REPORT

Algal turf consumption by sea urchins and fishes is mediated by fisheries management on coral reefs in Kenya

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Abstract Herbivory is a key process that controls the abundance and accumulation of algal turf on tropical coral reefs. The capacity of reefs to prevent algal accumulation hinges on the balance between algal production and consumption (i.e., grazing). In this study, we quantify algal turf biomass accumulation and grazing using experimental substrata and herbivore exclusion cages across sites in Kenya that represent different levels of fisheries management: heavily fished reefs, community marine-protected areas less than 10 yr old, and older government-managed marine-protected areas. These reefs had different assemblages of grazing herbivores with fished reefs being dominated by sea urchins, while government closures had a high abundance of grazing fishes, in particular parrotfishes. The community fisheries closures had an intermediate mix of sea urchins and grazing fishes, with the latter dominated by surgeonfishes. These management regimes mediated algal biomass on experimental substrata such that urchins consumed as much as 90% on fished reefs and fishes as much as 96% at the government marine-protected areas by the end of the 390-d trial. The younger community fisheries closures lacked the herbivory to significantly reduce algal biomass, and consumption was less than 50% of production and never greater than 2 g algae m^{-2} d^{-1}. These findings point to the importance of recovery dynamics of herbivorous fishes from heavy fishing pressure. They also suggest that while sea urchins might be effective grazers to prevent macroalgal dominance, they are not a functional replacement for fishes due to their ability to reduce reef accretion through bioerosion and prevent settlement of crustose coralline algae in this system.

Keywords Consumers · Ecosystem functioning · Grazing pressure · Phase shift · Western Indian Ocean

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Introduction

Herbivory is important in mediating benthic composition on coral reefs (McManus and Polsenberg 2004; Cheal et al. 2010). Some studies have shown that herbivory is more of a driving factor in preventing macroalgal dominance on reefs than bottom-up factors, such as sunlight and nutrients (Burkepile and Hay 2006; Heck and Valentine 2007; Rasher et al. 2013). Others, however, have shown that bottom-up processes are the dominant drivers of coral reef benthic composition (Enochs et al. 2015; Russ et al. 2015). Disturbances (e.g., coral bleaching) also play a key role in shaping the benthos with the loss of live coral and a concomitant increase in algal production (Ledlie et al. 2007). Therefore, the capacity of reefs to maintain coral dominance largely relies on the balance between ability of grazers to remove algae after a disturbance and rates of

algal production (McManus and Polsenberg 2004; Marshell and Mumby 2012). Thus, fisheries management can have substantial impacts on coral–algal relationships by influencing the abundance and types of herbivores present (McClanahan 1995; Mumby et al. 2007; Rasher et al. 2013; Bozec et al. 2016).

Quantifying the foraging by herbivores can be challenging in a natural setting because of their mobility, feeding behaviors, and the difficulty of making direct observations of multiple species or functional groups simultaneously. Previous studies have measured consumption rates of one or a few species of fish and generally found that total food intake, or grazing impact, increases linearly with fish biomass (Klumpp and McKinnon 1989; Montgomery et al. 1989; Bruggemann et al. 1994a, b, c; 1996). Others have found that algal turf intake increases nonlinearly with fish size (Bonaldo and Bellwood 2008; Lokrantz et al. 2008). It is clear that spatial and temporal variation exists among herbivore functional groups in their grazing rates and how this relates to size (Choat and Bellwood 1985; Marshell and Mumby 2015; Holbrook et al. 2016; Tebbett et al. 2017). For example, feeding differences may be a function of behavior (e.g., territoriality, predator avoidance, and method of feeding) as well as factors such as the influence of temperature on grazer metabolic requirements, algal nutritional quality, and algal abundance and availability (Carpenter 1988; Ferreira et al. 1998b; Smith 2008; Afeworki et al. 2011; Kelly et al. 2016). Interference competition between fishes and sea urchins has also been shown to impact algal consumption (Hay and Taylor 1985). Given this variation in algal foraging on coral reefs, there is a need to more accurately quantify herbivory by key functional groups such as algal turf grazers more accurately.

