTER 2**

**Figure S2.1 Location of survey sites.** For site abbreviations, surveys dates and coordinates refer to Table S2.1



**Figure S2.2 Moran's I similarity spline correlograms for lionfish and grouper raw data across all sites (top two panels) and for the glmmADMB model residuals (bottom panel).**

Note the strong spatial autocorrelation of the raw data (i.e., swirling lines around zero) and how the hierarchical structure of the random effects (sites nested in regions) of the full glmmADMB model eliminated this correlation in the model residuals. A Mantel test of the model Pearson residuals ( $r = 0.073$ ) corroborates the lack of spatial correlation of the residuals. Lines are the mean  $\pm$  95% confidence interval.



**Table S2.1 Reef site detailed information.** Location names, coordinates, and site characteristics used in the study. S&G, spur-and-groove.

Country	Sub Region	Latitude	Longitude	Site Name	Site	Depth	Survey	Windward/	Protection	Habitat
Bahamas	Abaco	25.99661	-77.4009	Rocky Point Slope	RP	11.00	2011	Leeward	n	Slope
Bahamas	Abaco	26.04617	-77.4773	Sandy Point	SP	3.00	2011	Leeward	n	Patch
Bahamas	Abaco	26.3239	-76.9916	Little Harbor	LH	11.00	2011	Windward	n	S&G
Bahamas	Abaco	26.39783	-76.9885	Pelican Cay	PC	8.00	2011	Leeward	y	Slope
Bahamas	Abaco	26.62122	-77.0055	Man o War	MW	11.00	2011	Windward	n	S&G
Bahamas	Abaco	26.63717	-77.0385	Fowls Cay	FC	8.00	2011	Leeward	y	Slope
Bahamas	Abaco	26.70967	-77.1541	Guana Cay	GC	11.00	2011	Windward	n	S&G
Bahamas	Eleuthera	24.8174	-76.2442	108	108	2.44	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.81817	-76.2495	106	106	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.8194	-76.261	94	94	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.82102	-76.2573	112	112	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.82422	-76.2533	102	102	2.64	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.82643	-76.2483	101	101	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.82758	-76.2663	104	104	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.82792	-76.2438	100	100	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.83282	-76.2727	71	71	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.83398	-76.2429	84	84	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.8367	-76.2608	93	93	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.84107	-76.2445	80	80	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.84423	-76.2473	79	79	2.95	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.84454	-76.2604	55	55	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.84635	-76.2542	90	90	2.95	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.84838	-76.2422	89	89	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.84968	-76.2511	91	91	2.74	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.85208	-76.2583	76	76	3.05	2009	Leeward	n	Patch

Bahamas	Eleuthera	24.85253	-76.2551	75	75	3.05	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.85275	-76.2471	78	78	3.35	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.85302	-76.2492	77	77	3.25	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.85712	-76.2574	74	74	3.15	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.85883	-76.2543	73	73	2.74	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.86077	-76.2594	72	72	3.35	2009	Leeward	n	Patch
Bahamas	Eleuthera	24.95058	-76.2871	70	70	3.05	2009	Leeward	n	Patch
Bahamas	New Providence	24.91062	-77.5263	RSP Group	RS	15.40	2010	Leeward	n	S&G
Bahamas	New Providence	24.97067	-77.5342	Mike's Reef	MK	13.00	2010	Leeward	n	S&G
Bahamas	New Providence	24.97443	-77.5352	Pumpkin Patch	PK	11.50	2010	Leeward	n	S&G
Bahamas	New Providence	25.0013	-77.5416	Power Plant	PW	7.00	2010	Leeward	n	S&G
Bahamas	New Providence	25.0045	-77.5538	DC3 Wall	DW	13.75	2010	Leeward	n	S&G
Bahamas	New Providence	25.00617	-77.552	David Tucker	DT	14.50	2010	Leeward	n	S&G
Bahamas	New Providence	25.0085	-77.5572	Bond Wrecks	BW	11.50	2010	Leeward	n	S&G
Bahamas	New Providence	25.01535	-77.5698	Willaurie	WI	15.00	2010	Leeward	n	S&G
Belize	Meso American	16.1123	-88.2559	Nicholas	NI	13.00	2012	Windward	y	S&G
Belize	Meso American	16.11247	-88.2711	Southwest	ST	13.00	2012	Windward	n	S&G
Belize	Meso American	16.28501	-88.1503	Ranguana	RA	13.00	2012	Windward	n	S&G
Belize	Meso American	16.3731	-88.0891	Pampion	PO	13.00	2012	Windward	n	S&G
Belize	Meso American	16.72875	-87.8287	South Middle Cay	SM	13.00	2012	Windward	y	S&G
Belize	Meso American	16.73703	-87.8054	Middle Cay	MC	13.00	2012	Windward	y	S&G
Belize	Meso American	16.81346	-88.0776	South Water	SW	13.00	2012	Windward	y	S&G
Belize	Meso American	16.91911	-88.0476	Tobacco	TO	13.00	2012	Windward	n	S&G
Belize	Meso American	17.1966	-88.0512	Alligator	AL	13.00	2012	Windward	n	S&G
Belize	Meso American	17.2056	-87.5468	Half Moon	HM	13.00	2012	Leeward	y	S&G
Belize	Meso American	17.26147	-87.8197	Calabash	CA	13.00	2012	Windward	n	S&G
Belize	Meso American	17.49592	-88.0426	Gallows	GA	13.00	2012	Windward	n	S&G
Belize	Meso American	17.86343	-87.9724	Hol Chan	HC	13.00	2012	Windward	y	S&G
Belize	Meso American	17.91056	-87.9508	Tackle Box	TB	13.00	2012	Windward	n	S&G
Belize	Meso American	17.98782	-87.9038	Mexico Rocks	MR	13.00	2012	Windward	n	S&G
Belize	Meso American	18.16282	-87.8222	Bacalar Chico	BC	13.00	2012	Windward	n	S&G

Cuba	Bay of Pigs	22.07914	-81.076	Ebano	EB	11.00	2010	Windward	n	Slope
Cuba	Bay of Pigs	22.11003	-81.1163	Punta Perdiz	PZ	9.00	2010	Leeward	n	Slope
Cuba	Bay of Pigs	22.16627	-81.1383	Cueva Peces	CP	9.00	2010	Leeward	n	Slope
Cuba	Jardines de la Reina	20.76177	-78.8522	Five Sea	CF	11.00	2011	Leeward	y	Slope
Cuba	Jardines de la Reina	20.78697	-78.9432	Anclita	AN	11.00	2011	Leeward	y	Slope
Cuba	Jardines de la Reina	20.82586	-78.9803	Pipin	PP	16.00	2011	Leeward	y	S&G
Cuba	Jardines de la Reina	20.84411	-79.0217	El Peruano	EP	11.00	2011	Leeward	y	Slope
Cuba	North Coast	23.14654	-81.6666	Bacunayaua	BA	10.00	2012	Windward	n	Slope
Mexico	Akumal	20.42689	-87.286	Xaak	XA	15.00	2012	Windward	n	S&G
Mexico	Banco Chinchorro	18.41008	-87.4169	Banco Chinchorro South	BCS	15.00	2012	Leeward	y	S&G
Mexico	Banco Chinchorro	18.57457	-87.4198	Banco Chinchorro Central	BCC	15.00	2012	Leeward	y	S&G
Mexico	Banco Chinchorro	18.74867	-87.3476	Banco Chinchorro North	BCN	15.00	2012	Leeward	y	S&G
Mexico	Cancun	21.02544	-86.7713	Gardener of Hope	GH	12.00	2012	Windward	n	S&G
Mexico	Cozumel	20.31961	-87.0266	Columbia Reef	CR	15.00	2012	Leeward	y	S&G
Mexico	Cozumel	20.47188	-86.9815	Paraiso Bajo	PB	10.00	2012	Leeward	y	S&G



**Table S2.2 Summary of the glmmADMB results.** Lionfish abundance (ind. 100 m<sup>-2</sup>) on grouper biomass (g 100 m<sup>-2</sup>), predators, and other co-factors.

Coefficients	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	3.19012	1.18970	2.68	0.0073 **
Habitat (Spur & Groove)	-3.34259	1.44490	-2.31	0.0207 *
Habitat (Slope)	-2.75324	1.33400	-2.06	0.0390 *
Windward	-1.27082	0.63682	-2.00	0.0460 *
Protection (yes)	-1.32074	0.48898	-2.70	0.0069 **
Depth	0.25256	0.30394	0.83	0.4060
Time since invasion	0.32035	0.34958	0.92	0.3595
Reef complexity	-0.00503	0.07948	-0.06	0.9496
Humans/Reef	0.09210	0.08807	1.05	0.2957
Predator biomass	-0.08192	0.09066	-0.90	0.3662
log(Grouper biomass)	-0.00709	0.04494	-0.16	0.8747

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Number of observations: total=363, Region=11, Region: Site.Code=71

Random effect variance(s):

Group=Region

	Variance	StdDev
(Intercept)	1.179	1.086

Group=Region/Site.Code

	Variance	StdDev
(Intercept)	0.3861	0.6214

Negative binomial dispersion parameter: 1.568 (std. err.: 0.16423)

Zero-inflation: 0.0083623 (std. err.: 0.0096232 )

Log-likelihood: -618.889 AIC: 1267.8

## APPENDIX 3: SUPPLEMENTARY MATERIAL FOR CHAPTER 3

### Appendix 3.1 Description of anthropogenic and environmental covariates used in the models

#### *Human population density*

We estimated the number of humans within 50 km of each Caribbean site (maximum number of people that occurred within 50-km radius of each site). We chose 50 km as radius because is a reasonable range of anthropogenic influence on Caribbean reefs (Mora 2008). Projection estimates of human population counts for the year 2010 were obtained from the Gridded Population of the World V.3 at 0.25 degree resolution (SEDAC 2010) and calculated in ArcGIS v10.0. For the Pacific island we extracted the population density for every inhabited island from Williams et al. (2011).

#### *Cultivated land*

We quantified the area of cultivated land that occurred within a 50 km radius of each Caribbean reef site, and on those Pacific islands with measurable agricultural activities. Data for this variable was obtained from the Global Land Cover Share database (Latham et al. 2014) at ([http://www.glcn.org/databases/lc\\_glcshare\\_en.jsp](http://www.glcn.org/databases/lc_glcshare_en.jsp)). This global database provides a set of major thematic land cover layers combining the best available high resolution national, regional and subregional land cover databases and it is calculated from satellite images at 1 km resolution. Cultivated land could be a surrogate of terrestrial run-offs with potential effects on macroalgae cover when herbivory is reduced (McCook 1999). Spatial analyses were performed in ArcGIS v10.

### ***Thermal stress anomalies***

We created a 28-year dataset (1982-2010) of weekly thermal stress anomalies (TSA) for every of the 39 reefs/islands from the Caribbean and the tropical Pacific using the National Oceanic and Atmospheric Administration's (NOAA) National Oceanographic Data Center (NODC) Coral Reef Temperature Anomaly Database (CoRTAD) Version 4.0 (Casey et al. 2010, Selig et al. 2010)(available at <http://www.nodc.noaa.gov/SatelliteData/Cortad>). Temperature anomalies for this database were calculated from the Pathfinder Version 5.2 data temperature with a spatial resolution of ~4 km grid cell (Casey et al. 2010, Selig et al. 2010) and with a quality flag of four or better (Kilpatrick et al. 2001). TSAs were defined as deviations of 1 week where sea surface temperature (SST) was 1°C or greater than the mean maximum climatological week or the long term average warmest week from 1982 to 2010. This threshold is generally accepted for environmental conditions that may cause bleaching and coral mortality (Glynn 1993, Liu et al. 2003). We calculated the long term (28 years) average weekly TSA for each grid cell that corresponded to each Caribbean site. For the Pacific islands, long term average weekly TSA were calculated by spatially averaging the 4 km pixel that were intersected by or contained within 30 km bathymetric contour for each island (sensu Gove et al. 2013). Spatial analyses were performed in ArcGIS 10.

