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Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs

Running header: Consequences of parrotfish defaunation

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ABSTRACT

The unique traits of large animals often allow them to fulfill functional roles in ecosystems that small animals cannot. However, large animals are also at greater risk from human activities. Thus, it is critical to understand how losing large animals impacts ecosystem function. In the oceans, selective fishing for large animals alters the demographics and size-structure of numerous species. While the community-wide impacts of losing large animals is a major theme in terrestrial research, the ecological consequences of removing large animals from marine ecosystems remain understudied. Here, we combine survey data from 282 sites across the Caribbean with a field experiment to investigate how altering the size-structure of parrotfish populations impacts coral reef communities. We show that Caribbean-wide, parrotfish populations are skewed towards smaller individuals, with fishes <11 cm in length comprising nearly 70% of the population in the most heavily fished locations versus ~25% at minimally fished sites. Despite these differences in size-structure, sites had similar overall parrotfish biomass. As a result, algal cover was unrelated to parrotfish biomass and instead, was negatively correlated with the density of large parrotfishes. To mechanistically explore how large parrotfishes shape benthic communities, we manipulated fishes' access to the benthos to create three distinct fish communities with different size-structure. We found that excluding large or large and medium-sized parrotfishes did not alter overall parrotfish grazing rates but caused respective 4- and 10-fold increases in algal biomass. Unexpectedly, branching corals benefited from excluding large parrotfishes whereas the growth of mounding coral species was impaired. Similarly, removing large parrotfishes led to unexpected increases in coral recruitment that were absent when both large and medium bodied fishes were excluded. Our data highlight the unique roles of large parrotfishes in driving benthic dynamics on coral reefs and suggests that diversity of size is an important component of how herbivore diversity impacts ecosystem function on reefs. This study adds to a growing body of literature revealing the ecological ramifications of removing large animals from ecosystems and sheds new light on how fishing down the size-structure of parrotfish populations alters functional diversity to reshape benthic reef communities.

Keywords: defaunation, herbivory, corallivory, overexploitation, marine conservation, coral recruitment, phase shifts, functional diversity

INTRODUCTION

Body size is one of the most important traits for determining an animal's role in their ecosystem (Peters 1983, Owen-Smith 1988). Metabolism, digestive physiology, and feeding morphology vary with body size, making size fundamental in structuring consumer-resource interactions (Peters 1983, Petchey et al. 2008, Arim et al. 2010). Additionally, in many species territoriality, aggression, and competitive ability increases with an individual's size, further differentiating the ecological impacts of large versus small animals (e.g. Slotow et al. 2000, Shanks 2002). As a result, there are often functional differences both between different sized species and within species across ontogeny, with differences within species rivaling those between species (Rudolf and Rasmussen 2013, Rudolf et al. 2014). To account for this intraspecific variability, size-based approaches that ignore taxonomic identity and groups individuals by body mass can be used to

describe the dynamics and structure of communities (Marquet et al. 2005, Ings et al. 2009). This size-based approach relies on empirical work showing that body size is a key determinant of ecological interactions and that natural communities typically possess regular size-abundance relationships (Rudolf et al. 2014). Accordingly, changes in population size-structure, even without the loss of individual species, can have cascading effects throughout ecosystems (Garcia et al. 2012).

Currently, human activity is driving defaunation across the planet. In the past four decades, terrestrial vertebrates have experienced a mean decline of 28% in population size (Dirzo et al. 2014), often with concomitant declines in species' average body size (Gardner et al. 2011). In the oceans, these changes can be extreme. Every year for the past thirty years humans have removed ~80,000,000 metric tons of wild animals from the oceans, endangering approximately one third of commercially fished species and contributing to the global defaunation of marine ecosystems (Pauly et al. 1998, McCauley et al. 2015a, FAO 2018). However, fishing is a highly selective process and the use of specialized gear, combined with regulations on catch sizes and the desire to maximize returns on effort, have resulted in larger fishes facing disproportionately higher rates of mortality (Garcia et al. 2012). Consequently, fishing can profoundly impact the size-structure, sex ratios, and fecundity of entire populations (Zhou et al. 2010, Garcia et al. 2012). While the potential genetic and evolutionary ramifications of size-selective fishing have been recognized since at least the 1950's (e.g. Miller 1957, Handford et al. 1977, Allendorf et al. 2008), the ecological consequences of size-selective fishing have been difficult to study (Fenberg and Roy 2008). As a result, we are only beginning to understand how the defaunation of the largest members of fish populations impacts the community dynamics and ecosystem function of marine environments.

Our incomplete understanding of the consequences of size-selective fishing is particularly important for coral reefs, which already face severe declines due to a myriad of human-induced stressors (Harborne et al. 2017, Hughes et al. 2017). On coral reefs, grazing by herbivores is a primary driver of benthic community structure (Randall 1961, Ogden and Lobel 1978, Burkepile and Hay 2006, Adam et al. 2015). Parrotfish in particular are some of the most important reef herbivores (Bonaldo et al. 2014, Hoey and Bonaldo 2018), and on Caribbean reefs their importance has been amplified by the 1980's mass mortality of the long spine sea urchin *Diadema antillarum* (Lessios 1988). Parrotfish biomass is commonly used as a proxy for grazing pressure on reefs and declines in

parrotfish biomass can erode reef resilience and promote phase shifts from coral- to algae-dominated reefs (Hughes et al. 2007, Graham et al. 2015). Both theoretical and experimental work suggest that the response of benthic communities to declining herbivore biomass are non-linear and that tipping points exist where herbivory can no longer keep pace with algal growth and phase shifts occur (Scheffer et al. 2001, Holbrook et al. 2016, Schmitt et al. 2019).

However, this emphasis on herbivore biomass and grazing rates overlooks the potential differences in the functional roles associated with different sized fishes. In particular, ontogenetic changes in parrotfish morphology and diet selection allow the functional roles of parrotfish to change with size (Bonaldo and Bellwood 2008, Shantz et al. 2017), with larger individuals having greater influence on functions such as bioerosion, corallivory, and removal of certain species of macroalgae (Bonaldo and Bellwood 2008, Bellwood et al. 2012, Adam et al. 2018). Yet, despite extensive studies assessing the impact of herbivore removal on coral reefs (*e.g.* Lewis 1986, Hughes et al. 2007, Zaneveld et al. 2016), only a handful of studies have explored how altering the size-structure of herbivorous fishes impacts reef dynamics (McCauley et al. 2010, Steneck et al. 2014, Cernohorsky et al. 2015, Mumby et al. 2016).

Here, we examine how changes in the size-structure of parrotfish communities on Caribbean reefs impact benthic communities. First, we used data from fish and benthic communities from over 280 sites across the wider Caribbean to examine the relationships between parrotfish density, biomass, and size on the abundance of algae. Next, based on the observed distributions of parrotfish size, we conducted an experiment using size-based herbivore exclosures to mechanistically explore the impacts of size-selective fishing on coral reef benthic communities. To do so, we constructed exclosures with different sized openings to manipulate fishes' access to the benthos, creating three distinct herbivorous fish communities with different size-structures. We predicted that medium-sized parrotfishes, which are often macroalgal browsers, would limit palatable macroalgae but would be unable to offset the loss of unique functional roles carried out by large fishes, leading to benthic communities dominated by turf and heavily defended algae species. In contrast, we predicted that when only the smallest herbivores were present, mimicking size-structure of herbivore communities in some of the most heavily fished areas of the Caribbean, palatable macroalgae species would dominate benthic communities, reducing coral growth rates and increasing coral mortality.