It is clear that parrotfishes (family *Labridae*) serve a critical role on coral reefs worldwide in promoting ecosystem functioning and coral dominance. Parrotfishes have been shown to have strong effects on algal abundance and thus preventing phase shifts while promoting reef resilience and structural complexity (Mumby et al. 2006, 2007). Parrotfishes are, however, often overfished on coral reefs (McClanahan and Mangi 2001; Bellwood et al. 2003; Hawkins and Roberts 2004; McClanahan et al. 2013). Overfishing results in not only declining abundances, but also reductions in mean body size due to size-selective harvesting (Russ 1991; Shin et al. 2005; Bellwood et al. 2012). Reefs dominated by small (< 15 cm) parrotfishes may not have consumption rates high enough to control turf algae (Mumby 2006; Lokrantz et al. 2008; Taylor et al. 2015; but see Bellwood et al. 2012). The recovery dynamics of parrotfishes are especially critical in Kenyan coral reef systems due to their ability to impede algal succession and maintain reefs with high coral cover

(McClanahan 1997; McClanahan and Humphries 2012; Humphries et al. 2014). Complementing the role of parrotfishes on coral reefs are surgeonfishes, or algal turf grazers primarily in the family Acanthuridae. For example, the brown surgeonfish (*Acanthurus nigrofuscus*) feeds on sparse algal turfs tearing filaments and thus preventing macroalgal establishment (Polunin et al. 1995). In many coral reefs, sea urchins are also important algal turf grazers that exert primary control of algae and their removal inhibits coral settlement (Hughes 1994). These various herbivores can play complimentary roles or compete for shared resources impacting functional redundancy in the ecosystem (Hay and Taylor 1985).

Herbivory rates on coral reefs have typically been estimated by the extrapolating results from a few select species, scaling up metabolic requirements of species, or using exclusion cages and experimental substrata (but see Robinson et al. 2019). The results from such experiments in the Caribbean and Great Barrier Reef suggest that even robust herbivorous fish populations may only be able to consume 30 to 40% of net algal production (Williams et al. 2001; Mumby et al. 2007). Other studies suggest herbivores are able to remove up to, and greater than, 100% of algal turf production (Hatcher 1981; Carpenter 1986; Van Rooij et al. 1998; Russ 2003; Kopp et al. 2010). Simulation models have estimated that sea urchins are able to graze as much as 40–50% of the substratum but also assume fish and sea urchins can graze the same areas (i.e., no interference competition; Mumby 2006; Sebastián and McClanahan 2013). To our knowledge, there have been no empirically derived algal consumption values for herbivore communities across reefs that include both fishes and sea urchins. Thus, in this study we measure algal production and consumption using a selective herbivore exclusion experiment across a gradient of herbivore abundance and composition. Specifically, we compare algal turf herbivory by fishes and sea urchins together, just fishes, and just sea urchins using exclusion cages in Kenyan reef lagoons. The fringing coral reefs of Kenya provide an ideal system to study these processes because they represent a wide range of herbivore community composition that is mediated by management (i.e., marine-protected areas; McClanahan 2019).

Materials and methods

Study sites

To sample across a gradient of herbivore assemblages, we collected data in 2011 and 2012 from sites representing distinct fisheries management regimes: two heavily fished open access reefs, two younger no-take marine-protected

areas (community closures), and two older marine-protected areas (government closures) (Humphries et al. 2014). We regarded management regimes as experimental treatments, and sites representing these treatments were interspersed (Fig. 1). The two community closures, Kuruwitu and Mradi, have received protection from fishing since 2005 and 2010, respectively, and are both approximately 0.3–0.4 km^2 in size. The other two marine-protected areas are government closures, Mombasa and Malindi, and have received protection from fishing since 1991 and 1968, respectively; Mombasa is approximately 6 km^2 in size, whereas Malindi is 10 km^2. Fishing at Kanamai and Ras Iwatine is intense and highly unselective with a variety of gear types being used (e.g., spear guns, nets, traps).