### ***Oceanic primary productivity***

We calculated the average oceanic primary production ( $\text{mg C m}^{-2} \text{ day}^{-1}$ ) for each Caribbean site between 2002 and 2012 from the Aqua Moderate Resolution Imaging Spectroradiometer satellite (MODIS) monthly data combined in the vertical generalized production model (Behrenfeld and Falkowski 1997) at a spatial resolution of 0.0833° (Oregon

State University 2013). We calculated the climatological mean of the last ten years period because primary production is inherently variable in time and we were interested on long term effects instead of specific variability. Calculations were performed in ArcGIS 10.0.

For the Pacific islands, Chlorophyll-*a* concentration ( $\text{mg m}^{-3}$ ) was used as proxy for ocean productivity. Eight-days,  $0.0417^\circ$ -resolution ( $\sim 4$  km) time series of Chlorophyll-*a* concentration was obtained from the Aqua MODIS satellite (<http://modis.gsfc.nasa.gov/>) for the July 2002 – May 2011 period. Land and shallow water areas ( $<30$  m) were removed to avoid unreliable data associated with bottom reflectance that is not related with Chlorophyll-*a* signal (Boss and Zaneveld 2003). The zone most proximate to the islands ( $\sim 3.3$ - $6.5$  km from the 30 m contour) was used to calculate chlorophyll-*a* values as it captures the most representative signal (Gove et al. 2013). As in the Caribbean, we used the long term climatological mean as predictors in the models. Average per island was extracted from Gove et al. (2013).

### ***Reef complexity***

For the Caribbean sites, we visually estimated structural reef complexity at each transect set on a scale of 0-5, where 0 was given to reefs with no vertical relief; 1, low and sparse relief; 2, low but widespread relief; 3, moderately complex relief; 4, very complex relief with numerous caves and fissures; and 5, reefs with exceptionally complex habitats, with numerous caves and overhangs (Polunin and Roberts 1993). This topographic measure provided an assessment of reef complexity at the seascape level which is relevant to large and medium-sized fish (Polunin and Roberts 1993, Wilson et al. 2007). For the Pacific islands, the same complexity index was estimated in each tow-diver survey and island mean was calculated for statistical analysis.

### ***Reef area***

Reef areas within 5 km and 10 km radius of each Caribbean site was calculated from the Global Distribution of Coral Reefs (2010) database as available at the Ocean Data Viewer United Nations Environment Program's World Conservation Monitoring Centre (UNEP-WCMC) (<http://data.unep-wcmc.org/datasets/13>) in ArcGIS v10.0. This database represents the global distribution of warm water coral reefs compiled mostly from the Millennium Coral Reef Mapping Project validated and un-validated maps as well as other sources acquired by UNEP-WCMC. For each Pacific islands, reef areas was calculated from the shoreline to 10 fathom line or ~18 m isobaths and obtained from Rohmann et al. (2005).

### ***Maximum island elevation***

Maximum land elevation for each Pacific island was obtained from CRED's Data/Information Products Team (<http://www.pifsc.noaa.gov/cred/>). We included island elevation because may have a positive effect on macroalgae richness probably due to more available space (Schils et al. 2013)

### ***Wave exposure***

Wave exposure for the Caribbean sites, given as the log of wind driven wave exposure ( $J m^{-3}$ ), was extracted in ArchGIS 10.0 from the wave stress map for the Caribbean basin built by Chollett et al. (2012) and available at (<http://www.marinespatialecologylab.org/wp-content/uploads/2010/11/PECS1.png>). This index does not include the influence of tides or swells, which are not generated by local wind, and it is an approximation of wave patterns in shallow areas over time (Chollett et al. 2012). Wave exposure in a given location is a function of

the basin shape (i.e. fetch), wind speed and direction and it is calculated using the method described by Ekeborn et al. (2003). Wind speed and direction were obtained from QuickSCAT satellite scatterometer data (1999-2008) available at (<http://www.ssmi.com/qscat>). The detailed description of the wave exposure calculations and assumptions can be found in Chollett & Mumby (2012).

For the Pacific, average wave exposure or energy ( $\text{kW m}^{-1}$ ) for each island was extracted from Gove et al. (2013). This variable was quantified using the global full spectral wave model Wave Watch III (<http://polar.ncep.noaha.gov/waves>). It was calculated at one-degree spatial resolution incorporating the 3-hour output of mean significant wave height, peak period, and direction from 1997 to 2010. Wave data were extracted from the one-degree grid cell in which each island was located. For detailed calculations of wave energy flux for each Pacific island refer to Gove et al. (2013).

Wave energy and exposure (given the dependence on wave period and height) are more realistic estimates of wave forcing and thus, more ecologically relevant variable to quantify wave impact on benthic communities (Friedlander et al. 2003, Storlazzi et al. 2005, Chollett and Mumby 2012). Wave exposure has been a good predictor of spatial variation in reef building corals such as *Orbicella* sp. (former *Montastrea* sp.) (Chollett and Mumby 2012) and can partially explain beta diversity patterns of benthic communities (Harborne et al. 2011). Wave exposure may also directly affect the biomass and diversity of tropical reef fish (Friedlander et al. 2003) and the distribution and abundance of temperate reef fish by compromising swimming abilities (Fulton and Bellwood 2004).

**Table S3.1 Survey locations, regions, and protection level for reef sites in the Caribbean.**

Date of survey is month and year(s). Protection level, NTZ: No-take zone, MPA: marine protected area. P code is protection level divided in two categories: N (none, MPA) and P (NTZ).

Site name	Site code	Depth (m)	Date of survey	Latitude	Longitude	Protection level	P code
<i>Mesoamerican Barrier, Mexico</i>							
Cancún	GH	12	Jul 12	21.02544	-86.7713	none	N
Cozumel North	PB	10	Jul 12	20.47188	-86.9815	NTZ	P
Akumal	XA	15	Jul 12	20.42689	-87.2860	none	N
Cozumel South	CR	15	Jul 12	20.31961	-87.0266	NTZ	P
Chinchorro North	BCN	15	Jul 12	18.74867	-87.3476	MPA	N
Chinchorro Central	BCC	15	Jul 12	18.57457	-87.4198	MPA	N
Chinchorro South	BCS	15	Jul 12	18.41008	-87.4169	MPA	N
<i>Mesoamerican Barrier, Belize</i>							
Bacalar Chico	BC	12-15	May 10/12	18.16282	-87.82222	NTZ	P
Mexico Rocks	MR	12-15	May 10/12	17.98782	-87.90382	none	N
Tackle Box	TB	12-15	May 10/12	17.91056	-87.95083	none	N
Hol Chan	HC	12-15	May 10/12	17.86343	-87.97238	NTZ	P
Gallows	GA	12-15	May 10/12	17.49592	-88.04255	none	N
Calabash Caye	CA	12-15	May 10/12	17.26147	-87.81970	none	N
Half Moon Caye	HM	12-15	May 10/12	17.20560	-87.54679	NTZ	P
Alligator Caye	AL	12-15	May 10/12	17.19660	-88.05115	none	N
Tobacco Caye	TO	12-15	May 10/12	16.91911	-88.04757	none	N
South Water Caye	SW	12-15	May 10/12	16.81346	-88.07756	MPA	N
Middle Caye	MC	12-15	May 10/12	16.73703	-87.80536	MPA	N
South Middle Caye	SM	12-15	May 10/12	16.72875	-87.82867	MPA	N
Pampion Caye	PO	12-15	May 10/12	16.37310	-88.08913	none	N
Ranguana Caye	RA	12-15	May 10/12	16.28501	-88.15031	none	N
Southwest Caye	ST	12-15	May 10/12	16.11247	-88.27107	none	N
Nicholas Caye	NI	12-15	May 10/12	16.11230	-88.25586	MPA	N
<i>Dry Tortugas, USA</i>	LG	12	Jun 12	24.68508	-82.91050	NTZ	P
<i>Cuba</i>							
Cueva Peces	CP	10-12	Jun 10/12	22.16627	-81.13827	none	N
Punta Perdiz	PZ	10-12	Jun 10/12	22.11003	-81.11626	none	N
Ebano	EB	10-12	Jun 10	22.07914	-81.07599	none	N
Brinco	BR	10-12	Jun 12	22.06939	-81.05588	none	N
Bacunayagua, Cuba	BC	10-12	Jun 12	23.14653	-81.66664	none	N
El Peruano	EP	10-12	Jun 11	20.84411	-79.02166	NTZ	P
Pipin	PP	12-15	Jun 11	20.82586	-78.98026	NTZ	P
Anclita	AN	10-12	Jun 11	20.78697	-78.94317	NTZ	P
Cueva Pulpo	CF	10-12	Jun 11	20.75266	-78.83634	NTZ	P
<i>Abaco, Bahamas</i>							
Guana Cay	GC	10-12	Jul 11/12	26.70967	-77.15408	none	N
Fowls Cay	FC	10	Jul 11/12	26.63717	-77.03848	NTZ	P
Man o' War	MW	10-12	Jul 11/12	26.62122	-77.00550	none	N
Pelican Cay	PC	10	Jul 11/12	26.39783	-76.98850	NTZ	P
Little Harbor	LH	10-12	Jul 11/12	26.32390	-76.99160	none	N
Rocky Point	RP	10-12	Jul 11/12	25.99661	-77.40092	none	N