METHODS

Caribbean Wide Patterns in Herbivore and Algal Communities

To explore patterns in herbivorous fish population size-structure across the Caribbean, we compiled data from the Atlantic and Gulf Rapid Reef Assessment fish surveys conducted between 2012 – 2017 (AGRRA 2017; see Appendix S1 for survey details). The AGRRA dataset contains over 20 years of basic standardized data on fish and benthic communities across the Caribbean, providing an extensive and under-utilized dataset for researchers. We extracted survey data on the biomass and size of parrotfish and surgeonfish, and the percent cover of algae and corals from AGRRA surveys conducted on forereef, bank reef, and subtidal reef crests between 3 – 30 m depth. Fish surveys were conducted by AGRRA trained divers who swam 30 x 2 m belt transect to record the species and size of every fish encountered in the survey area. Benthic surveys were conducted using a point-intercept method, recording the taxonomic identity or substrate type encountered by divers every 10 cm along 10 m transects. Detailed survey descriptions and protocol are available from AGRRA (<http://www.agrra.org>). Due to the challenging taxonomy of many algal species and potential bias introduced by the number of different surveyors, we used the sum of turf and macroalgae categories for our measurements of algal cover, rather than focusing on individual algal groups or species and risking observer bias from misclassification. For sites that had been surveyed multiple times during the 5-year time span, we only used the most recent survey data. To increase our coverage, we included our own survey data from the upper Florida Keys (Burkepile et al. 2013), which was collected in an identical manner along 25 x 4 m belt transects and converted to the same area and categories as the AGRRA data. For each country or territory where surveys occurred, we calculated the average biomass and density of parrotfishes and surgeonfishes in 10 cm size bins defined by AGRRA (<11, 11-20, 21-30, 31-40, >40cm) by pooling surveys from sites across the country.

Caribbean-wide Analyses

The Florida Keys National Marine Sanctuary (FKNMS) has been protected for over 25 years. Fish traps are prohibited and the FKNMS does not have an active parrotfish fishery, making it a useful, if somewhat conservative baseline for unfished Caribbean parrotfish communities. Therefore, to look for shifts in the size-structure that would be indicative of overfishing we used one-sided Mann-Whitney U-tests corrected for multiple comparisons to test whether the size frequency distribution of parrotfish populations across the Caribbean were significantly skewed towards smaller individuals than the Florida Keys population. Additionally, we used a generalized linear mixed effects model with a gamma distribution followed by Tukey's HSD post hoc comparisons to test for differences in parrotfish biomass between countries or territories. For this model we included a random effect for site to account for multiple transects within a site and added a negligible value (1g) to sites with zero biomass.

We used model selection to examine the relationships for parrotfish density, biomass, and size vs. algal cover across the Caribbean. We first modeled the algal cover at each site as a response to either the biomass or abundance of parrotfishes present. Because abundance does not explicitly account for parrotfish size-structure and a few large fishes could have the same biomass as numerous small fishes, we included two additional models that incorporated an interaction between average parrotfish length and biomass or abundance and biomass respectively. Since we could not identify whether benthic transects were conducted along the same transect lines as the fish transects, we used the average site-wide values for these models. All models included the country where each site is located, the survey depth, and the surgeonfish biomass at the site as random effects. However, because surgeonfish biomass did not account for any of the residual variance, this term was dropped from the models. We used AICc to determine the most parsimonious model and tested for significance against a null model that included only the random effects via a likelihood ratio test.

Size-selective Herbivore Exclusion Experiment

To mechanistically test the impacts of size-selective fishing on the benthos, we deployed eighteen, 1 x 1 x 0.9 m (length x width x height) fish exclosures at 6 – 8 m depth on a forereef near the Conch Reef Sanctuary Preservation Area in the Florida Keys National Marine Sanctuary

(24°57.695'W, 80°27.230'N). Each enclosure was constructed from a welded stainless-steel frame wrapped in plastic coated wire mesh (2.5 cm diameter mesh size). To manipulate the size distribution of fishes that could enter the enclosures, we cut openings of different sizes into the mesh to create six replicates each of: (i) Full enclosures with no additional openings cut into the mesh (2.5cm diameter holes) designed to exclude parrotfishes >10 cm total length; (ii) Partial enclosures with 7.5 cm diameter holes cut throughout the mesh designed to exclude parrotfishes > 20 cm; and (iii) Control enclosures with one 50 x 50 cm panel of mesh removed from each side and two removed from the top to allow access to all parrotfishes (see Appendix S1, Fig. S1 for schematic of experimental design).

Enclosures were deployed for 14 months beginning in July 2013 and scrubbed monthly to prevent fouling. Every two months, we deployed GoPro video cameras to film the enclosures and assess the efficacy of the treatments. During each camera deployment, we randomly selected three plots from each treatment to film, as well as haphazardly selected a 1 m² section of open benthos, hereafter referred to as External plots, to act as an unmanipulated control to test whether the structure created by Control enclosures impacted herbivory rates. The borders of the External plots were marked with 1/8" polyester rope stretched across the benthos and weighted down in each corner with a small diving weight and filmed in an identical manner as our treatments. For each camera deployment, plots were filmed for ~120 minutes, during which divers avoided the area until the cameras were recovered. Videos were scored to record the species, length, and number of bites taken by every fish ≥5 cm that fed within the plots. Due to the difficulty of tracking fishes <11 cm in the Full enclosures, we used the average bite rates of confamilial fishes <11 cm, calculated from recordings of the Control and Partial enclosures, to estimate their bites in the Full enclosures. Therefore, bite rates of fishes <11 cm in the Full enclosure treatments represent conservative estimates. We calculated the biomass of each herbivorous fish observed feeding using published length-weight relationships (Bohnsack and Harper 1988, Marks and Klomp 2003) and calculated biomass-corrected bite rates by multiplying each individual's weight by the number of bites they took (Holbrook et al. 2016). Based on their lengths, we binned fishes into 5 cm size classes and summed the bite rates and biomass-corrected bite rates from each video for each size class.

We tracked changes in the benthic community by surveying each plot before deploying our exclusion cages and every two months thereafter. During our initial surveys, we identified, tagged,

and photographed every coral >1 cm in diameter in each plot. In all subsequent surveys, we re-photographed each coral from the same position. We used ImageJ v1.5 to calculate the two-dimensional surface area of each colony and tracked changes in live surface area as a proxy for coral growth. Additionally, we estimated benthic cover during each survey by identifying canopy and understory organisms to the lowest taxonomic level possible below 100 points, spaced every 10 cm throughout each plot. Algal percent cover was calculated for each genus observed as well as binned into functional groups for groups with challenging taxonomy in the field (e.g., crustose coralline algae (CCA), filamentous turf algae) based on (Steneck 1988).

To assess coral recruitment, we deployed four limestone settlement tiles (10 x 10 x 1 cm, length x width x height) in every plot. Each tile was secured ~0.5 cm above the substrate on a single stainless-steel bolt and left in place for the full duration of the study. At the end of the experiment the tiles were photographed *in situ*. Each tile was then collected, placed in individual 4 l plastic bags with fresh seawater, and transported to the lab on ice. In the lab, macroalgae were removed from each tile, dried to a constant weight at 60° C, and weighed to estimate algal biomass. We then placed the algae-free tiles in a 10% bleach solution for 24 hours and examined each under a dissecting microscope to count the number of coral recruits present.

Exclusion Experiment Analyses

To determine whether the structure created by the exclusion cages influenced herbivory, we tested for differences in the size distribution of fishes feeding in our Control and External plots via Mann Whitney U-tests. Additionally, we used linear mixed-effects models that included date as a random effect to test for differences in the bite rates and biomass corrected bite rates of parrotfishes and surgeonfishes in the Control and External plots. Because we detected no significant differences in any of these tests (see Supplemental Results in Appendix S1) we only include the Control, Partial, and Full exclosures in all the remaining analyses.

To assess the efficacy of our treatments in altering population size-structure we tested for differences in the size distribution of fishes feeding between each treatment using Mann-Whitney U-

tests. To understand how these differences in size-structure impacted herbivory, we used linear mixed-effects models similar to those described above to test for differences in the bite rates and biomass-corrected bite rates among treatments. Thus, each model included treatment as a fixed factor with three levels (Full, Partial, and Control) and plot number and date as random effects to account for repeated measurements of the same plots and lack of independence between plots filmed on the same day. Because surgeonfish have deeper bodies than parrotfish of the same length, we expected the size-structure of fishes that could access our enclosures to differ between the two families. Therefore, for all our tests of herbivore access and grazing within our enclosures, surgeonfishes and parrotfishes were examined independently. Both bite rates and biomass-corrected bite rates were square root transformed to conform to assumptions of parametric statistics. When significant treatment differences were detected, we used Tukey's HSD post hoc analyses to identify differences between treatments.