Herbivore surveys

Sea urchins were identified to species and counted in 10 m^2, haphazardly placed circular plots ($n = 9$–18 per site). Wet weight was estimated by multiplying the number of individuals by wet weights per species using locally derived values from species collected previously in these sites (McClanahan and Shafir 1990). Herbivorous fishes were counted and identified to species with fish size (total length, TL), estimated to the nearest 10 cm by underwater visual census (via snorkel) using 2-4 haphazardly placed replicate belt transects (5 × 100 m) per site. Parrotfishes under 10 cm TL were grouped together as "juveniles" due to the difficulty of identifying them to the species level in the field. Transects were conducted during neap tides when the water was between ∼ 1 and 4 m deep. Mass was

Fig. 1 Study sites differing in management where government closures are administered by the Kenya Wildlife Service and are older than the more newly established community closures administered by fishers, both of which do not allow fishing. Open access reefs have no restrictions on fishing. Modified from Humphries et al. (2014)

determined by converting fish counts to biomass using published length–weight relationships (Letourneur et al. 1998; Froese and Pauly 2006). Herbivorous fishes were assigned to functional groups based on published information on diets as well as morphology and behavior (Froese and Pauly 2006; Green et al. 2009). For example, fishes that consume fleshy macroalgaeHoey were considered browsers (excluded in this study) and those feeding on algal turf were either scrapers (parrotfishes) or grazers (i.e., algal croppers and surgeonfishes). There are only two species of rabbitfishes at the study sites (Humphries et al. 2015), *Siganus sutor* and *Siganus argenteus*, and they were not considered algal turf grazers because previous research in this system (Humphries et al. 2014, 2015) and associated video recordings have shown them to exclusively consume seagrass or be primarily croppers of red and green macroalgae (Hoey et al. 2013). Algal croppers and detritivores were combined into one functional group (herein referred to as "grazers"). No excavating parrotfishes were recorded during these surveys.

Algal biomass

To determine algal biomass accumulation at reefs, experimental substrata were made from ∼ 2.5-cm cross sections of massive *Porites* coral (mean plate size ± SE was 184 ± 11 cm^2; $n = 288$ plates). Plates had flat surfaces but irregularly shaped edges. Holes were drilled in individual plates allowing them to be attached to plastic cage flooring (1 × 1 m), which was nailed into bare substratum. Individual plates were deployed in sets of 4 and attached at least 5 cm apart from one another on the same piece of flooring to form a single replicate. Three experimental treatments were created to allow access to the plates by different groups of herbivores: (1) cage treatments, which represented a control for site-specific, bottom-up differences in environmental variables, or herbivore exclusion preventing animals > 2.5 cm minimum dimension (defined as "large herbivores"), (2) fence treatments that allowed herbivory only by fishes, and (3) open treatments that allowed herbivory by both fishes and sea urchins.

Cages and fences were made from plastic mesh material (2.5 × 2.5 cm square holes) and attached to bare substratum using u-bolts. Cages were approximately 1 ×1 × 0.5 m (L × W × H) in size. The previous work has found that cages similar to these had no significant effect of on algal standing crop or species composition other than the effect of excluding grazers (Humphries et al. 2014). Sea urchins were unable to climb the sides of the fences and enter the treatments (Humphries personal observation). At each reef site, treatments were deployed in four blocks, each including one replicate from each treatment. Blocks were placed > 20 m apart from one another, and
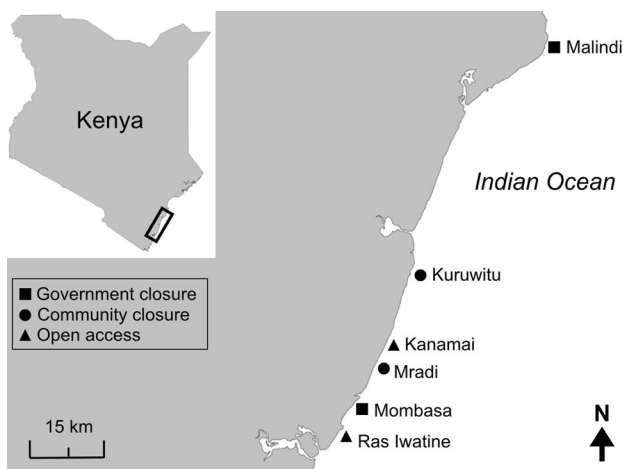
treatments within blocks were < 3 m apart. Areas for deployment were typical of the larger reef areas and away from damselfish territories. We began the algal production experiment during the southeast monsoon season between September and October 2011, which is the beginning of the calm season.