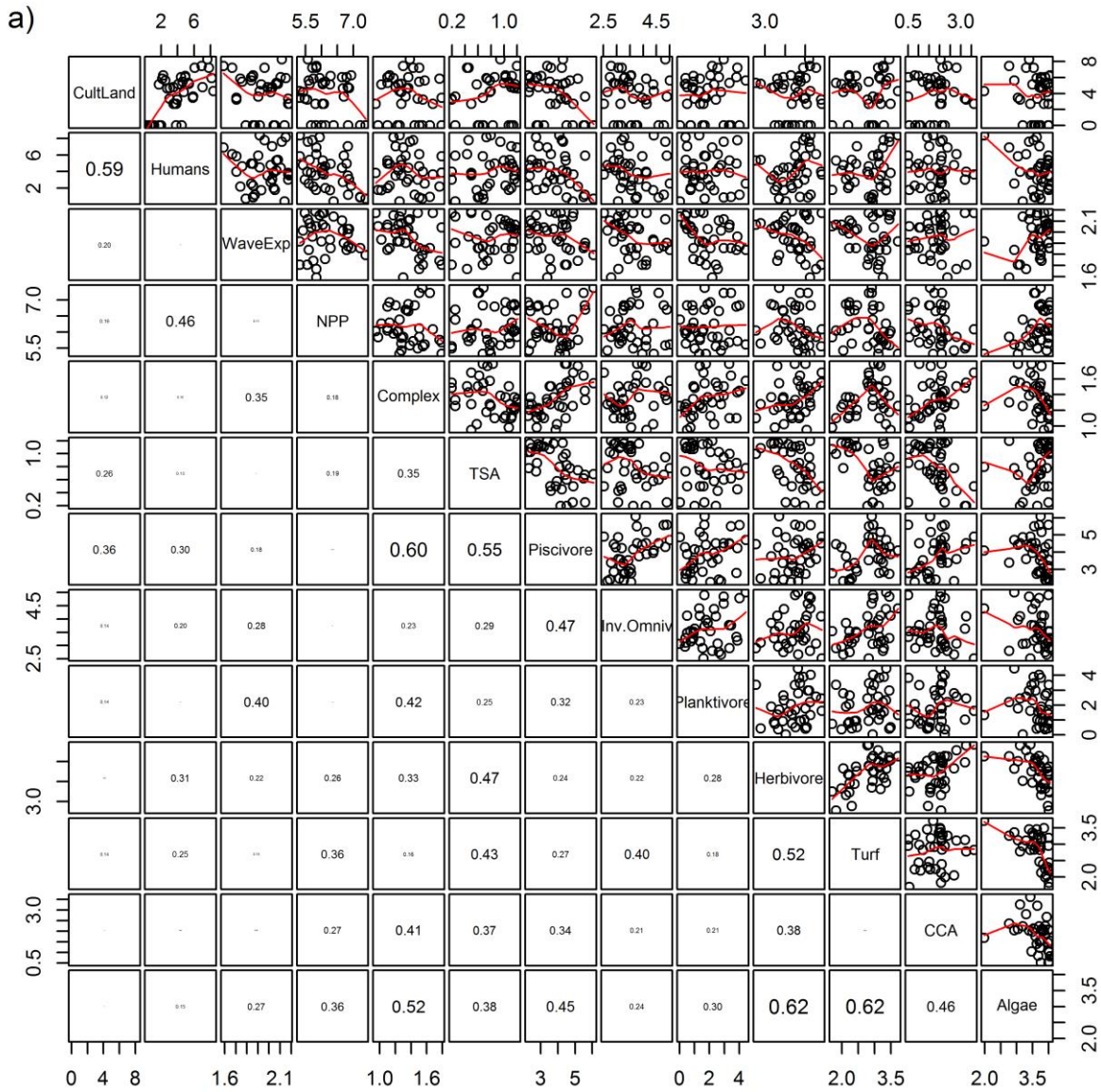
**Table S3.2 Survey locations, regions, and status for US Pacific islands used in this study.**

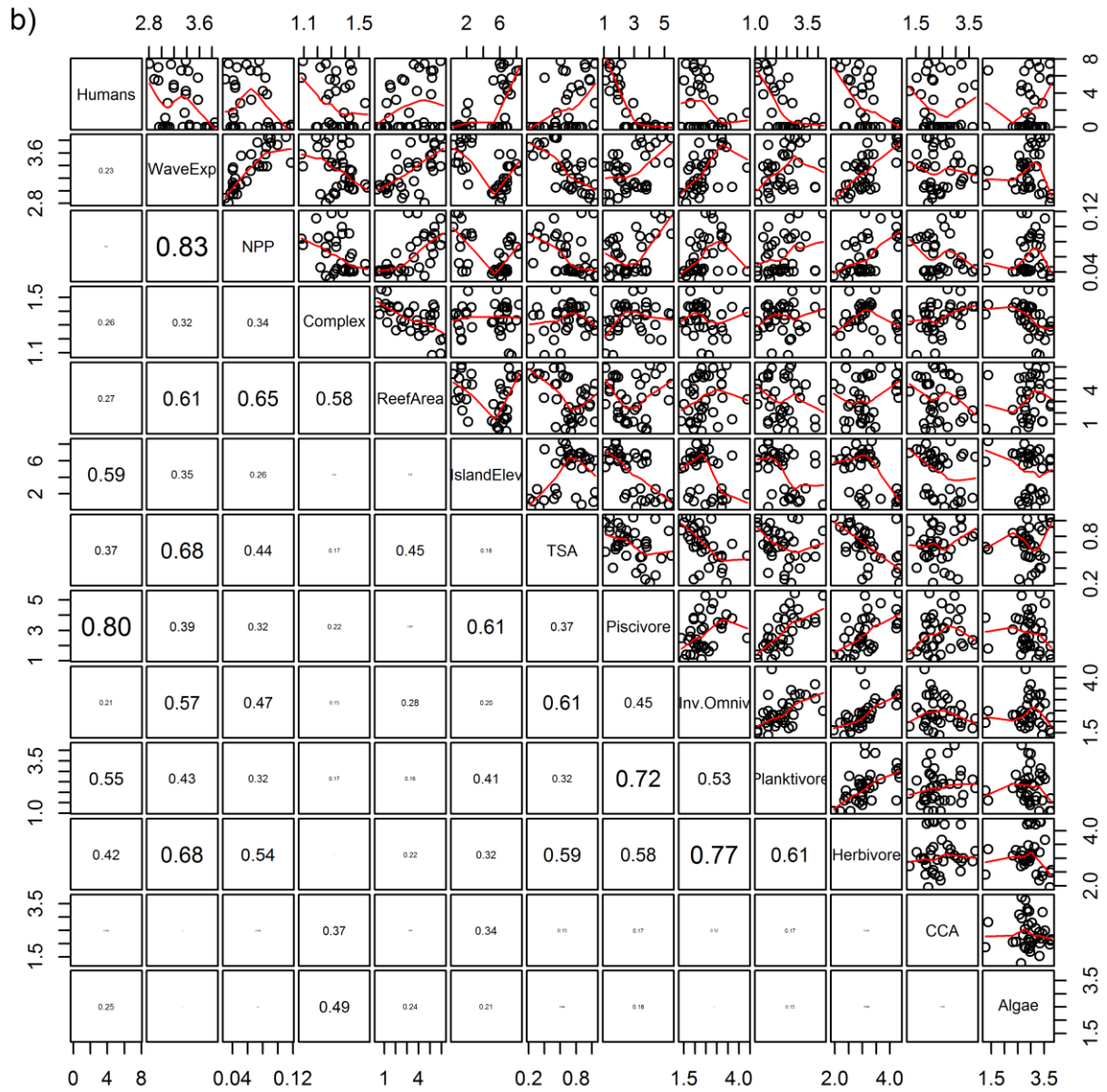
P/R, populated versus remote islands.

Island	Island code	Latitude	Longitude	P/R
<i>Hawaiian archipelago</i>				
Kauai	KAU	22.09119	-159.570	P
Niihau	NII	21.89792	-160.151	P
Oahu	OAH	21.48649	-158.003	P
Molokai	MOL	21.14063	-157.091	P
Lanai	LAN	20.82110	-156.918	P
Maui	MAI	20.81507	-156.400	P
Hawaii	HAW	19.52631	-155.416	P
Kure	KUR	28.42340	-178.331	R
Midway	MID	28.22690	-177.380	R
Pearl and Hermes	PHR	27.85629	-175.847	R
Lisianski	LIS	26.00917	-173.950	R
Laysan	LAY	25.77585	-171.732	R
Maro	MAR	25.41415	-170.579	R
French Frigate	FFS	23.79099	-166.213	R
<i>Mariana archipelago</i>				
Saipan	SAI	15.18538	145.7533	P
Tinian	TIN	14.99162	145.6324	P
Aguijan	AGU	14.85228	145.5548	P
Rota	ROT	14.16038	145.2103	P
Guam	GUA	13.46281	144.7875	P
Farallon de Pajaros	FDP	20.54689	144.8934	R
Maug	MAU	20.02211	145.2219	R
Asuncion	ASC	19.69406	145.4011	R
Agrihan	AGR	18.76091	145.6564	R
Pagan	PAG	18.11034	145.7565	R
Alamagan	ALA	17.60291	145.8253	R
Guguan	GUG	17.30801	145.8373	R
Sarigan	SAR	16.70606	145.7757	R
<i>Pacific remote islands</i>				
Wake	WAK	19.30113	166.6156	R
Johnston	JOH	16.74147	-169.516	R
Kingman	KIN	6.39852	-162.379	R
Palmyra	PAL	5.54049	-162.104	R
Howland	HOW	0.80441	-176.621	R
Baker	BAK	0.19631	-176.479	R
Jarvis	JAR	-0.37374	-159.997	R
<i>American Samoa</i>				
Ofu-Olesoga	OFU	-14.1736	-169.649	P
Tau	TAU	-14.2390	-169.469	P
Tutuila	TUT	-14.2972	-170.695	P
Rose	ROS	-14.5460	-168.156	R
Swains	SWA	-11.0562	-171.082	R



**Figure S3.1 Spearman rank correlations (lower panel) and scatterplot matrix (upper panel) of covariates used in the GLMMs for the Caribbean (a) and Pacific (b).** Red lines in the upper panel are smooth lowess curves with span of 2/3. Sizes of numbers in lower panel are proportional to the correlation. Covariates with correlation > 0.50 were not included in the same global model.





**Table S3.3 Top generalized linear mixed-effect models (GLMMs) for percent cover of corals, CCA, and macroalgae across 38 Caribbean reefs and 36 US Pacific islands.** Different model sets account for collinearity among predictors with symbols as in coefficient plots (Fig. 3.2). Variables selected in top models are marked by “+”, those included in global models but did not make top models are unmarked, and variables not included in global models due to correlation are shaded. Degree of freedom is df.  $\Delta$ AICc is the difference in AICc values between model *i* and the best model considered in the group. Model weight is the probability that model *i* is the best of the group. Relative variable importance (importance) is the sum of the weights of all models with that variable within the set. Variables with zero importance did not make the top models. Top models are those with  $\Delta$  AICc < 2 for the Caribbean and  $\Delta$  AICc < 3 for the Pacific. Note that explanatory variables are coded differently from the Caribbean and Pacific.

<b>Coral</b>	1	2	3	4	5	6	7	8	9	10	11	12	13	df	logLik	AICc	$\Delta$ AICc	Weight
● Set A		+		+	+	+			+	+				8	-106.01	232.98	0.00	0.37
Caribbean		+		+	+	+		+		+				8	-106.50	233.96	0.98	0.23
		+		+	+	+		+	+	+				9	-104.84	234.11	1.13	0.21
		+		+	+	+				+				7	-108.31	234.35	1.37	0.19
importance	0.0	1.0	0.0	1.0	1.0	1.0		.44	.58	1.0								
■ Set B		+					+	+				+		6	-114.99	244.69	0.00	0.23
Caribbean		+					+	+				+	+	7	-113.55	244.83	0.14	0.22
		+					+					+	+	6	-115.08	244.87	0.18	0.21
		+					+					+		5	-116.98	245.83	1.14	0.13
	+	+					+					+	+	7	-114.29	246.32	1.63	0.10
		+	+				+	+				+		7	-114.34	246.42	1.73	0.10
importance	.10	1.0	.10				1.0	.55	0.0			1.0	.54					
▲ Set C		+		+	+				+		+			7	-108.12	233.98	0.00	0.26
Caribbean		+		+	+			+	+		+			8	-106.69	234.34	0.36	0.21
		+		+	+			+			+			7	-108.52	234.78	0.80	0.17
		+		+	+				+					6	-110.30	235.31	1.33	0.13
		+		+	+						+			6	-110.46	235.63	1.65	0.11
		+		+	+			+						6	-110.48	235.68	1.70	0.11
importance	0.0	1.0	0.0	1.0	1.0			.50	.60		.76							

Variables: 1. Human/Reef; 2. Wave exposure; 3. NPP; 4. Reef complexity; 5. TSA; 6. Herbivore : TSA; 7. Piscivore; 8. Omnivore/Invertivore; 9. Planktivore; 10. Herbivore; 11. Turf; 12. CCA; 13. Macroalgae.