To analyze how excluding different sized fishes impacted benthic communities, we calculated Bray-Curtis dissimilarity indices based on the percent cover of benthic organisms from our surveys. At each timepoint, we used ANOSIM to test for differences in the benthic community among treatments and plotted the differences in non-metric, multidimensional space. We tested how total algae cover, articulated calcareous algae, and turf, as well as the most common components of the algal community in the treatments, *Dictyota* spp., and *Sargassum* spp. changed through time using linear mixed effects models with date and treatment as interacting fixed effects and plot as a random effect to account for repeated measures. For all these models, we logit transformed the response variable to conform to assumptions of normality. However, even after transformation the distribution of residuals from our models of *Dictyota* spp. and *Sargassum* spp. deviated from normality and p-values should be interpreted with caution. At the culmination of the study we calculated the species diversity of the algal community and tested for differences between treatments via ANOVA. Additionally, we tested for differences in total algal biomass among treatments via a linear mixed-effects model that used the dried algal biomass collected from our settlement tiles as a response variable, treatment as a fixed effect, and a random intercept for plot number.

Algae can have detrimental effects on coral (Tanner 1995, Lirman 2001, Zaneveld et al. 2016), but branching coral species that can grow upward to overtop and grow away from algal competitors

may be more resistant to algal competition (Meesters et al. 1996). Therefore, to test how herbivore size affected coral growth we used a linear mixed effects model that included an interaction between treatment and coral colony morphology (branching versus encrusting/mounding) as fixed effects and plot as a random effect. To determine whether algae mediated the effects of parrotfish size on the coral growth, we regressed the average change in area of branching or mounding and encrusting morphologies from each exclusion against the respective final percent cover of macroalgae. Additionally, we used a generalized linear mixed-effects model (GLMM) with a binomial distribution to test for differences in the survival of coral colonies in each treatment, again including an interaction with coral morphology.

Parrotfish also influence the survival of coral larvae directly by consuming settlers while feeding (Nozawa 2008) and indirectly via their effects on the algal community (Kuffner *et al.* 2006). Therefore, we used a GLMM with a Poisson distribution to test the impact of treatment and algal biomass on coral recruitment. For this model, we regressed the number of recruits on our settlement tiles against the algal biomass on the tile, including an interaction with treatment and random effect for plot number to account for multiple tiles in each plot.

All analyses were conducted in R v3.4.1 (R Core Team 2017). Generalized mixed effects models and linear mixed effects models were analyzed using the lme4 package (Bates et al. 2015). We used the Vegan package (Oksanen et al. 2019) for ANOSIM. All data are presented as means \pm 1 standard error.

RESULTS

Caribbean-wide Patterns in Parrotfish Size-structure and Algal Cover

Across the Caribbean, the size-structure of parrotfish populations was heavily skewed towards small individuals (Fig. 1a). The Turks and Caicos Islands were the only territory we examined where the size-distribution of parrotfishes was similar to the protected population in the Florida Keys (Appendix S1, Table S1; Figs 1a & b). However, despite the significantly smaller size-distributions of parrotfish across the Caribbean, overall parrotfish biomass in the Florida Keys did not differ

significantly from any of the other Caribbean countries or territories examined (Fig. 1b; Appendix S1, Table S2).

Model selection indicated that parrotfish density provided the most parsimonious explanation of algal cover across the Caribbean, accounting for 29% of the observed variance in algal cover ($R^2_m = 0.06$; Table 1). However, contrary to our expectations algal cover was positively correlated with parrotfish density in this model (Fig. 2a). In contrast, our model that included the interaction between parrotfish density and average parrotfish size performed equally well ($\Delta AICc = 1.47$). Furthermore, the fixed factors in this model explained slightly more of the observed variance ($R^2_m = 0.08$) and suggested a significant decline in algal cover as the average length and density of parrotfishes increased, (LRT $\chi^2(3) = 15.573$, $p = 0.001$; Fig. 2b). Thus, when not accounting for size algal cover increased with parrotfish density but when parrotfish size was included, this pattern reversed, and algal cover declined as the density of larger parrotfishes increased. Surprisingly, parrotfish biomass, which is commonly used as a proxy for herbivory on reefs, showed no correlation with algal cover (Fig. 2c).

Size-selective Herbivore Exclusion Experiment

Our exclusion cages created significant differences in the size-structure of fishes feeding in each treatment (Fig. 3a, Appendix S1, Table S3). Parrotfishes >30 cm length never fed in the Full or Partial exclosures. Although fish in these size classes averaged just under 2 bites•hour⁻¹ in the Control exclosures, this equated to ~1,500 g•bites•hour⁻¹, or ~30% of the average biomass-corrected parrotfish feeding in these plots. Similarly, over the entire year only a single parrotfish >25 cm fed in our Partial exclosures (due to a brief breach in the mesh at the beginning of the experiment), whereas parrotfishes between 26-30 cm averaged 2.87 ± 1.22 bites•hour⁻¹ (~600–1,400 g•bites•hour⁻¹) in Control exclosures. The largest of surgeonfishes we observed were 26 - 30 cm in length and only fed in Control exclosures. For surgeonfishes <26 cm, grazing was similar in the Control exclosures and Partial exclosures (Appendix S1, Fig. S3). However, due to their deeper bodies, no surgeonfishes >10cm fed in the Full exclosures.

Despite the altered size-structure, overall bite rates did not differ between treatments for parrotfishes or surgeonfishes (Fig. 3b). In contrast, there were significant differences in parrotfish biomass-corrected bite rates between treatments ($\chi^2(2) = 24.912$, $p < 0.001$; Fig. 3c). Biomass-corrected grazing for parrotfishes was significantly higher in Control enclosures than Partial enclosures (Tukey's HSD: $t = 3.742$, $p = 0.014$) and Full enclosures ($t = 4.535$, $p = 0.001$) but did not differ between Partial and Full enclosures ($t = 1.466$, $p = 0.334$). Biomass corrected bite rates for surgeonfishes were more variable and did not differ between the Control and Partial enclosures but were so low as to preclude analysis in the Full enclosures (Fig. 3c).

Full enclosures also caused a slight decline in the diversity of parrotfishes feeding within the plots (Fig. 3a). In Control enclosures, 8 of the 11 parrotfish species in the region were recorded feeding versus just 6 species in the Partial and Full enclosures. *Scarus guacamaia* and *Sc. coeruleus*, two of the largest species in the region, accounted for ~12 and 17% of the biomass-corrected bites in Control enclosures respectively but never fed in the Partial or Full enclosures. Similarly, *Sparisoma rubripinne* was responsible for nearly 35% of biomass-corrected bites in Control enclosures but <2% of biomass-corrected bites in Partial and Full enclosures. In response to exclusion of these larger species, smaller species appeared to compensate for some of these declines in grazing. For instance, biomass-corrected bite rates for *Sp. aurofrenatum* were 150% higher in Partial enclosures compared to Control enclosures.

Effects on Algal Community Structure

Restricting the size of fishes that could access our plots substantially changed the benthic community. When we deployed our cages in July of 2013, benthic communities were indistinguishable among the three treatments ($R = -0.078$, $p = 0.876$). After just two months, the communities began to differentiate, with Full enclosures differing from Controls ($R = 0.29$, $p = 0.002$). By November 2013, each treatment had developed distinct benthic communities that remained significantly different throughout the remainder of the experiment (Fig 4a). By the end of the experiment there was an average of 14 macroalgal species in Control enclosures versus 22 in Partial enclosures and 32 in Full enclosures ($F_{2,15} = 77.031$, $p < 0.001$; Fig 4b). Restricting large herbivore

access also caused a significant increase in total algal biomass ($\chi^2(2) = 72.331$; $p < 0.001$), with 4x more algae in Partial exclosures and 10x more in Full exclosures than in Controls (Fig 4c).