Algal biomass (expressed per unit area; g algae m^{-2}) was quantified as (dry) algal biomass. To do this, we followed methods similar to Russ (2003) and scraped a 5 × 5 cm area on each plate at all treatments at regular time intervals (Samples were taken a total of 6 times over the ∼ 390 d duration of the experiment.) We sampled areas that seemed typical of the whole plate, and it was not possible to determine the area of the plate that was previously scraped. All algal samples were immediately placed on ice and returned to the laboratory where wet weight was initially recorded. Samples were then dried at 60 °C to a constant weight and ground in a Wiley mill and weighed (dry calcified weight). To remove calcium carbonate and determine dry algal weight (or weight of organic matter only), we placed the samples in 10% acetic acid for 24 h (stirring regularly), vacuum-filtered them onto Whatman ashless filters, rinsed them with deionized water, and dried them at 60 °C to a constant weight (hereafter referred to as "algae"). All weights were measured to the nearest 0.001 g. Samples were processed in this manner to have units comparable to those in similar studies (Bruggemann et al. 1994a, b; Van Rooij et al. 1998; Russ 2003; Paddack et al. 2006; Marshell and Mumby 2012), where units represent grams of dry organic material or algae.

Algal consumption

To calculate the proportion of algal biomass consumed by herbivores, we quantified the percentages consumed by fishes (C_F) and sea urchins (C_{SU}) at each sampling event using the equations

$$C_F = \left(1 - \left[\frac{B_F}{B_C}\right]\right) \times 100$$

and

$$C_{SU} = \left(\left[1 - \left\{\frac{B_0}{B_C}\right\}\right] \times 100\right) - C_F$$

where B_C is algal biomass at the cage treatment, B_F is algal biomass at the fence treatment, and B_O is algal biomass at the open treatment (i.e., the observed percentage of algal biomass consumed). The total percentage consumed by both fishes and sea urchins was calculated by summing C_F and C_{SU}. To calculate algal turf consumption rates (g algae m^{-2} d^{-1}), we divided the algal biomass removed at each treatment as described above (B_F, B_C, B_O), but divided

each by the number of days between sampling events to get a daily average.

Data analyses

We used separate one-way analyses of variance (ANOVA) to test for a site effect on: (a) fish biomass (by functional group and total) and (b) sea urchin biomass. Significant differences were followed by Tukey tests. Using a two-way ANOVA, we tested for the effects of site and treatment, and their interaction, on algal biomass at the final sampling event. Finally, algal consumption was compared using one-way ANOVA with site as the main effect for: (a) all herbivores and (b) each functional group. All data analyses were performed using the software program "R" (v. 3.1.2; R Development Core Team 2014).

Results

Herbivore surveys

Total grazing fish biomass was significantly different across sites (df = 5, F-value = 61.23, p < 0.001; Fig. 2). It was lowest at the fished sites and greatest at the government closure sites, with community closures in between (Table S1). Mombasa, a government closure site, however, was not significantly different from either community closure site. Fish biomass of both grazers (df = 5, F-value = 198.98, p < 0.001) and scrapers (df = 5, F-value = 10.08, p < 0.05) was significantly different across sites. For grazers, the open access sites of Kanamai and Ras Iwatine had significantly less biomass than the community closures, Mradi and Kuruwitu, as well as one government closure site, Mombasa (Table S1). Malindi had significantly greater grazer biomass than any other site. The government closures had significantly greater biomass of scraping fishes than all the other sites, and there was no significant difference between the fished sites and the community closure sites (Table S1). Sea urchins were significantly different across sites (df = 5, F-value = 13.95, p < 0.01); the greatest urchin biomass was at the fished sites and community closures, which were significantly less than the government closure sites, Mombasa and Malindi (Fig. 1, Table S1).