CCA	1	2	3	4	5	6	7	8	9	10	11	12	13	df	logLik	AICc	$\Delta$ AICc	Weight
● Set A	+		+		+	+		+		+				8	-94.49	209.94	0.00	0.31
Caribbean	+		+		+	+		+	+	+				9	-93.26	210.95	1.01	0.19
	+				+	+		+		+				7	-96.95	211.64	1.70	0.13
	+				+	+		+	+	+				8	-95.36	211.68	1.74	0.13
	+		+	+	+	+		+		+				9	-93.73	211.88	1.95	0.12
					+	+		+	+	+				7	-97.08	211.90	1.96	0.12
importance	.88	0.0	.62	.12	1.0	1.0		1.0	.44	1.0								
■ Set B	+		+					+	+				+	7	-103.08	223.90	0.00	0.27
Caribbean	+		+					+					+	6	-104.86	224.44	0.54	0.21
	+							+	+				+	6	-105.00	224.70	0.81	0.18
	+	+	+					+	+				+	8	-102.15	225.27	1.37	0.14
	+							+					+	5	-106.95	225.78	1.89	0.11
	+	+						+	+				+	7	-104.04	225.82	1.93	0.10
importance	1.0	.24	.61				0.0	1.0	.69				1.0					
▲ Set C			+	+				+			+			6	-104.14	222.99	0.00	0.73
Caribbean		+	+	+				+			+			7	-103.60	224.93	1.94	0.27
importance	0.0	.27	1.0	1.0	0.0			1.0	0.0		1.0							

Variables: 1. Human/Reef; 2. Wave exposure; 3. NPP; 4. Reef complexity; 5. TSA; 6. Herbivore : TSA; 7. Piscivore; 8. Omnivore/Invertivore; 9. Planktivore; 10. Herbivore; 11. Turf; 12. CCA; 13. Macroalgae.

Macroalgae	1	2	3	4	5	6	7	8	9	10	11	12	13	df	logLik	AICc	$\Delta$ AICc	Weight
● Set A		+	+	+						+				6	-155.83	326.38	0.00	0.14
Caribbean	+	+	+	+						+				7	-154.37	326.47	0.09	0.13
			+	+						+				5	-157.59	327.06	0.68	0.10
	+		+	+						+				6	-156.27	327.25	0.87	0.09
	+	+		+	+	+				+				8	-153.25	327.46	1.08	0.08
		+	+	+	+					+				7	-154.87	327.48	1.10	0.08
		+	+	+	+	+				+				8	-153.29	327.55	1.18	0.08
			+	+	+					+				6	-156.59	327.90	1.52	0.06
	+			+	+	+				+				7	-155.09	327.92	1.54	0.06
	+	+	+	+	+	+				+				9	-151.77	327.96	1.58	0.06
	+	+	+	+	+					+				8	-153.52	328.00	1.62	0.06
	+			+						+				5	-158.17	328.22	1.85	0.05
importance	.54	.63	.80	1.0	.49	.28				1.0								
■ Set B		+	+				+				+			6	-156.49	327.68	0.00	0.43
Caribbean		+	+				+	+			+			7	-155.68	329.10	1.42	0.21
		+	+								+			5	-158.75	329.38	1.70	0.18
	+	+	+				+				+			7	-155.85	329.43	1.75	0.18
importance	.18	1.0	1.0				.82	.21	0.0		1.0							

Variables: 1. Human/Reef; 2. Wave exposure; 3. NPP; 4. Reef complexity; 5. TSA; 6. Herbivore : TSA; 7. Piscivore; 8. Omnivore/Invertivore; 9. Planktivore; 10. Herbivore; 11. Turf; 12. CCA; 13. Macroalgae.

<b>Coral</b>	1	2	3	4	5	6	7	8	9	10	11	12	13	df	logLik	AICc	ΔAICc	Weight
● Set A				+			+							4	-122.47	254.24	0.00	0.65
Pacific				+			+	+						5	-121.73	255.46	1.22	0.35
importance				1.0			1.0	.35	0.0			0.0	0.0					
■ Set B													+	3	-146.83	300.42	0.00	0.19
Pacific	+												+	4	-145.63	300.55	0.13	0.18
	+													3	-147.34	301.43	1.01	0.11
												+	+	4	-146.09	301.47	1.06	0.11
	+				+							+	+	5	-144.77	301.53	1.11	0.11
	+											+	+	5	-144.92	301.85	1.43	0.09
	+											+		4	-146.47	302.24	1.82	0.08
	+				+									4	-146.54	302.38	1.96	0.07
importance	.63				.25						0.0	.28	.74					
▲ Set C				+	+									4	-116.52	242.33	0.00	0.26
Pacific				+	+			+						5	-115.18	242.37	0.03	0.26
				+	+					+				5	-115.28	242.55	0.22	0.24
				+	+		+	+						6	-114.48	243.85	1.51	0.12
importance				1.0	1.0		.21	.45		.35		0.0	0.0	6	-114.58	244.05	1.71	0.11
▼ Set D				+										3	-124.78	256.31	0.00	0.47
Pacific		+		+										4	-123.83	256.94	1.64	0.34
				+									+	4	-124.45	258.20	1.89	0.18
importance		.34		1.0								0.0	.18					

Variables: 1. Human/Reef; 2. Wave exposure; 3. NPP; 4. Reef complexity; 5. Reef area; 6. Island elevation; 7. TSA; 8. Piscivore; 9. Omnivore/Invertivore; 10. Planktivore; 11. Herbivore; 12. CCA; 13. Macroalgae.

CCA	1	2	3	4	5	6	7	8	9	10	11	12	13	df	logLik	AICc	$\Delta$ AICc	Weight
● Set A								+	+					4	-110.90	231.10	0.00	0.33
Pacific							+	+	+					5	-109.73	231.45	0.36	0.28
								+	+				+	5	-109.88	231.76	0.67	0.24
importance				0.0			.28	1.0	.85				.24		-112.97	232.69	1.59	0.15
■ Set B					+						+			4	-110.15	229.58	0.00	0.45
Pacific											+			3	-111.84	230.42	0.84	0.30
					+						+		+	5	-109.39	230.79	1.20	0.25
importance	0.0	0.0			.70						1.0		.25					
▲ Set C						+							+	4	-111.06	231.42	0.00	0.28
Pacific				+			+							4	-111.10	231.49	0.07	0.27
				+		+							+	5	-110.13	232.26	0.84	0.18
				+	+		+							5	-110.31	232.61	1.20	0.15
importance			.72	.15		.46	.54			0.0			+	5	-110.64	233.27	1.86	0.11
▼ Set D		+											+	4	-112.10	233.49	0.00	0.39
Pacific		+												3	-113.44	233.64	0.15	0.36
		+		+										4	-112.50	234.30	0.81	0.26
importance		1.0		.26									.39					

Variables: 1. Human/Reef; 2. Wave exposure; 3. NPP; 4. Reef complexity; 5. Reef area; 6. Island elevation; 7. TSA; 8. Piscivore; 9. Omnivore/Invertivore; 10. Planktivore; 11. Herbivore; 12. CCA; 13. Macroalgae.

Macroalgae	1	2	3	4	5	6	7	8	9	10	11	12	13	df	logLik	AICc	$\Delta$ AICc	Weight
● Set A				+			+							4	-152.87	315.03	0.00	0.41
Pacific				+			+		+					5	-151.86	315.72	0.69	0.29
				+			+	+						5	-152.25	316.49	1.47	0.20
importance				1.0			1.0	.30	.39					6	-151.45	317.80	2.77	0.10
■ Set B	+													3	-177.17	361.10	0.00	0.43
Pacific	+										+			4	-176.72	362.74	1.64	0.19
	+				+									4	-177.01	363.31	2.21	0.14
											+			3	-178.48	363.71	2.62	0.12
importance	.77				.26						.42			4	-177.21	363.71	2.62	0.12
▲ Set C			+	+		+	+							6	-132.97	280.84	0.00	0.79
Pacific			+	+		+	+			+				7	-132.74	283.49	2.65	0.21
importance			1.0	1.0		1.0	1.0			.21								
▼ Set D				+										3	-160.98	328.72	0.00	0.59
Pacific		+		+										4	-160.06	329.42	0.70	0.41
importance		.41		1.0														

Variables: 1. Human/Reef; 2. Wave exposure; 3. NPP; 4. Reef complexity; 5. Reef area; 6. Island elevation; 7. TSA; 8. Piscivore; 9. Omnivore/Invertivore; 10. Planktivore; 11. Herbivore; 12. CCA; 13. Macroalgae.



## Appendix 3.2 References

- Behrenfeld, M. J., and P. G. Falkowski. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and oceanography*:1–20.
- Boss, E., and J. R. Zaneveld. 2003. The effect of bottom substrate on inherent optical properties: Evidence of biogeochemical processes.
- Casey, K. S., T. B. Brandon, P. Cornillon, and R. Evans. 2010. The past, present, and future of the AVHRR pathfinder SST program. Pages 273–287 *in* V. Barale, J. F. R. Gower, and L. Alberotanza, editors. *Oceanography from Space*. Springer Netherlands, Dordrecht.
- Chollett, I., and P. J. Mumby. 2012. Predicting the distribution of *Montastraea* reefs using wave exposure. *Coral Reefs* 31:493–503.
- Chollett, I., P. J. Mumby, F. E. Müller-Karger, and C. Hu. 2012. Physical environments of the Caribbean Sea. *Limnology and Oceanography* 57:1233–1244.
- Ekeboom, J., P. Laihonon, and T. Suominen. 2003. A GIS-based step-wise procedure for assessing physical exposure in fragmented archipelagos. *Estuarine, Coastal and Shelf Science* 57:887–898.
- Friedlander, A. M., E. K. Brown, P. L. Jokiel, W. R. Smith, and K. S. Rodgers. 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305.
- Fulton, C. J., and D. R. Bellwood. 2004. Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. *Marine Biology* 144:429–437.
- Glynn, P. W. 1993. Coral reef bleaching: ecological perspectives. *Coral Reefs* 12:1–17.
- Gove, J. M., G. J. Williams, M. A. McManus, S. F. Heron, S. A. Sandin, O. J. Vetter, and D. G. Foley. 2013. Quantifying climatological ranges and anomalies for Pacific coral reef ecosystems. *PloS one* 8:e61974.
- Harborne, A. R., P. J. Mumby, K. Żychaluk, J. D. Hedley, and P. G. Blackwell. 2011. Modeling the beta diversity of coral reefs. *Ecology* 87:2871–2881.
- Kilpatrick, K. A., G. P. Podestá, and R. Evans. 2001. Overview of the NOAA/NASA advanced very high resolution radiometer Pathfinder algorithm for sea surface temperature and associated matchup database. *Journal of Geophysical Research: Oceans* 106:9179–9197.
- Latham, J., R. Cumani, I. Rosati, and M. Bloise. 2014. FAO Global Land Cover SHARE (GLC-SHARE) database Beta-Release Version 1.0-2014. FAO.