Changes in both algal composition and abundance were responsible for driving the differences between treatments in benthic communities. Upright algal cover was highest in the Full exclosures, followed by the Partial exclosures, and finally the Control plots ($\chi^2(12) = 81.958$; $p < 0.001$; Fig 5a). Articulated calcareous algae proliferated in both Partial and Full exclosures, remaining significantly higher than in Control exclosures throughout the study but showing seasonal dynamics between the Partial and Full exclosures that suggest competition with other algae was important in mediating these patterns ($\chi^2(12) = 66.035$; $p < 0.001$; Fig 5b). Filamentous turf algae showed the opposite pattern, slowly declining in the Full exclosures while peaking in the Control exclosures, suggesting algal competition may have suppressed turf cover in Partial and Full exclosures ($\chi^2(12) = 74.264$; $p < 0.001$; 5c). When examining the most common algal genera, *Acanthophora* spp. increased dramatically in Full exclosures but remained so low in both Partial and Control exclosures as to preclude analysis (Fig. 5d). In contrast, unpalatable *Dictyota* spp. declined from summer to winter in all our treatments before diverging the following summer, with the percent cover in our Control exclosures returning to previous levels but remaining significantly depressed in Partial and Full exclosures ($\chi^2(12) = 33.477$; $p = 0.001$; Fig 5e). This pattern contrasted with *Sargassum* spp. ($\chi^2(12) = 47.847$; $p < 0.001$; Fig 5f), which showed the opposite trend, again suggesting an interaction between herbivory and algal competition mediates benthic communities.

Effects on Coral Growth and Recruitment

Across treatments, the coral community consisted primarily of branching *Porites* spp., encrusting *Agaricia* spp., and mounding *Porites*, *Orbicella*, *Montastraea*, and *Siderastrea* spp. Coral growth was influenced by the interaction between colony morphology and exclusion treatment ($\chi^2(2) = 6.883$, $p = 0.032$). In Control exclosures, mounding and encrusting coral species grew by ~25% over the course of the experiment whereas branching morphologies lost ~27% of their live tissue area (Fig. 6a). In contrast, when large parrotfishes were excluded in the Partial exclosures, branching corals grew by roughly 43% while mounding and encrusting morphologies did not grow appreciably.

In the Full enclosures, branching corals did not grow, on average, but the data were extremely variable. In contrast, mounding and encrusting species in the Full enclosures declined in size by ~12%. For branching morphologies, the percent cover of algae had no effect on the average change in live tissue area ($F_{(1,13)} = 0.379$; $p = 0.55$) but there was a marginal decline in the live tissue on mounding and encrusting corals as algal cover increased ($F_{(1,15)} = 3.972$; $p = 0.064$; Fig. 6b).

Finally, we found a significant effect of herbivore access on coral recruitment. Recruits were more abundant in Partial enclosures than in Control enclosures, with Full enclosures showing an intermediate effect on coral recruits ($\chi^2(5) = 18.3$, $p = 0.003$; Fig. 6c). We also found a significant interaction between algal biomass and enclosure treatment on coral recruitment (Fig. 6c). In Full enclosures, coral recruitment declined as algal biomass increased. Yet, for Control and Partial enclosures, there was no relationship between algal biomass and the abundance of coral recruits, likely due to the restricted range of algal biomass in these treatments.

DISCUSSION

Defaunation is a pervasive consequence of human activity (Estes et al. 2011, Dirzo et al. 2014, McCauley et al. 2015b), and large animals, particularly herbivores, have experienced some of the greatest declines. The ecological ramifications of losing the largest herbivores on community dynamics has become a major emphasis in terrestrial ecology (e.g. Ripple et al. 2015a, Bakker et al. 2016a, Burkepile et al. 2017). By comparison, relatively few studies have assessed how removing large herbivores affects community dynamics in marine ecosystems, with most of the focus on marine mammals (e.g. dugongs and manatees) or sea turtles (Christianen et al. 2012, Bakker et al. 2016b).

Here, we show that across the Caribbean, populations of parrotfish, the largest herbivorous fishes on tropical reefs, are heavily skewed towards smaller individuals. Caribbean-wide, this loss of large parrotfishes, but not parrotfish biomass, correlates with increases in algal abundance. Furthermore, using a manipulative experiment, we show that removing large parrotfishes increases macroalgal abundance and diversity and decreases the growth of massive, reef-building corals. Interestingly, maintaining intermediate sized fishes mitigates some of these adverse effects, limiting

the increase in macroalgae species richness and biomass and moderating the decline in growth of mounding corals. Mechanistically, our experiment suggests that the loss of the largest parrotfishes does not affect reef benthic communities by reducing bite rates on the benthos, but instead eliminates the unique functional roles carried out by these fishes. Our study adds to the growing body of literature revealing the ecological ramifications of losing large animals and sheds new light on how fishing down the size-structure of parrotfish populations alters the benthic dynamics of coral reefs.

Unique Impacts of Large Parrotfishes on Algal Community Dynamics

The shifts in size-structure of parrotfish communities on reefs across the Caribbean are striking. Compared to our protected reference reefs in the Florida Keys, parrotfishes <11 cm in length were 2-15x more abundant in all but three of the other Caribbean regions we studied. Small parrotfishes often increase in abundance when large individuals are overfished (Hawkins and Roberts 2004, Bellwood et al. 2012), and the areas in our study where small fishes were abundant are historically some of the most heavily fished reefs in the Caribbean (Vallès and Oxenford 2014). Unexpectedly, we found that the greater abundance of small parrotfishes often compensated for the biomass lost from harvesting larger fishes, resulting in few differences in biomass across reefs with widely varying size-structure. In the most striking example, parrotfish populations around Haiti were the most heavily skewed towards small individuals yet had comparable parrotfish biomass to the Florida Keys where large individuals are abundant ($\sim 1,973 \pm 136$ g 100 m⁻² versus $1,678 \pm 349$ g 100 m⁻², respectively).

Parrotfish biomass is often considered critical for mediating algal abundance and is used as an indicator of a reefs' ability to recover after disturbances (Hughes et al. 2007, Mumby et al. 2007, MacNeil et al. 2015). Yet, other studies show no relationship between herbivore biomass and algal abundance or coral dynamics (Russ et al. 2015, Suchley et al. 2016). In this study, we found no relationship between parrotfish biomass and algal cover across 249 sites (Fig. 2c). Instead, an interaction between parrotfish density and average parrotfish size explained the most variance in algal cover across the Caribbean, with an $\sim 0.5\%$ decline in algal cover for every 1 cm increase in average parrotfish length (Fig. 2b). After accounting for reef depth and regional location, this model explained

27% of the total variance in algal cover. A large portion of the unexplained variance was likely due to differences between sites in factors such as water quality, coral cover, or disturbance history (e.g. storms, bleaching), all of which can strongly influence algal cover. Differences in the abundance of invertebrate herbivores such as *Diadema*, which have shown incomplete but spotty recovery in some regions, could also account for some of the unexplained variance (Idjadi et al. 2010). Unfortunately, the standardized AGRRA surveys do not provide the specific details on disturbance history or abiotic conditions at each site that would be needed to resolve less prominent drivers of benthic dynamics. However, collectively our study suggests that without accounting for population size-structure, parrotfish biomass may be an unreliable indicator of top-down pressure and reef resilience. This conclusion is supported by examples from the literature. For instance, following disturbances in Micronesia, herbivore size was a consistently better predictor of community resilience than herbivore biomass (Houk et al. 2014). Thus, larger parrotfishes likely play unique and underappreciated roles in community dynamics.

Our field experiments complement our Caribbean-wide analyses to reveal the importance of parrotfish size in shaping benthic communities. Several mechanisms may contribute to these functional differences across fish size. For example, larger parrotfish with more robust jaw morphology can eat food that smaller fishes are physically incapable of consuming (Bellwood and Choat 1990). Furthermore, parrotfish bite size increases with fish length (Adam et al. 2018) so that larger fishes consume more algae with a single bite. This increased bite size may also result in the incidental removal of non-target species such as unpalatable macroalgae that smaller fishes avoid, as the feeding morphology of large herbivores can physically constrain their ability to selectively target individual resources (Pollard and Cooke 1994, Scott et al. 2018). In fact, many parrotfish species appear to be microphages that target cyanobacteria and other autotrophic microorganisms living on or within the algae and substrate they consume, suggesting the majority of macroalgae consumption by parrotfishes may be incidental (Clements et al. 2016).