Algal biomass

Overall, algal biomass over the ∼ 390-d period is grouped by management category for the open and caged treatments. At the fished sites, algal production was significantly limited by sea urchin herbivory; at the community closure sites, algal biomass increased in all three
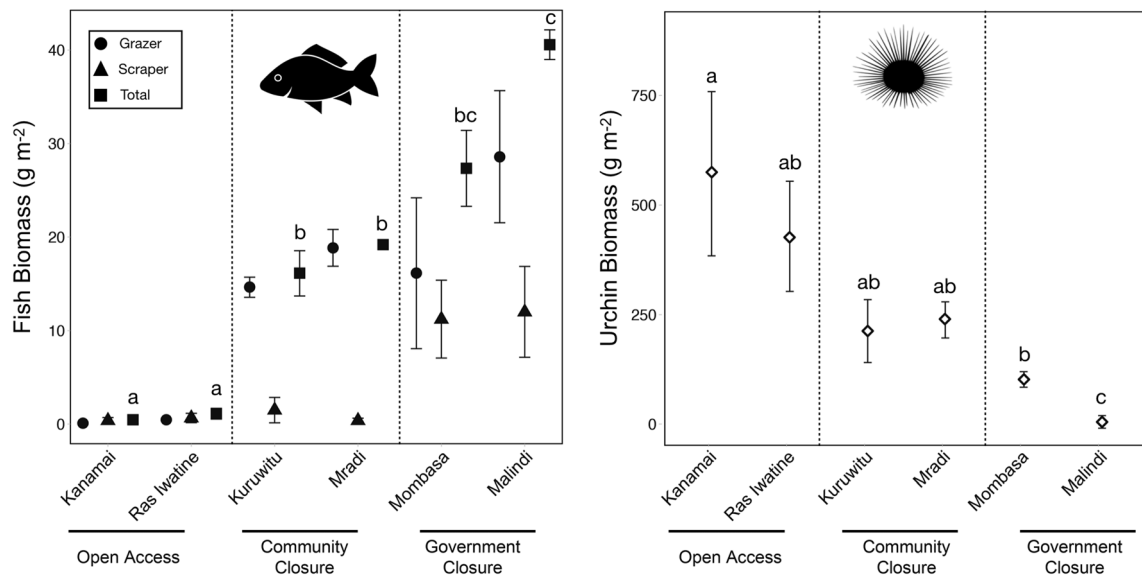
Fig. 2 Mean (± SE) grazing herbivorous fish and sea urchin biomass (g m^{-2}) by study site and management. Letters represent homogeneous subgroups for total turf grazing fishes and sea urchins ($p < 0.05$) identified using one-way ANOVA and individual contrasts

treatments, suggesting that fish herbivory, either alone or together with urchin herbivory, was insufficient to prevent accumulation of algal biomass; at the government closure sites, algal production was significantly limited by fish herbivory (Fig. 3). The interaction term (site * treatment) was statistically significant in this model (df = 10, F-value = 13.01, $p < 0.05$), meaning that algal biomass at the final sampling event is differed by site across the treatment levels.