- Liu, G., A. E. Strong, and W. Skirving. 2003. Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. *Eos, Transactions American Geophysical Union* 84:137–141.
- McCook, L. J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:357–367.
- Mora, C. 2008. A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society B: Biological Sciences* 275:767–773.
- Oregon State University. 2013. Ocean Productivity: Online VGPM Data. <http://orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.vgpm.m.chl.m.sst4.php>.
- Polunin, N. V. C., and C. M. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* 100:177–183.
- Rohmann, S. O., J. J. Hayes, R. C. Newhall, M. E. Monaco, and R. W. Grigg. 2005. The area of potential shallow-water tropical and subtropical coral ecosystems in the United States. *Coral Reefs* 24:370–383.
- Schils, T., P. S. Vroom, and A. D. Tribollet. 2013. Geographical partitioning of marine macrophyte assemblages in the tropical Pacific: a result of local and regional diversity processes. *Journal of Biogeography* 40:1266–1277.
- SEDAC, (Socioeconomic Data and Applications Center). 2010. Global rural-urban mapping project – settlement points. Columbia University, New York. <http://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-density/data-download>.
- Selig, E. R., K. S. Casey, and J. F. Bruno. 2010. New insights into global patterns of ocean temperature anomalies: implications for coral reef health and management. *Global Ecology and Biogeography* 19:397–411.
- Storlazzi, C. D., E. K. Brown, M. E. Field, K. Rodgers, and P. L. Jokiel. 2005. A model for wave control on coral breakage and species distribution in the Hawaiian Islands. *Coral Reefs* 24:43–55.
- UNEP-WCMC, WorldFish Centre, WRI, and TNC. 2010. Global distribution of warm-water coral reefs, compiled from multiple sources, including the Millennium Coral Reef Mapping Project. UNEP World Conservation Monitoring Centre. Cambridge (UK). <http://data.unep-wcmc.org/datasets/13>.
- Williams, I. D., B. L. Richards, S. A. Sandin, J. K. Baum, R. E. Schroeder, M. O. Nadon, B. Zgliczynski, P. Craig, J. L. McIlwain, and R. E. Brainard. 2011. Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western pacific. *Journal of Marine Biology* 2011.
- Wilson, S., N. Graham, and N. Polunin. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology* 151:1069–1076.

## APPENDIX 4: SUPPLEMENTARY MATERIAL FOR CHAPTER 4

### Appendix 4.1 Description of variables used as predictors in the generalized linear mixed effect models.

#### *Humans per reef area*

Humans per reef area were used as a proxy of anthropogenic disturbance because human activities have a direct and indirect negative effect on coral assemblages (Hughes et al. 2003, Mora 2008, Bellwood et al. 2011, Barott et al. 2012). Human population size was estimated as the maximum number of people that occurred within 50-km radius of each site. We chose 50 km as radius because is a reasonable range of anthropogenic influence on Caribbean reefs (Mora 2008). Projection estimates of human population counts for the year 2010 were obtained from the Gridded Population of the World V.3 at 0.25 degree resolution (SEDAC 2010). Reef areas within 10 km radius of each site was calculated from the Global Distribution of Coral Reefs (2010) database as available at the Ocean Data Viewer United Nations Environment Program's World Conservation Monitoring Centre (UNEP-WCMC) (<http://data.unep-wcmc.org/datasets/13>). All spatial calculations were performed in ArcGIS v10.0. Humans/ Reef Area (humans/km<sup>2</sup> reef) was calculated as: number of humans within 50km/Reef area within 10km/ ( $\pi 10^2$ ) (km<sup>2</sup>)

#### *Cultivated land*

Cultivated land could be a surrogate of terrestrial run-offs with potential effects on coral and macroalgae cover when herbivory is reduced (McCook 1999, Mora 2008). We quantified the area of cultivated land that occurred within a 50 km radius of each reef site. The raster data for this variable was obtained from the Global Land Cover Share 2013 database (Latham et al.

2014). Specifically, we used the regional dataset (North and Central America) that depicts the spatial distribution of 29 different land attributes for the year 2010 as calculated from satellite images at 1 km resolution. Spatial analyses were performed in ArcGIS v10.

### ***Reef structural complexity***

Reef structural complexity was estimated at the seascape level. This topographic measure provided an assessment of overall complexity accounting for living benthic organisms and reef structure that have built over time (Polunin and Roberts 1993, Wilson et al. 2007). For each transect set at each site we visually estimated structural reef complexity on a scale of 0-5, where 0 was given to reefs with no vertical relief; 1, low and sparse relief; 2, low but widespread relief; 3, moderately complex relief; 4, very complex relief with numerous caves and fissures; and 5, reefs with exceptionally complex habitats, with numerous caves and overhangs (Polunin and Roberts 1993). To minimize estimation subjectivity among observers, at least two divers estimated reef structural complexity for each transect set and the average was calculated to be used in the models. We evaluated the accuracy of the estimations among observers by comparing the standard deviations (SD) among transects per site and found that SDs were 0-0.7 in all cases, meaning that average estimation differences were never over 1 unit.

### ***Ocean productivity***

Mean oceanic net primary productivity ( $\text{mg C m}^{-2} \text{ day}^{-1}$ ) was estimated for each site between 2002 and 2012 using remote-sensing. This was obtained from Aqua MODIS satellite monthly data combined in the vertical generalized production model (Behrenfeld and Falkowski 1997) at a spatial resolution of  $0.0833^\circ$  (Oregon State University 2013). We used the mean of the last ten years period because primary productivity is inherently variable in time and established

benthic communities may respond better to long term trends in primary productivity than to survey year or monthly mean values. Calculations were performed in ArcGIS 10.0.

### ***Wave exposure***

Wave exposure is a good predictor of spatial variation in reef-building corals such as *Orbicella* spp. (former *Montastrea* spp.) (Chollett and Mumby 2012) and can partially explain beta diversity patterns of benthic communities (Harborne et al. 2011). The log of wind driven wave exposure ( $J m^{-3}$ ) was extracted in ArcGIS 10.0 from the wave stress map for the Caribbean basin built by Chollett *et al.* (2012) and available at (<http://www.marinespatialecologylab.org/wp-content/uploads/2010/11/PECS1.png>). The detailed description of the wave exposure calculations and assumptions can be found in Chollett & Mumby (2012).

### ***Fish biomass***

Piscivore and herbivorous fishes can indirectly affect coral assemblages through cascading effects (Dulvy et al. 2004, Mumby et al. 2006, 2007). Underwater visual censuses (UVC) were used to characterize the fish assemblages. At each reef site we randomly placed six to eight belt transect sets along the fore reef's spur-and-groove or slope formations and recorded, identified, and estimated body size of all reef fish species. Each set consisted in a 50 x 10 m transect area to estimate fish  $\geq 40$  cm in total length (TL) (McCauley et al. 2012) and a nested 30 x 2 transect area to estimate fish  $< 40$  cm TL (Lang et al. 2010). Fish size was estimated to the nearest 10 cm, except for fish  $< 10$  cm where a 5 cm interval was used. Each transect belt set was surveyed in ~15 minutes, covered the entire visible water column, and were at least ~10 m apart.

Fish biomass was calculated using the allometric conversion relationship  $W = aL^b$  (Froese and Pauly 2013) where  $W$  is the weight of each fish in grams,  $L$  is the total length ( $TL$ ) or fork length ( $FL$ ) in cm, and the parameters  $a$  and  $b$  are species specific. Length-length conversion parameters were used to convert  $TL$  to  $FL$  for those species that  $L$  was based on  $FL$ . When the allometric parameters ( $a$  and  $b$ ) were not available we used those values from congeneric species of similar size and shape and of similar geographical range (Froese and Pauly 2013).

**Table S4.1 General descriptive information of surveyed sites.** S&G means spur-and-groove.

Country	Site name	Site code	Latitude	Longitude	Habitat type	Depth (m)	Date of survey
Mexico	Cancún	GH	21.02544	-86.7713	S & G	12	Jul 12
	Cozumel North	PB	20.47188	-86.9815	S & G	10	Jul 12
	Akumal	XA	20.42689	-87.2860	S & G	15	Jul 12
	Cozumel South	CR	20.31961	-87.0266	S & G	15	Jul 12
	Chinchorro North	BCN	18.74867	-87.3476	S & G	15	Jul 12
	Chinchorro Central	BCC	18.57457	-87.4198	S & G	15	Jul 12
	Chinchorro South	BCS	18.41008	-87.4169	S & G	15	Jul 12
Belize	Bacalar Chico	BC	18.16282	-87.82222	S & G	12-15	May 10/12
	Mexico Rocks	MR	17.98782	-87.90382	S & G	12-15	May 10/12
	Tackle Box	TB	17.91056	-87.95083	S & G	12-15	May 10/12
	Hol Chan	HC	17.86343	-87.97238	S & G	12-15	May 10/12
	Gallows	GA	17.49592	-88.04255	S & G	12-15	May 10/12
	Calabash Caye	CA	17.26147	-87.81970	S & G	12-15	May 10/12
	Half Moon Caye	HM	17.20560	-87.54679	S & G	12-15	May 10/12
	Alligator Caye	AL	17.19660	-88.05115	S & G	12-15	May 10/12
	Tobacco Caye	TO	16.91911	-88.04757	S & G	12-15	May 10/12
	South Water Caye	SW	16.81346	-88.07756	S & G	12-15	May 10/12
	Middle Caye	MC	16.73703	-87.80536	S & G	12-15	May 10/12
	South Middle Caye	SM	16.72875	-87.82867	S & G	12-15	May 10/12
	Pampion Caye	PO	16.37310	-88.08913	S & G	12-15	May 10/12
	Ranguana Caye	RA	16.28501	-88.15031	S & G	12-15	May 10/12
	Southwest Caye	ST	16.11247	-88.27107	S & G	12-15	May 10/12
Nicholas Caye	NI	16.11230	-88.25586	S & G	12-15	May 10/12	
USA	Dry Tortugas, USA	LG	24.68508	-82.91050	S & G	12	Jun 12
Cuba	Cueva Peces	CP	22.16627	-81.13827	Slope	10-12	Jun 10/12
	Punta Perdiz	PZ	22.11003	-81.11626	Slope	10-12	Jun 10/12
	Ebano	EB	22.07914	-81.07599	Slope	10-12	Jun 10
	Brinco	BR	22.06939	-81.05588	Slope	10-12	Jun 12
	Bacunayagua, Cuba	BC	23.14653	-81.66664	Slope	10-12	Jun 12
	El Peruano	EP	20.84411	-79.02166	Slope	10-12	Jun 11
	Pipin	PP	20.82586	-78.98026	S & G	12-15	Jun 11
	Anclita	AN	20.78697	-78.94317	Slope	10-12	Jun 11
	Cueva Pulpo	CF	20.75266	-78.83634	Slope	10-12	Jun 11
Bahamas	Guana Cay	GC	26.70967	-77.15408	S & G	10-12	Jul 11/12
	Fowls Cay	FC	26.63717	-77.03848	Slope	10	Jul 11/12
	Man o' War	MW	26.62122	-77.00550	S & G	10-12	Jul 11/12
	Pelican Cay	PC	26.39783	-76.98850	Slope	10	Jul 11/12
	Little Harbor	LH	26.32390	-76.99160	S & G	10-12	Jul 11/12
	Rocky Point	RP	25.99661	-77.40092	Slope	10-12	Jul 11/12

**Table S4.2 Classification of Caribbean scleractinian coral species in three life history strategies** after Darling et al. (2012) These species were identified during our surveys.