Large herbivores can also substantially modify community structure by physically altering their environment as they feed, simultaneously creating and destroying habitat for other species (Bakker et al. 2016a). Feeding by parrotfishes often excavates the benthos and opens bare substrate for colonization (Hoey 2018). Importantly, these regular disturbances could favor algae, especially

filamentous algae, with ruderal life histories that are more likely to be palatable to other herbivores (Steneck and Dethier 1994) rather than competitively dominant species that develop in undisturbed habitats (Grime 1988). The role of grazing in resetting algal succession on reefs was recognized by (Birkeland et al. 1985) yet the importance of herbivore size in this process has remained untested. While parrotfishes as small as 5 cm can leave grazing scars, the frequency with which bites create grazing scars increases with size and significant excavation of substrate does not occur until fishes exceed ~20 cm (Bruggemann et al. 1996, Lokrantz et al. 2008, Adam et al. 2018). This threshold is also the size at which our Partial enclosures began limiting parrotfish access and algal communities became dominated by heavily calcified, articulated algae (Fig. 5). Thus, in addition to feeding on algae, the physical disturbance of the benthos by large parrotfishes may be a critical component of their ability to control less palatable macroalgae species.

Interestingly, while larger parrotfishes were essential for controlling algae in our experiment, another recent study showed grazing by fishes <22.5 cm was sufficient to prevent algal proliferation over four months on a shallow backreef in the Indian Ocean (Cernohorsky et al. 2015). These contrasting results could be due to differences in study duration, with our longer study allowing for the succession of algal communities. Alternatively, differences in habitat (backreef versus forereef) or functional differences in the herbivore communities present in the two regions could have contributed to the disparate effects of excluding herbivores. For instance, restricting large fishes' access to settlement tiles in the Atlantic caused larger increases in algal biomass than an identical experiment in the Pacific (Steneck et al. 2014, Mumby et al. 2016). Thus, it will be important to consider how regional species diversity and environmental context influence the importance of parrotfish size.

Complex Relationships Between Large Parrotfish and Coral Communities

Parrotfish of almost every size consume algae but only the largest parrotfishes frequently prey on live coral (Rotjan and Lewis 2008). While the benefits to corals from parrotfish removing algal competitors are assumed to outweigh the costs of parrotfish corallivory (Mumby 2009), our data suggest that this relationship is complex and depends on coral morphology. For example, branching *Porites* spp. are a favored prey of Caribbean parrotfishes (Burkepile 2012) and parrotfish corallivory

can completely extirpate *P. divaricata* from some reefs and impair *P. porites* growth as much as algal competition (Miller and Hay 1998). Accordingly, the loss of large parrotfishes appeared to benefit branching *Porites* spp. by reducing corallivory, as these species lost tissue in Control enclosures but grew significantly larger in Partial enclosures. However, when medium-sized fishes were excluded and only the smallest herbivores were present, proliferation of algal competitors appeared to offset any benefits of reduced corallivory for branching species as they merely maintained their size in the Full enclosures. Notably, this tradeoff between herbivory and corallivory by large parrotfishes may not be present for *Acropora* spp., which are some of the most important branching corals in the Caribbean, since parrotfishes rarely, if ever, feed on *Acropora* (Burkepile 2012). Thus, large parrotfishes may play an important role in facilitating crucial *Acropora* spp. while negatively impacting other branching coral species.

In contrast to branching corals, mounding corals benefitted from the presence of the largest parrotfishes, despite potential corallivory. Mounding corals typically recover quickly from most parrotfish bite wounds (Bonaldo and Bellwood 2011, Bonaldo et al. 2011) but are often susceptible to the negative effects of algal competition (Vega Thurber et al. 2012). In our study, mounding and encrusting species only lost tissue when both large and intermediate sized parrotfishes were excluded and algal cover was high. Furthermore, we found a marginally significant decline in growth for mounding and encrusting corals with increasing algal cover within the plots (Fig 6b). Thus, the positive effect of large parrotfishes on mounding corals was likely due to limiting algal competition. Because mounding coral species comprise some of the most important reef-building species in the Caribbean, such as *Orbicella*, *Siderastrea*, and *Montastraea*, the loss of large parrotfishes may be particularly detrimental for reef accretion.

Eliminating large fishes also influenced coral recruitment in complex ways. In the Full enclosures, the increase in algal abundance appeared to inhibit coral recruitment, consistent with other studies showing algae impair recruitment (Kuffner et al. 2006, Bulleri et al. 2018); Fig. 5b). In contrast, the Partial enclosures had roughly 4X the algal biomass of the Control enclosures, but recruitment in these plots was over two times greater than in the Control enclosures, suggesting that the presence of large parrotfishes in Control plots suppressed coral recruitment. These findings are

also consistent with previous studies showing that intense parrotfish grazing impairs coral recruitment through incidental or even intentional consumption of recruits (Nozawa 2008, Edmunds et al. 2014).

However, because we counted recruits from the skeletons on bleached settlement tiles at the end of our experiment, it is difficult to make inferences regarding the survival of coral recruits in the different treatments. Importantly, algae reduce coral recruitment by preventing settlement but also reduce the survival of corals that do recruit (e.g. Rasher *et al.* 2011; Smith *et al.* 2006). Furthermore, the skeletons of these dead recruits likely remain visible in the absence of bioeroding parrotfishes. Therefore, the greater number of coral recruits in our Partial exclosures may not have actually led to an increase in successful recruitment if the increased algal biomass resulted in higher rates of mortality. Similarly, the coral recruits we counted in the Full exclosures may not have reflected successful recruitment as these corals may have died due to intense algal competition in these low herbivory regimes. Notably, (McCauley et al. 2010) found that coral recruitment on the reefs of Palmyra Atoll was initially higher when fishes were excluded but the number of newly settled and surviving recruits dropped quickly over time and, by 4 months, did not differ from open plots. Together these data suggest that large parrotfishes may reduce initial recruitment rates due to incidental, or even intentional predation, on recently settled corals, but their presence likely increases overall coral survivorship and growth by limiting competition with algae over the long term.

The Role of Large Herbivores in Ecosystem Function

Across ecosystems, herbivore species diversity is often emphasized as an important driver of community dynamics and ecosystem function (Burkepile 2013, Lefcheck et al. 2015). On coral reefs, more species diverse herbivore assemblages increase overall herbivory rates and can consume a broader suite of macroalgae. In turn, this greater level of top-down control benefits corals and facilitates reef resilience after disturbances (Burkepile and Hay 2008, Cheal et al. 2010). Here, our data suggests that the diversity of sizes of herbivorous fishes may be an important component of how herbivore diversity impacts ecosystem function of coral reefs. Restricting fish size reduced the species diversity of parrotfishes feeding within the plots, as some species, such as *Scarus coeruleus* and *Sc. guacamaia*, were only observed feeding in our Control exclosures. Importantly, both of these species

spend their immature life-stages in mangroves and seagrass beds before migrating to the reef as adults (Nagelkerken and van der Velde 2003), making the presence of small individuals on reefs extremely rare. In fact, in the 2,581 transects we analyzed from across the Caribbean, only two *Sc. guacamaia* and four *Sc. coeruleus* < 20 cm in length were observed on forereef sites. Thus, size-selective fishing is particularly likely to extirpate species that undergo ontogenetic shifts in habitat and move to the reef as adults. Interestingly, there were no differences in the parrotfish species diversity or biomass corrected grazing rates between our Partial and Full Enclosures (Fig. 3) but the algal communities within the two treatments differed substantially (Fig. 4), suggesting different sized fishes of the same species carry out different functional roles that strongly impact community dynamics.

Previous studies have identified larger parrotfish species or larger individuals of specific species that feed in unique ways, cover larger territories, or simply target different foods (Bruggemann et al. 1996, Bonaldo and Bellwood 2008, Adam et al. 2018). Each of these traits can influence the functional niche that parrotfishes fill, creating varying degrees of functional redundancy and complementarity within and between species. For instance, after a bleaching event in the Seychelles, the loss of habitat caused small parrotfish populations to decline but large parrotfish populations were unaffected. As a result, size-based differences in habitat requirements proved to be a critical element of fishes functional diversity and reefs where large roving parrotfishes were present prior to bleaching were more likely to recover (Nash et al. 2016). However, there is still much to be learned about the impact of losing the largest parrotfishes on coral reefs.