Generally, algal biomass increased rapidly in the cage treatments (no herbivory) at all six sites and then leveled off after ~ 100–150 d and remained at ~ 150 g algae
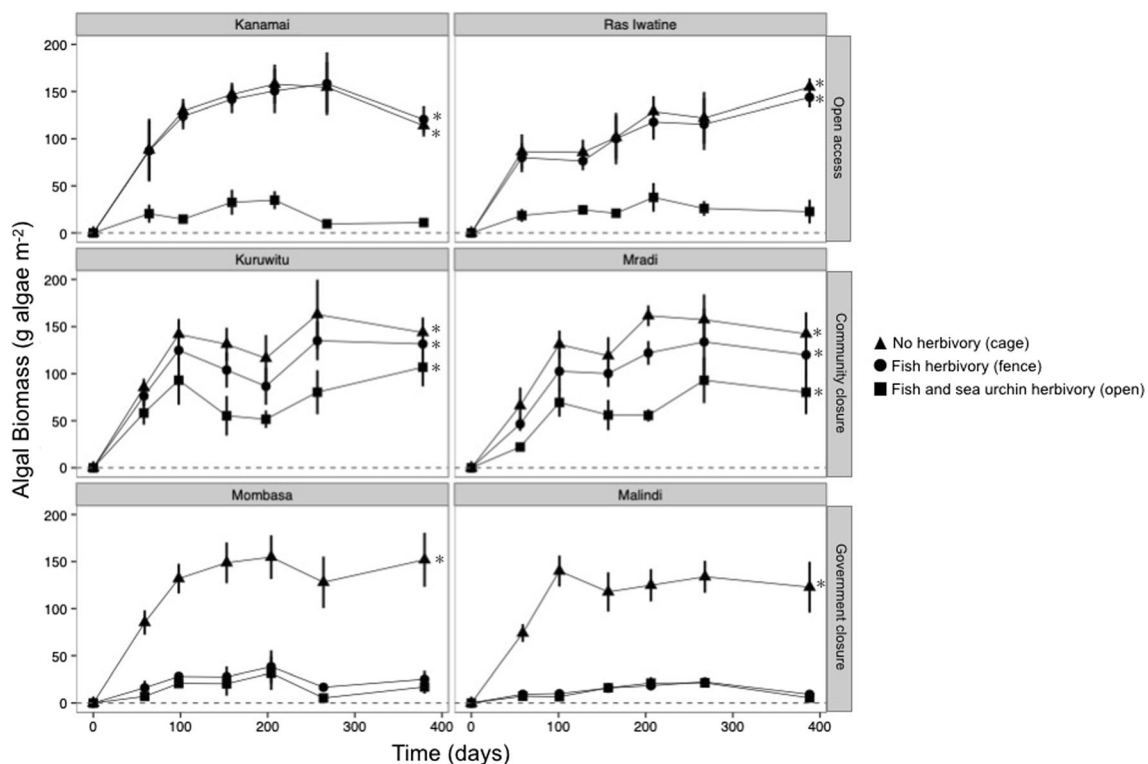

Fig. 3 Time series of the mean (± SE) algal biomass (g algae m^{-2}) at the six study sites, grouped by management. Shapes indicate treatment, and asterisks indicate significant differences between the first and last sampling events ($p < 0.05$)

m^{-2} for the remainder of the experiment at each site. These values were all significantly greater ($p > 0.05$) than at the beginning of the experiment (Fig. 3). The open access fished reefs showed significant increases in algal biomass by the end of the experiment at the fence treatments ($p < 0.05$), but not the open treatments where sea urchins could access the plates. At the community closures, all treatments tracked similar trajectories and were significantly different from zero at the end of the experiment ($p < 0.001$); these experimental substrata all had greater than 80 g algae m^{-2} at the conclusion of the experiment. At the government closure sites, the only treatment to show a significant increase in algal biomass was the cage treatment ($p < 0.001$). The fence and open treatments never reached above 35 g algae m^{-2} throughout the experimental period. Accumulation of algal biomass after ~ 390 d did not differ between sites at the caged treatments (df = 5, F-value = 0.627, $p = 0.681$).

Algal consumption

Total algal turf consumption was greatest at the open access fished sites (> 2.6 g algae m^{-2} d^{-1}) and the government closures (total > 2.3 g algae m^{-2} d^{-1}), but did not differ significantly among sites (df = 5, F-value = 0.08, $p = 0.99$; Fig. 4). Total algal turf consumption at the community closure sites of Mradi and Kuruwitu was 1.65 and 1.56 g algae m^{-2} d^{-1}, respectively. Sea urchin consumption varied significantly by site (df = 5, F-value = 8.82, $p < 0.01$). Consumption at both of the open access sites, Kanamai and Ras Iwatine, was significantly greater than at the government closures, Mombasa and Malindi (t-values < -3.72, $p < 0.05$). Fish consumption of algae varied significantly by site (df = 5, F-value = 13.38, $p < 0.001$), with the open access and community closure

Fig. 4 Mean ($\pm$ SE) algal turf consumption rate (g algae m^{-2} d^{-1}) of fishes and sea urchins across sites and management categories

sites exhibiting lower values than the government closures (Fig. 4).