Family	Species	Code	Life history
Acroporidae	<i>Acropora cervicornis</i>	AcrCer	Competitive
Acroporidae	<i>Acropora palmata</i>	AcrPal	Competitive
Agaricidae	<i>Agaricia agaricites</i>	Agaaga	Weedy
Agaricidae	<i>Agaricia fragilis</i>	Agafra	Weedy
Agaricidae	<i>Agaricia grahamae</i>	Agagra	Weedy
Agaricidae	<i>Agaricia humilis</i>	Agahum	Weedy
Agaricidae	<i>Agaricia lamarcki</i>	Agalam	Weedy
Agaricidae	<i>Agaricia tenuifolia</i>	Agaten	Weedy
Mussidae	<i>Colpophyllia natans</i>	Colnat	Stress-tolerant
Meandrinidae	<i>Dendrogyra cylindrus</i>	Dencyl	Competitive
Meandrinidae	<i>Dichocoenia stokesi</i>	Dicsto	Stress-tolerant
Mussidae	<i>Diploria labyrinthiformis</i>	Diplab	Stress-tolerant
Caryophyllidae	<i>Eusmilia fastigiata</i>	Eusfas	Stress-tolerant
Faviidae	<i>Favia fragum</i>	Favfra	Stress-tolerant
Mussidae	<i>Isophyllia sinuosa</i>	Isosin	Stress-tolerant
Agaricidae	<i>Leptoseris cucullata</i>	Lepcuc	Weedy <sup>1</sup>
Pocilloporidae	<i>Madracis decactis</i>	Maddec	Weedy
Pocilloporidae	<i>Madracis mirabilis</i>	Madmir	Weedy <sup>2</sup>
Mussidae	<i>Manicina areolata</i>	Manare	Weedy
Meandrinidae	<i>Meandrina meandrites</i>	Meamea	Stress-tolerant
Milleporidae	<i>Millepora alcicornis</i>	Milalc	Hydrocoral
Milleporidae	<i>Millepora complanata</i>	Milcom	Hydrocoral
Montastreidae	<i>Montastraea cavernosa</i>	Moncav	Stress-tolerant
Mussidae	<i>Mussa angulosa</i>	Musang	Weedy <sup>1</sup>
Mussidae	<i>Mycetophyllia aliciae</i>	Mycali	Weedy
Mussidae	<i>Mycetophyllia danae</i>	Mycdan	Weedy
Mussidae	<i>Mycetophyllia ferox</i>	Mycfer	Weedy
Mussidae	<i>Mycetophyllia lamarckiana</i>	Myclam	Weedy
Merulinidae	<i>Orbicella annularis</i>	Orbann	Stress-tolerant
Merulinidae	<i>Orbicella faveolata</i>	Orbfav	Stress-tolerant
Merulinidae	<i>Orbicella franksi</i>	Orbfra	Stress-tolerant
Poritidae	<i>Porites astreoides</i>	Porast	Weedy
Poritidae	<i>Porites divaricata</i>	Pordiv	Weedy
Poritidae	<i>Porites furcata</i>	Porfur	Weedy
Poritidae	<i>Porites porites</i>	Porpor	Weedy
Mussidae	<i>Pseudodiploria clivosa</i>	Psecli	Stress-tolerant
Mussidae	<i>Pseudodiploria strigosa</i>	Psestr	Stress-tolerant
Siderastreidae	<i>Siderastrea radians</i>	Sidrad	Weedy
Siderastreidae	<i>Siderastrea siderea</i>	Sidsid	Stress-tolerant
Mussidae	<i>Scolymia lacera</i>	Scolac	Weedy <sup>1</sup>
<i>incertae sedis</i> <sup>3</sup>	<i>Solenastrea buornoni</i>	Solbuo	Stress-tolerant
Astrocoeniidae	<i>Stephanocoenia intersepta</i>	Steint	Stress-tolerant

<sup>1</sup>Life history assigned from species in family

<sup>2</sup>Life history assigned from congeneric species

<sup>3</sup>Classification still dubious (Budd et al. 2012)

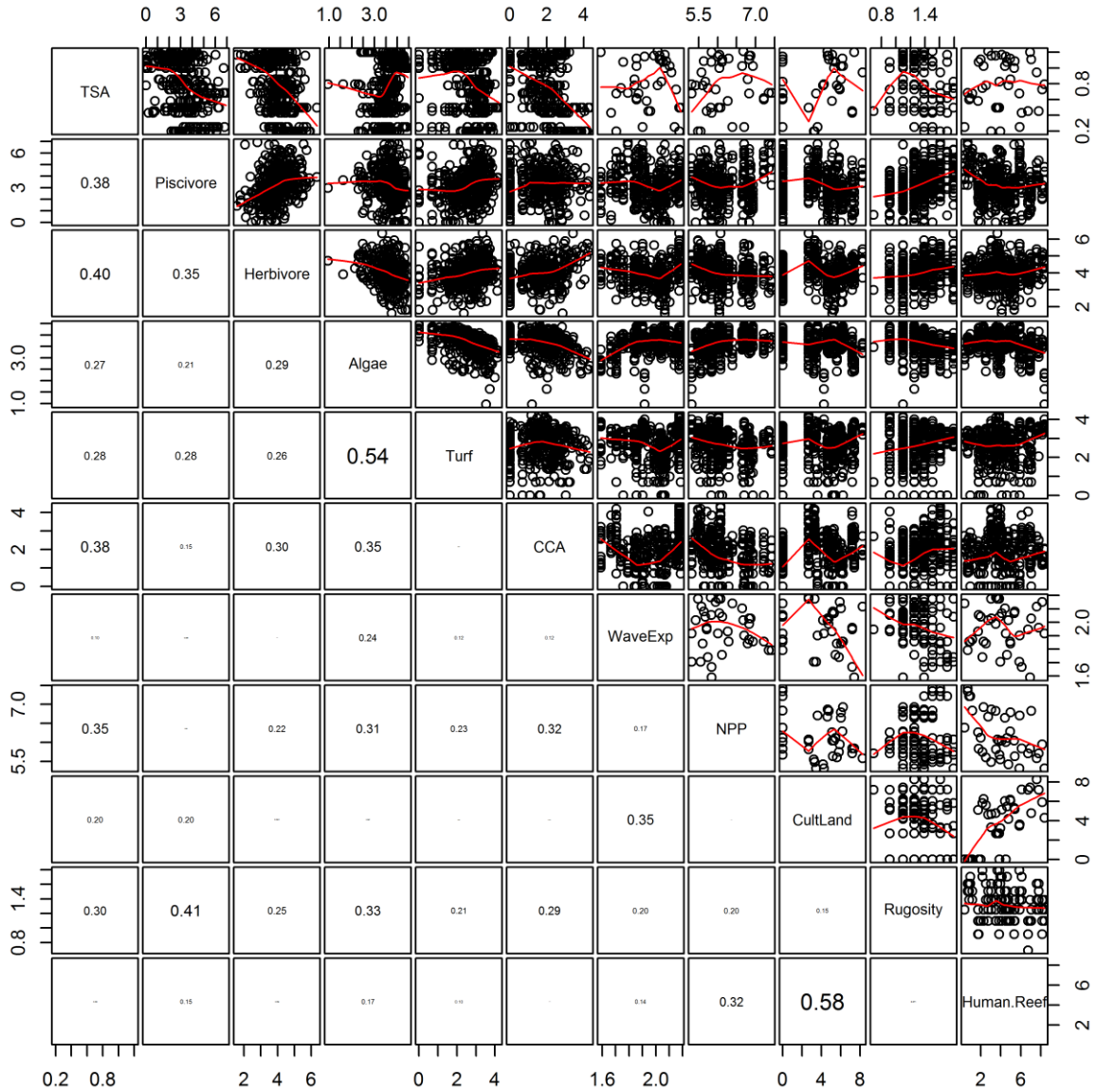


**Table S4.3 Summary of the linear regression models parameters of the trend of thermal stress anomalies on years for each study sites.** For site codes refer to Table S1. Significance

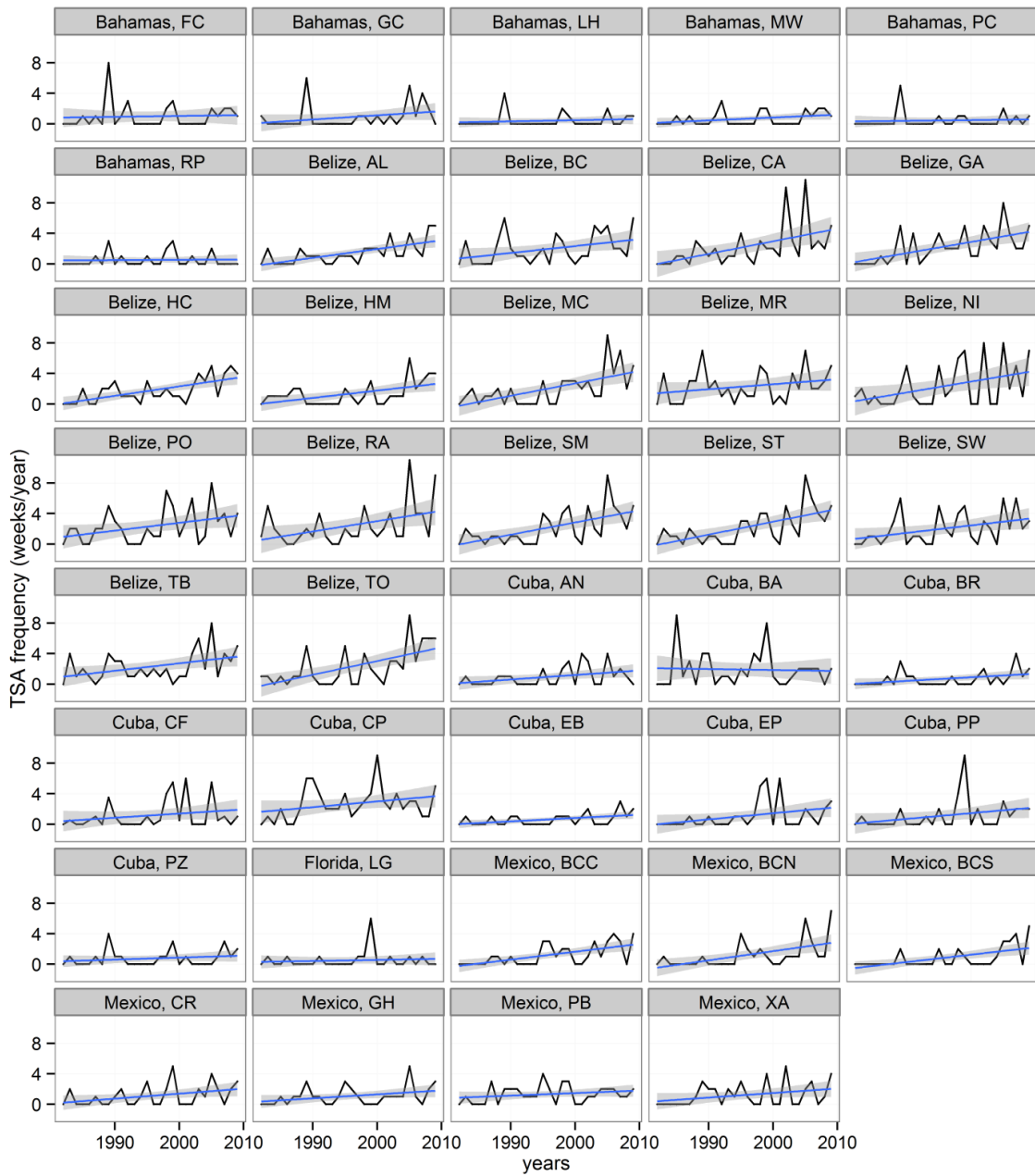
codes are: 0 ‘\*\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’