Although increases in the number of small fishes on overfished reefs may help compensate for the loss of herbivore biomass (e.g. (Kuempel and Altieri 2017), small individuals cannot replace the functional roles that are lost when larger parrotfishes are extirpated. Future studies will be needed to determine the minimum parrotfish size required to maintain functional diversity, but our results indicate it will require protecting fishes >20 cm in length. Given the unique physiological, evolutionary, and ecological roles that large fishes play in ecosystems, managing fishing pressure via size-based regulations that allow harvest of the largest fishes may be selectively removing some of the most ecologically important individuals. Similarly, temporary closures that are based on fish biomass are likely to be ineffective at protecting functionally important large individuals, as biomass can recover quickly whereas it can take decades characteristics such as maximum fish size to return to

baseline levels (McClanahan and Graham 2015). Consequently, many authors have advocated size-based metrics to manage fisheries (Johannes 1998, Shin et al. 2005) and moving towards slot-based regulations or balanced harvesting strategies may be an effective method of mitigating the adverse consequences of fishing on ecosystem function (Garcia et al. 2012).

As defaunation accelerates, larger herbivores are often among the first species lost (Ripple et al. 2015b). Our data joins a growing body of literature across ecosystems showing that these large animals play unique, often irreplaceable, roles in community dynamics and ecosystem function. For example, in African savannas, elephants (*Loxodonta africana*) are ecosystem engineers that knock down trees creating habitat heterogeneity (Owen-Smith 1988). While white rhinoceros (*Ceratotherium simum*) and hippopotamus (*Hippopotamus amphibius*) create short-grass grazing lawns which can facilitate grazing and nutrient acquisition by smaller herbivores (Waldram et al. 2008, Cromsigt and te Beest 2014). Parallel processes are likely to take place in the oceans but compared to terrestrial ecosystems, far less is known about the ecosystem-wide consequences of losing large herbivores in marine systems. Recent work has shown the powerful impact of manatees, dugongs, and turtles in seagrass ecosystems (Burkholder et al. 2013, Christianen et al. 2019) while the loss of the largest parrotfish, *Bolbometopon muricatum*, correlates with reduced rates of bioerosion across the Indo-Pacific (Bellwood et al. 2012). Our work here strongly supports the growing realization that size-biased removal of large parrotfishes has major impacts on coral reef community dynamics at both local and regional scales. While parrotfishes may not rival other megaherbivores in terms of sheer mass, the body size of reef fishes changes by orders of magnitude as they grow, making adult parrotfishes by far the largest herbivores on reefs and far larger than most reef grazers and the resources they consume. Accordingly, when these large herbivores are lost, their outsized roles in ecosystems often disappear with them.

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Data Availability

Data are available on the Dryad Digital Repository: <https://doi.org/10.5061/dryad.70rxwdbsz>

Table 1: AICc results from model selection assessing the relationship between the average percent cover of macroalgae at sites across the Caribbean and characteristics of the parrotfish community. R_m^2 is the variance explained by the fixed effect alone while R_c^2 is the variance explained by the fixed effect, depth of the site, and country in which each site is located. Models with a ΔAICc value <2 are considered to perform equally well.

Model	d.f.	AICc	ΔAICc	R_m^2	R_c^2
Parrotfish Density	6	2012.78	0	0.06	0.29
Parrotfish Density x Proportion $>20\text{cm}$	8	2014.25	1.47	0.08	0.27
Parrotfish Biomass x Proportion $>20\text{cm}$	8	2016.14	3.36	0.06	0.24
Null	5	2023.52	10.74	0.00	0.23
Parrotfish Biomass	6	2024.98	12.1	0.00	0.24

Figure Legend:

Figure 1: **(a)** Histograms of the density of parrotfish in 10 cm size bins surveyed by AGRRA divers across the Caribbean. Density ranges from zero to 50 and the scales in all panels are identical to the axes on panel 1. **(b)** Parrotfish biomass averaged from sites within each country. Letters indicate significant differences between the countries. Error bars are ± 1 SE.

Figure 2: Average percent cover of macroalgae at each site plotted against the density of parrotfish **(a)**, average length and density of parrotfish **(b)**, and average parrotfish biomass **(c)** at each site. Marginal R^2 values are provided and indicate the amount of variance explained by fixed effects in the models.

Figure 3: **(a)** The average biomass-corrected bites per hour measured for different sized parrotfishes recorded on video feeding within our different exclusion treatments. Biomass-corrected bite rates were calculated by multiplying the number of bites that a fish took within a given treatment by the fish's weight. Illustrations represent the community size-structure created by the treatments **(b)** Average bites per hour taken by surgeonfishes and parrotfishes recorded feeding in each of the three treatments. **(c)** Biomass-corrected bite rates for all surgeonfishes and parrotfishes recorded feeding within the treatments. Note, for surgeonfishes our analysis only compared Control and Partial exclosures as the extremely low biomass-corrected bite rates in Full exclosures precluded including this treatment. Letters indicated significant differences based on Tukey's HSD post hoc analysis of our linear mixed effects models. Error bars are ± 1 SE.

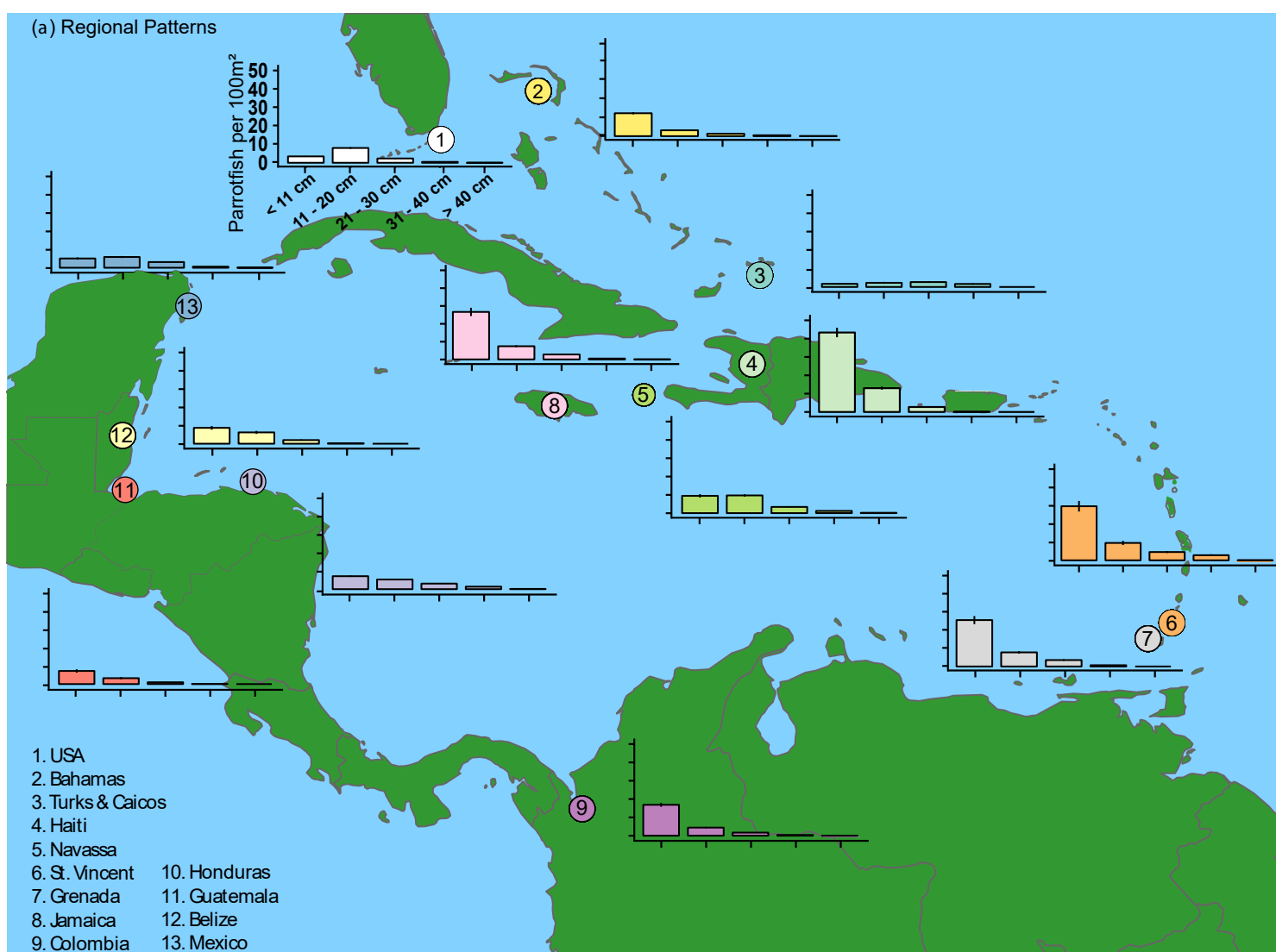
Figure 4: **(a)** Results from Nonmetric multidimensional scaling tracking changes in the benthic community within each of the exclusion treatments through time. Triangles represent the position of the initial communities measured in July 2013 at the start of the experiment. Squares indicate the final community measured in September 2014. Grey arrows show the loadings for each respective component of the benthic community. **(b)** The number of macroalgae species present within each of

the enclosure treatments in September 2014 at the conclusion of our caging experiment. **(c)** The average final dried algal biomass measured from 24, 10 cm x 10 cm settlement tiles placed in each treatment. Letters represent significant differences between treatments. Error bars are ± 1 SE.