Country	Site	Estimate	Std. Error	t-value	F-statistic	Pr(> t )	R <sup>2</sup>
Bahamas	FC	0.01122	0.04019	0.279	0.079	0.7823	0.002
Bahamas	GC	0.05473	0.03611	1.516	2.297	0.1417	0.081
Bahamas	LH	0.01505	0.02165	0.695	0.483	0.4931	0.018
Bahamas	MW	0.03777	0.02043	1.849	3.418	0.0759.	0.116
Bahamas	PC	0.00931	0.02458	0.379	0.143	0.7081	0.005
Bahamas	RP	0.00438	0.02199	0.199	0.039	0.8437	0.002
Belize	AL	0.11549	0.02695	4.286	18.37	0.0002***	0.414
Belize	BC	0.09031	0.04229	2.136	4.560	0.0423*	0.149
Belize	CA	0.16530	0.05483	3.015	9.089	0.0057**	0.259
Belize	GA	0.14614	0.04044	3.164	13.06	0.0012**	0.334
Belize	HC	0.12397	0.02872	4.317	18.64	0.0002***	0.418
Belize	HM	0.09606	0.03086	3.112	9.687	0.0044**	0.271
Belize	MC	0.16284	0.04218	3.860	14.90	0.0007***	0.364
Belize	MR	0.06513	0.04723	1.379	1.902	0.1800	0.065
Belize	NI	0.14231	0.06065	2.347	5.506	0.0269*	0.175
Belize	PO	0.10208	0.04964	2.056	4.228	0.0499*	0.139
Belize	RA	0.13547	0.05678	2.386	5.692	0.0246*	0.179
Belize	SM	0.16010	0.04300	3.723	13.86	0.0009***	0.348
Belize	ST	0.16845	0.04147	4.062	16.50	0.0004***	0.388
Belize	SW	0.09797	0.04459	2.197	4.827	0.0371*	0.157
Belize	TB	0.09743	0.04164	2.340	5.474	0.0273*	0.174
Belize	TO	0.17950	0.04630	3.878	15.04	0.0006***	0.366
Cuba	AN	0.05911	0.02809	2.105	4.430	0.0451*	0.146
Cuba	BA	-0.01286	0.05436	-0.237	0.056	0.8148	0.002
Cuba	BR	0.04735	0.02248	2.106	4.434	0.0450*	0.146
Cuba	CF	0.05446	0.04329	1.258	1.583	0.2200	0.057
Cuba	CP	0.07553	0.04768	1.584	2.509	0.1253	0.088
Cuba	EB	0.04351	0.01668	2.608	6.804	0.0149*	0.207
Cuba	EP	0.08046	0.04001	2.011	4.045	0.0548.	0.135
Cuba	PP	0.07526	0.04312	1.745	3.046	0.0928.	0.105
Cuba	PZ	0.02600	0.02514	1.034	1.070	0.3105	0.039
USA	LG	0.01423	0.02777	0.512	0.263	0.6126	0.010
Mexico	BCC	0.10317	0.02622	3.935	15.48	0.0006***	0.373
Mexico	BCN	0.12014	0.03605	3.333	11.11	0.0026**	0.299
Mexico	BCS	0.09661	0.02793	3.459	11.96	0.0019**	0.315
Mexico	CR	0.06541	0.03073	2.128	4.530	0.0429*	0.148
Mexico	GH	0.05200	0.02711	1.918	3.678	0.0662.	0.124
Mexico	PB	0.03311	0.02600	1.274	1.623	0.2140	0.059
Mexico	XA	0.05966	0.03440	1.734	3.008	0.0947	0.104

**Figure S4.1 Spearman's rank correlation matrix of absolute values and pairs plot for explanatory variables used in the GLMMs.** The size of the correlation numbers is proportional to the amount of correlation. *Turf algae* and *Cultivated land* were dropped from the models because they were correlated ( $r_s > 0.50$ ) with *Algae* cover and *Humans/reef*, respectively.

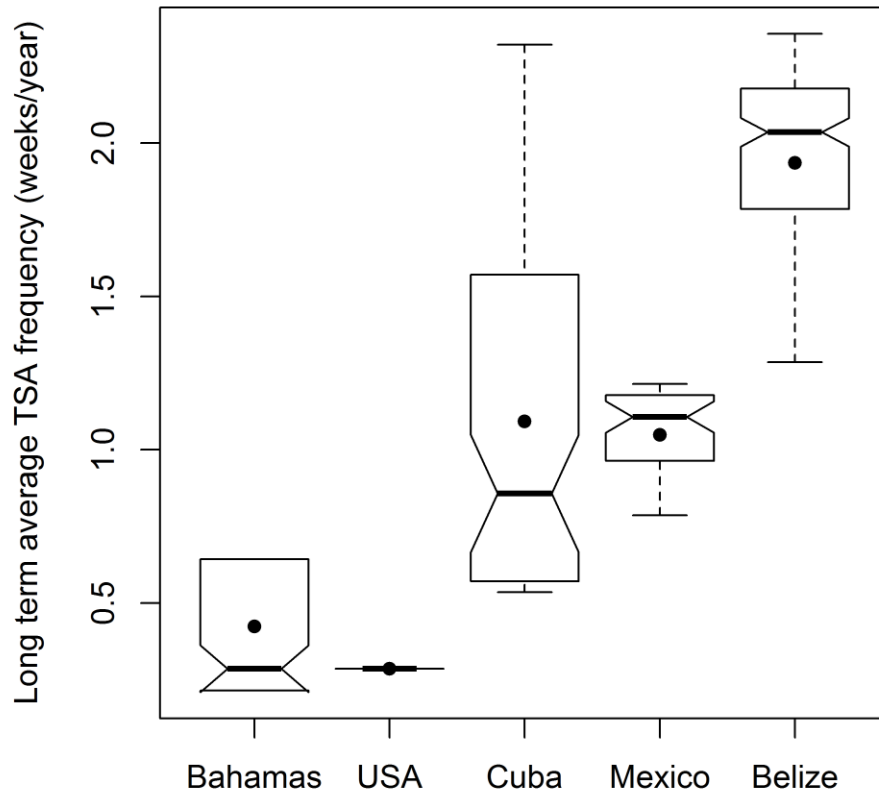


**Figure S4.2 Frequency of thermal stress anomalies for each surveyed site from 1982 to 2010.** Blue line is the predicted simple linear model regression bounded by 95% confidence interval. Most sites in Belize and Mexico have increased the frequency of TSA over ~30 year. For site labels refer to Supplementary Table S4.1. For the results of the linear model see Table

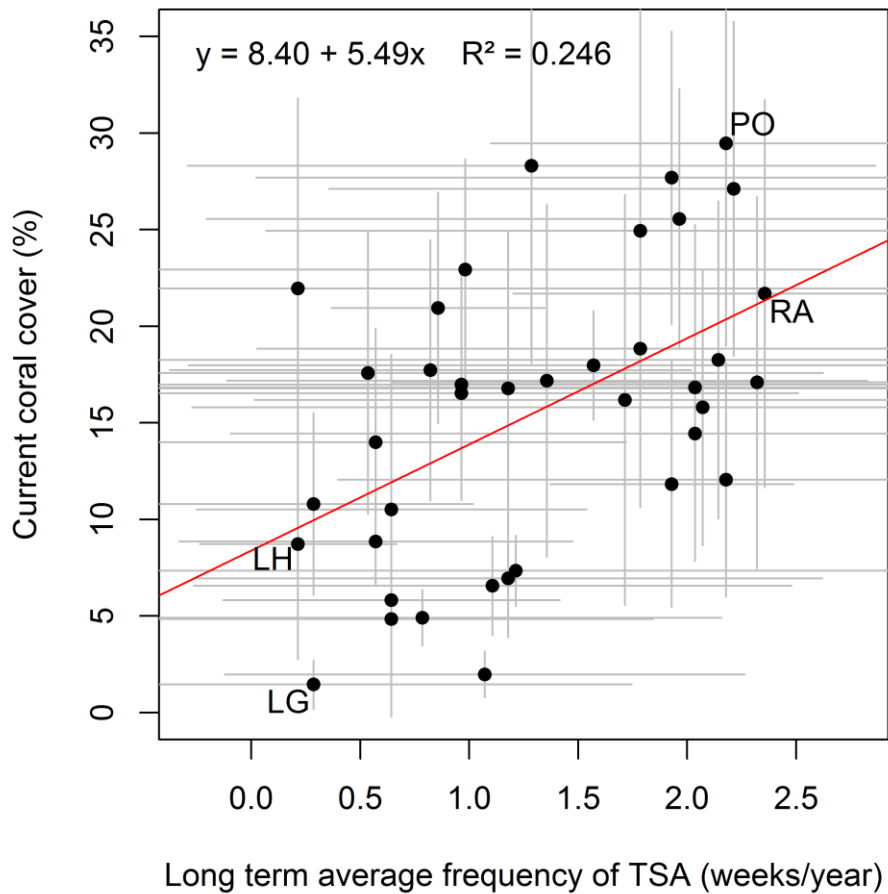


S4.3.

**Figure S4.3 Notched boxplot of average TSA frequency over 29 years for each sub-region (country).** Non-overlapping notches indicate statistically significant differences between medians (horizontal black line). Black dot is the mean value for each sub-region.



**Figure S4.4 Scatterplot of means ( $\pm$  standard deviation) of current coral cover on TSA frequency over 29 years (1982-2010). Red lined is the predicted regression slope from the averaged GLMMs. LH (Little Harbor, Bahamas) had the lowest TSA frequency while RA (Ranguana, Belize) had the highest. LG (Loggerhead, Dry Tortugas, Florida) was the site with the lowest coral cover while PO (Pompion, Belize) had the highest coral cover. For site coordinates of those reefs refer to Table S4.1. Some standard deviations are trunked for easy visualization.**



## Appendix 4.2 Mechanisms of acquisition of thermal tolerance

Thermal tolerance of different coral species can occur via genetic adaptation or physiological acclimatization (i.e., phenotypic plasticity), two mechanisms that have been widely studied for coral species and genotypes over the past decade (Edmunds and Gates 2008, Bellantuono et al. 2012, Hoegh-Guldberg 2012, Palumbi et al. 2014). Adaptation occurs through natural selection of heat-tolerant lineages of algal symbionts and/or coral host (Baker et al. 2004, Guest et al. 2012, Hoegh-Guldberg 2012). Micro-evolutionary adaptation to rapid warming may take decades (Hoegh-Guldberg 2012), especially for major reef building broadcasting corals (e.g., *Acropora* spp., *Siderastrea* spp., and *Orbicella* spp. in the Caribbean) that reproduce annually or biannually and that reach maturity after several years (Darling et al. 2012). Physiological acclimatization of either or both host and symbiont in response to frequent thermal anomalies (Edmunds and Gates 2008, Bellantuono et al. 2012, Palumbi et al. 2014) can occur much faster than genetic adaptation in slow-growing organisms (like corals) and may bolster resistance to future temperature stress (Edmunds and Gates 2008, Palumbi et al. 2014), especially for weedy and brooder corals (e.g., *Porites* spp. and *Agaricia* spp.) that reproduce often (Green et al. 2008).