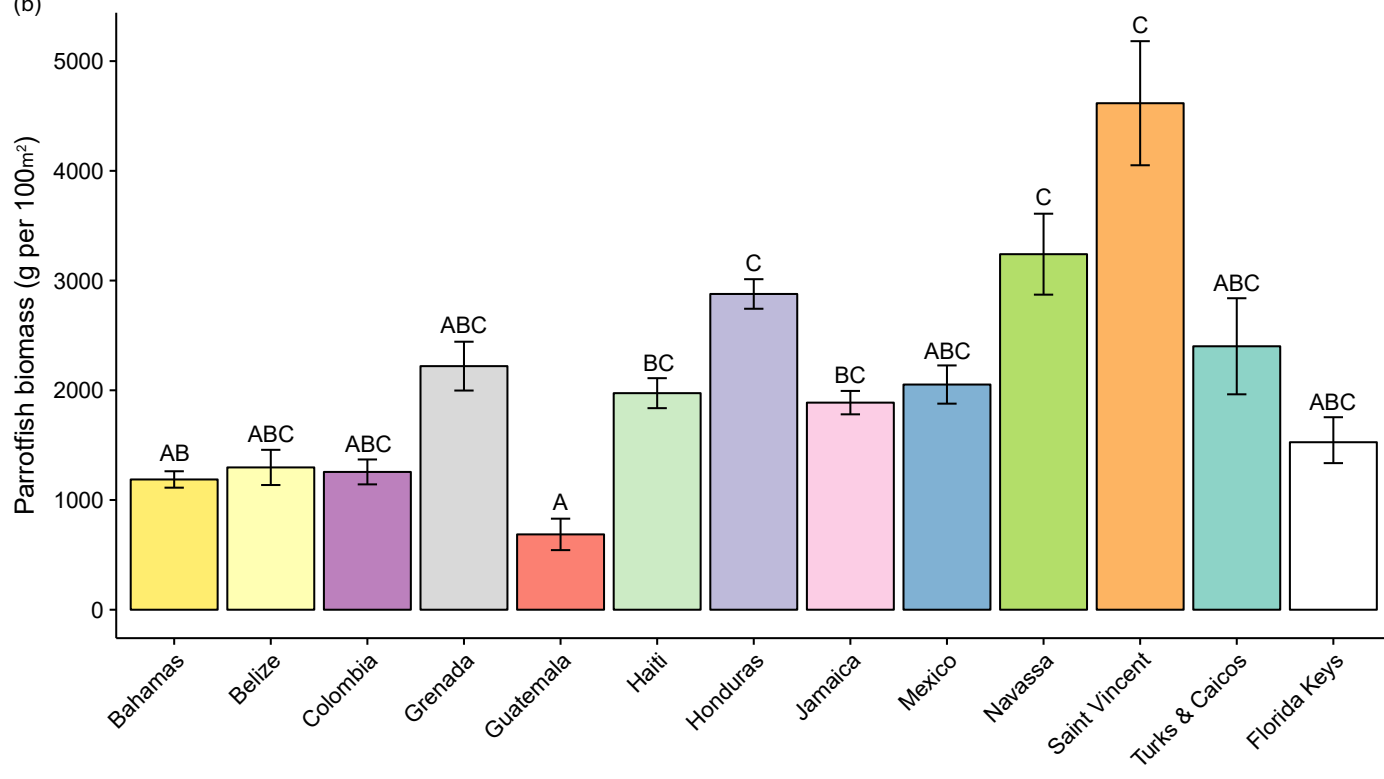
Figure 5: Changes in the percent cover of different groups (a, b, & c) and species (d, e, f) of macroalgae present in our experimental enclosures through time. P-values are from linear mixed effects models that include percent cover and time as interacting fixed effects. Error bars are ± 1 SE.

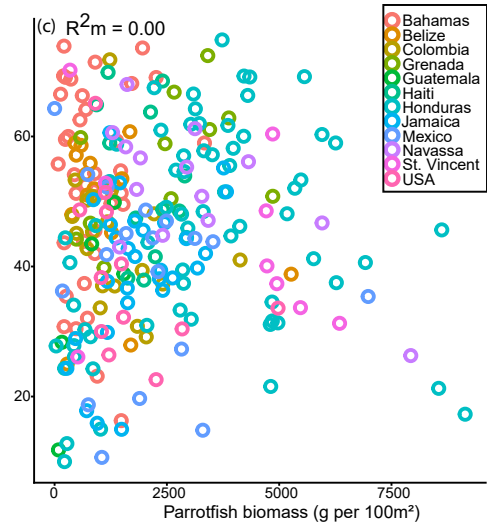
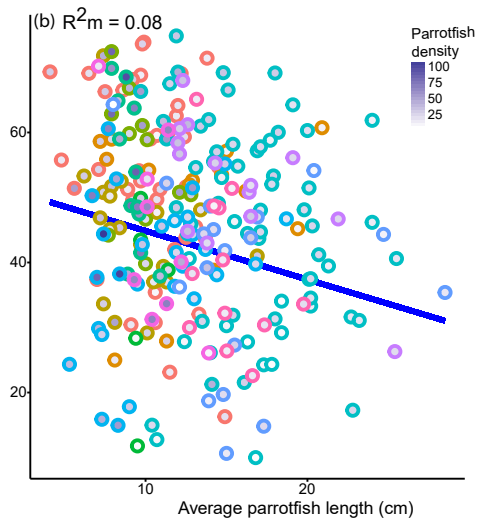
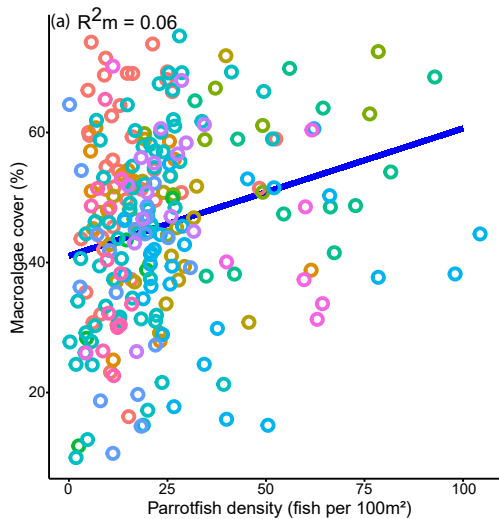
Figure 6: **(a)** The average growth, measured as change in live tissue area over the course of the experiment, of branching versus mounding and encrusting corals growing in our exclusion treatments. P-values are from linear mixed effects model with treatment and coral colony morphology (branching versus encrusting/mounding) as interacting fixed effects **(b)** Change in the average live tissue area of branching and mounding and encrusting corals regressed against final percent cover of macroalgae in each plot. The dashed trend line shows the marginally significant effect of algae on mounding and encrusting coral growth. **(c)** The number of recruits counted on settlement tiles placed in each enclosure regressed against the dry weight of algae measured on the tile while the inset panel shows the average number of recruits per tile within each treatment. Letters indicate significant differences between treatments. Error bars are ± 1 SE.

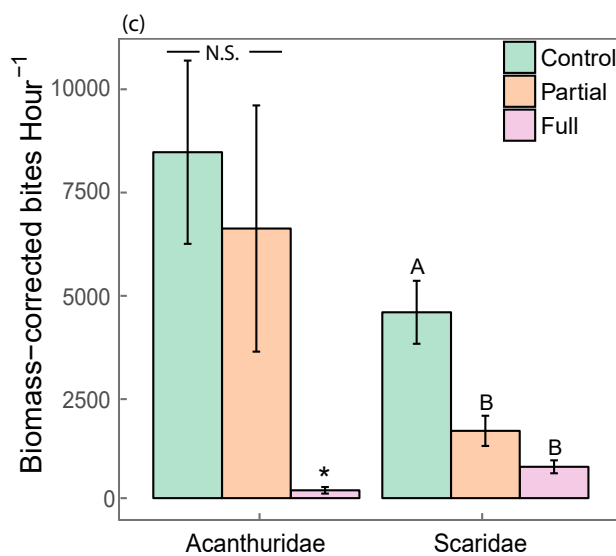
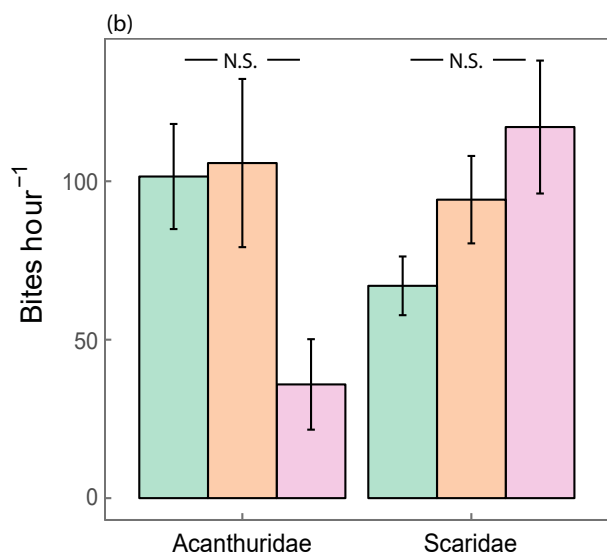
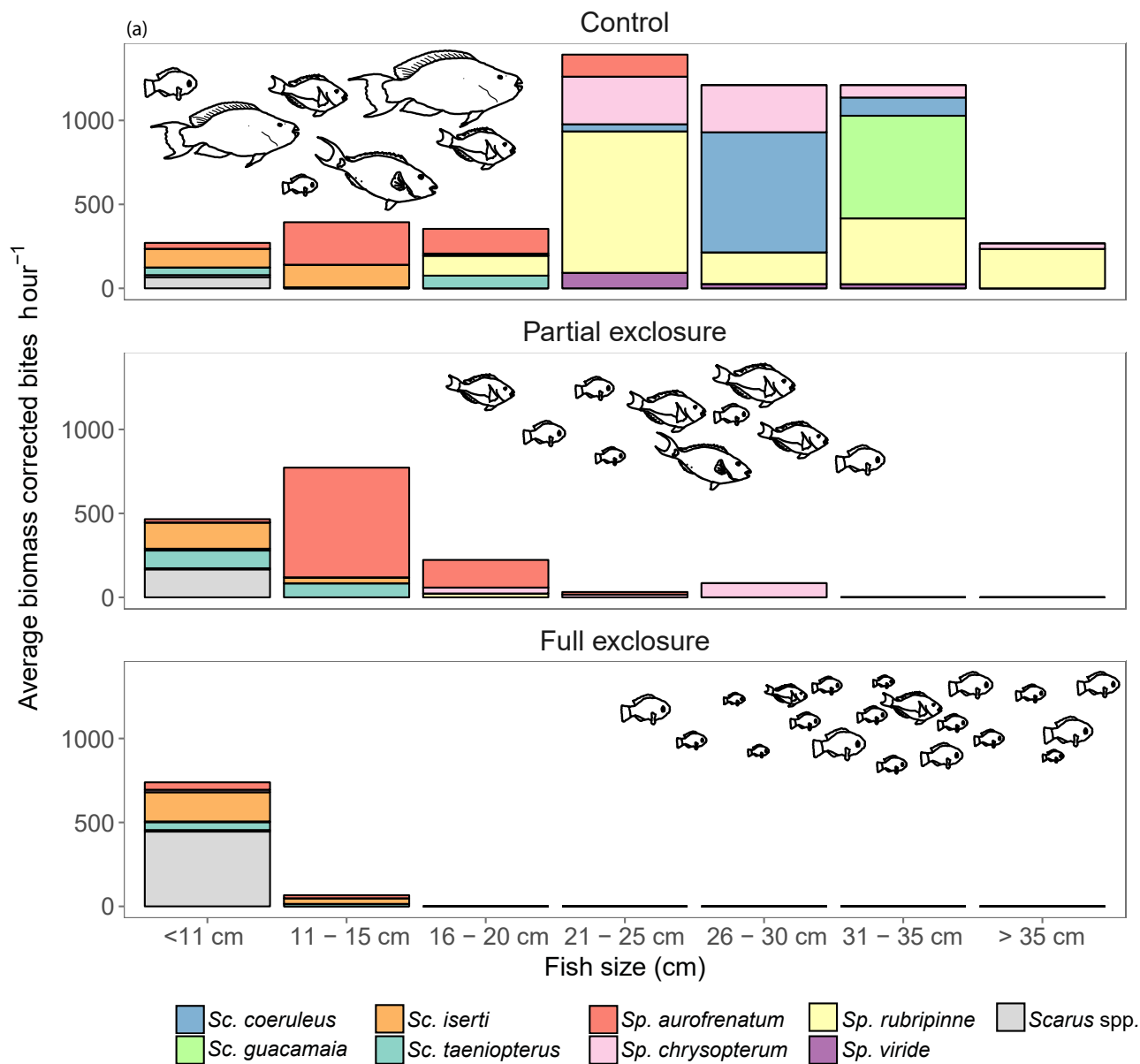
(a) Regional Patterns

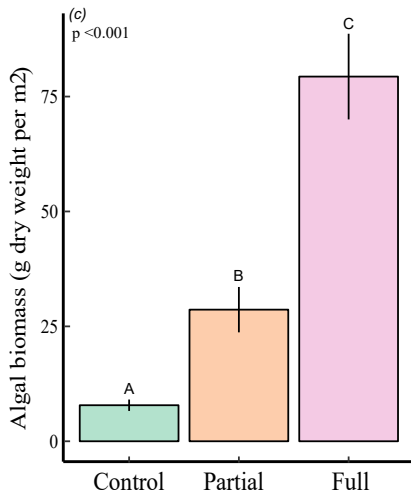
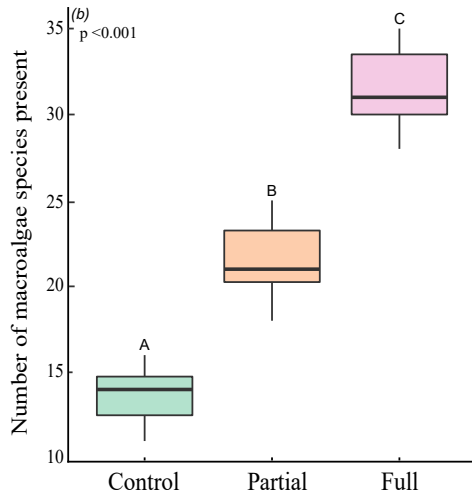
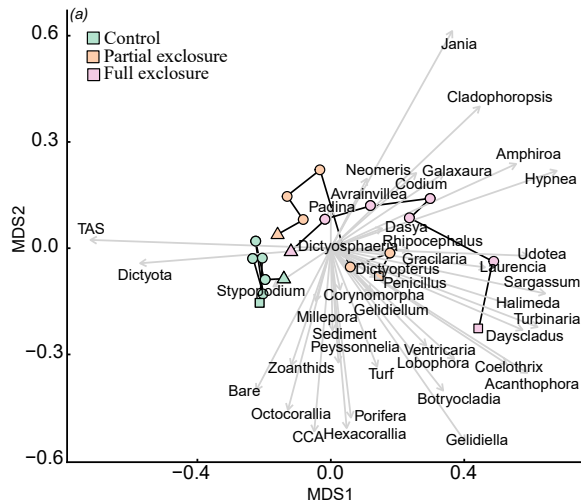


(b)









Control Partial Exposure Full Exposure