Acclimatization may work through at least two major pathways that promote thermal tolerance of corals, first by hosting, shifting or acquiring stress-tolerant algal symbionts (Baker et al. 2004, Berkelmans and Oppen 2006, Oliver and Palumbi 2011) and second by physiological changes of coral host and/or endosymbionts (Baird et al. 2009, Barshis et al. 2010, LaJeunesse et al. 2010, Bellantuono et al. 2012). Many corals can host, exchange or shift algal symbiont composition to thermally resistant clades which may confer them distinct thermal tolerance in high-temperature habitats (Berkelmans and Oppen 2006, Oliver and Palumbi 2011). For

example, during warming events in the Pacific, corals that host specific members of *Symbiodinium* clade D, and to lesser extent C1 subtype, suffered less bleaching and mortality than those harboring different clades (Baker et al. 2004, Berkelmans and Oppen 2006, Oliver and Palumbi 2011) . Previous studies have suggested that members of stress-tolerant clade D may showed in higher proportions in hotter, higher-stress environments, and during different seasons (Jones et al. 2008, LaJeunesse et al. 2010, Oliver and Palumbi 2011, Barshis et al. 2013, Palumbi et al. 2014). Additionally, some scleractinian coral species may host multiple algal symbiont clades with the potential to shift towards thermal-stress tolerant ones when necessary(Oliver and Palumbi 2011). In fact, after natural bleaching events, some corals (e.g., *Acropora* spp. in the Pacific) can increase the density of thermal tolerant symbiont clades (Jones et al. 2008, LaJeunesse et al. 2010, Oliver and Palumbi 2011). However, not all coral species that resist thermal stress change symbiont composition with environmental conditions (LaJeunesse et al. 2010, Bellantuono et al. 2012). For example, hydrocorals such as *Millepora divaricata* are common in higher-temperature habitats in the Pacific but harbor a single symbiont type (Oliver and Palumbi 2011). This implies that although changes in symbiont composition may be important for certain coral species, other species can successfully acclimate to local high-frequency of thermal stress anomalies without changing algal symbiont identity(Bellantuono et al. 2012, Palumbi et al. 2014).

Acclimatization can be also achieved through physiological plasticity of the host and/or symbiotic algae in response to temperature anomalies (Bellantuono et al. 2012). Increasing the expression of certain genes that promote high protein turnover has been associated with thermal tolerance in the host by providing protection from bleaching without altering *Symbiodinium* dynamics (Palumbi et al. 2014). For example, acquire tolerance of preconditioned *Acropora*

*millepora* corals to thermal stress was not associated to changes in endosymbionts or bacterial community in experimental studies (Bellantuono et al. 2012). In fact, the aposymbiotic larvae of *A. millepora* show pronounced gene expression that leads to production of heat-shock proteins in response to thermal stress (Rodriguez-Lanetty et al. 2009). Similarly, exposure of *Orbicella franksi* to elevated temperature result in the upregulation of heat-shock HSP70 proteins (i.e., which are involved in protein folding processes) after 6 and 48 hours of heat stress (Edmunds and Gates 2008). Other experiments have shown that host genotypes of *Pocillopora damicornis* originating from non-upwelling thermal-stressed areas showed greater thermal tolerance than genotypes originating from upwelling areas that exhibit lower thermal stress regime (D’Croz and Maté 2004). Reciprocal transplant experiments of genetically distinct populations of *Porites lobata* between back-reef and forereef environments also demonstrate host physiological acclimatization to stress driven by colony genotype (Barshis et al. 2010). In this species, thermal tolerance of back-reef individuals was associated with higher levels of ubiquitin-conjugate proteins in response to highly fluctuating back reef environment (Barshis et al. 2010). On the other hand, differences in photo-acclimation of algae symbionts, by reductions of Chlorophyll-*a* or by dissipating excess excitation energy through non-photochemical pathways in response to elevated irradiance, may partially explain why fore-reef generalist corals such as *Orbicella annularis* are less thermally tolerant than back-reef weedy species such as *Siderastrea radians* (Warner et al. 1996) in the Caribbean.



### Appendix 4.3 References

- Baird, A. H., R. Bhagooli, P. J. Ralph, and S. Takahashi. 2009. Coral bleaching: the role of the host. *Trends in Ecology & Evolution* 24:16–20.
- Baker, A. C., C. J. Starger, T. R. McClanahan, and P. W. Glynn. 2004. Coral reefs: Corals' adaptive response to climate change. *Nature* 430:741–741.
- Barott, K. L., G. J. Williams, M. J. A. Vermeij, J. Harris, J. E. Smith, F. L. Rohwer, and S. A. Sandin. 2012. Natural history of coral–algae competition across a gradient of human activity in the Line Islands. *Marine Ecology Progress Series* 460:1–12.
- Barshis, D. J., J. T. Ladner, T. A. Oliver, F. O. Seneca, N. Traylor-Knowles, and S. R. Palumbi. 2013. Genomic basis for coral resilience to climate change. *Proceedings of the National Academy of Sciences*.
- Barshis, D. J., J. H. Stillman, R. D. Gates, R. J. Toonen, L. W. Smith, and C. Birkeland. 2010. Protein expression and genetic structure of the coral *Porites lobata* in an environmentally extreme Samoan back reef: does host genotype limit phenotypic plasticity? *Molecular Ecology* 19:1705–1720.
- Behrenfeld, M. J., and P. G. Falkowski. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and oceanography*:1–20.
- Bellantuono, A. J., O. Hoegh-Guldberg, and M. Rodriguez-Lanetty. 2012. Resistance to thermal stress in corals without changes in symbiont composition. *Proceedings of the Royal Society B: Biological Sciences* 279:1100–1107.
- Bellwood, D. R., A. S. Hoey, and T. P. Hughes. 2011. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B: Biological Sciences*.
- Berkelmans, R., and M. J. H. van Oppen. 2006. The role of zooxanthellae in the thermal tolerance of corals: a “nugget of hope” for coral reefs in an era of climate change. *Proceedings of the Royal Society B: Biological Sciences* 273:2305–2312.
- Budd, A. F., H. Fukami, N. D. Smith, and N. Knowlton. 2012. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society* 166:465–529.
- Chollett, I., and P. J. Mumby. 2012. Predicting the distribution of *Montastraea* reefs using wave exposure. *Coral Reefs* 31:493–503.
- Chollett, I., P. J. Mumby, F. E. Müller-Karger, and C. Hu. 2012. Physical environments of the Caribbean Sea. *Limnology and Oceanography* 57:1233–1244.

- Darling, E. S., L. Alvarez-Filip, T. A. Oliver, T. R. McClanahan, and I. M. Côté. 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters* 15:1378–1386.
- D’Croze, L., and J. L. Maté. 2004. Experimental responses to elevated water temperature in genotypes of the reef coral *Pocillopora damicornis* from upwelling and non-upwelling environments in Panama. *Coral Reefs* 23:473–483.
- Dulvy, N. K., R. P. Freckleton, and N. V. C. Polunin. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* 7:410–416.
- Edmunds, P. J., and R. D. Gates. 2008. Acclimatization in tropical reef corals. *Marine Ecology Progress Series* 361:307–310.
- Froese, R., and D. Pauly. 2013. FishBase. <http://www.fishbase.org>.
- Green, D., P. Edmunds, and R. Carpenter. 2008. Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Marine Ecology Progress Series* 359:1–10.
- Guest, J. R., A. H. Baird, J. A. Maynard, E. Muttaqin, A. J. Edwards, S. J. Campbell, K. Yewdall, Y. A. Affendi, and L. M. Chou. 2012. Contrasting Patterns of Coral Bleaching Susceptibility in 2010 Suggest an Adaptive Response to Thermal Stress. *PLoS ONE* 7:e33353.
- Harborne, A. R., P. J. Mumby, K. Żychaluk, J. D. Hedley, and P. G. Blackwell. 2011. Modeling the beta diversity of coral reefs. *Ecology* 87:2871–2881.
- Hoegh-Guldberg, O. 2012. The adaptation of coral reefs to climate change: Is the Red Queen being outpaced? *Scientia Marina* 76:403–408.
- Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nyström, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933.
- Jones, A. M., R. Berkelmans, M. J. H. van Oppen, J. C. Mieog, and W. Sinclair. 2008. A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization. *Proceedings of the Royal Society B: Biological Sciences* 275:1359–1365.
- LaJeunesse, T. C., R. Smith, M. Walther, J. Pinzón, D. T. Pettay, M. McGinley, M. Aschaffenburg, P. Medina-Rosas, A. L. Cupul-Magaña, A. L. Pérez, H. Reyes-Bonilla, and M. E. Warner. 2010. Host–symbiont recombination versus natural selection in the response of coral–dinoflagellate symbioses to environmental disturbance. *Proceedings of the Royal Society B: Biological Sciences*:rsob20100385.

- Lang, J. C., K. W. Marks, P. A. Kramer, P. Richards Kramer, and R. N. Ginsburg. 2010. AGRRA Protocols version 5.4 Atlantic and Gulf Rapid Reef Assessment Program. University of Miami, Florida.
- Latham, J., R. Cumani, I. Rosati, and M. Bloise. 2014. FAO Global Land Cover SHARE (GLC-SHARE) database Beta-Release Version 1.0-2014. FAO.
- McCauley, D. J., K. A. McLean, J. Bauer, H. S. Young, and F. Micheli. 2012. Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations. *Ecological Applications* 22:385–392.
- McCook, L. J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:357–367.
- Mora, C. 2008. A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society B: Biological Sciences* 275:767–773.
- Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, J. N. Sanchirico, K. Buch, S. Box, R. W. Stoffle, and A. B. Gill. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101.
- Mumby, P. J., A. R. Harborne, J. Williams, C. V. Kappel, D. R. Brumbaugh, F. Micheli, K. E. Holmes, C. P. Dahlgren, C. B. Paris, and P. G. Blackwell. 2007. Trophic cascade facilitates coral recruitment in a marine reserve. *Proceedings of the National Academy of Sciences* 104:8362–8367.
- Oliver, T. A., and S. R. Palumbi. 2011. Many corals host thermally resistant symbionts in high-temperature habitat. *Coral Reefs* 30:241–250.
- Oregon State University. 2013. Ocean Productivity: Online VGPM Data. <http://orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.vgpm.m.chl.m.sst4.php>.
- Palumbi, S. R., D. J. Barshis, N. Traylor-Knowles, and R. A. Bay. 2014. Mechanisms of reef coral resistance to future climate change. *Science*:1251336.
- Polunin, N. V. C., and C. M. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* 100:177–183.
- Rodriguez-Lanetty, M., S. Harii, and O. Hoegh-Guldberg. 2009. Early molecular responses of coral larvae to hyperthermal stress. *Molecular Ecology* 18:5101–5114.
- SEDAC, (Socioeconomic Data and Applications Center). 2010. Global rural-urban mapping project – settlement points. Columbia University, New York. <http://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-density/data-download>.
- UNEP-WCMC, WorldFish Centre, WRI, and TNC. 2010. Global distribution of warm-water coral reefs, compiled from multiple sources, including the Millennium Coral Reef

Mapping Project. UNEP World Conservation Monitoring Centre. Cambridge (UK).  
<http://data.unep-wcmc.org/datasets/13>.

Warner, M. E., W. K. Fitt, and G. W. Schmitt. 1996. The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: a novel approach. *Plant, Cell & Environment* 19:291–299.

Wilson, S., N. Graham, and N. Polunin. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology* 151:1069–1076.