At the open access sites, greater than 85% of algal turf was consumed at the end of the experiment on the open treatments (urchin and fish herbivory; Table 1). Similarly, at the government closures, 89% and 96% of algal production were consumed for Mombasa and Malindi, respectively. In contrast, the community closures had only 26% (Kuruwitu) and 44% (Mradi) of total algal production consumed at the end of the experiment.

Discussion

The level of fishing pressure reflected marine-protected area management and mediated herbivore community composition in this study, which led to different rates of algal accumulation and consumption. The two management regimes characterized by herbivore communities able to prevent significant algal biomass by the end of the experiment were the government fisheries closures and the fished reefs, but each was maintained by different grazing functional groups: fishes in the closures and sea urchins at the fished reefs. In these two management systems, at least 85% of algal biomass was consumed. In fact, herbivores were able to consume as much as 96% of algal turf biomass where herbivory was greatest. In contrast, the relatively small, new community-based marine protected areas had an intermediate mix of algal turf grazing functional groups containing both fishes and sea urchins. These herbivores were not able to suppress algal turf biomass, which seemed to stabilize at between 100 and 150 g m^{-2} within the first 150 d. These results show how fishing and marine-protected area management can shape the algal turf grazing community on reefs and how closures that are transitioning from fishing may lack the herbivory necessary to prevent algal accumulation.

In the absence of significant herbivory, algal biomass stabilized on the experimental substrata in this study after 100–150 d. This seems to represent an upper limit to algal biomass in this system, which is 7-25 times greater than where herbivory was high due to either sea urchins or fishes. This is consistent with other studies that displayed a significant effect of grazing on algal biomass, with biomass quickly reaching a plateau in the absence of herbivores (e.g., Sammarco et al. 1974; Adey et al. 1977; Connor and Adey 1977; Carpenter 1986; McClanahan 1997). Similar patterns have also been demonstrated at a regional scale in the Caribbean since the mass mortality of the urchin *Diadema antillarum* (Carpenter 1988; Schutte et al. 2010). Additionally, several other studies outside the Caribbean have documented large increases in macroalgae following exclusion of herbivores (e.g., Hughes et al. 2007; Smith
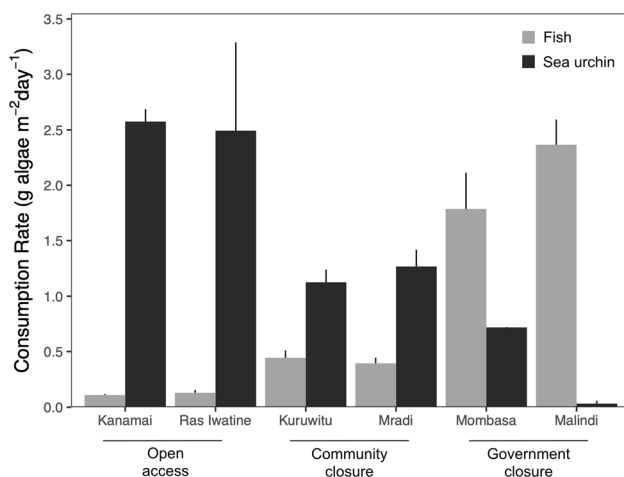
Table 1 Algal turf biomass biomass (g algae m^{-2}) from caged treatments and amount (%) consumed by herbivores in open treatments after ~ 390 d

Management	Site	Algal biomass (g algae m^{-2})	Algal turf consumed (%)
Open access	Kanamai	113.9	90
	Ras Iwatine	154.8	86
Community closure	Kuruwitu	143.8	26
	Mradi	142.3	44
Government closure	Mombasa	151.9	89
	Malindi	122.8	96

et al. 2010; Doropoulos et al. 2013; Webster et al. 2015). Nutrient concentrations and ratios were not measured in this study directly, but controlled for with the caged treatments (no herbivory), and algal production was not significantly different among sites. Thus, any possible increases in nutrient supply from increased fish biomass and waste or riverine discharge (e.g., Rasher et al. 2012, Burkepile et al. 2013) could have been masked by local-level differences in nutrient concentrations as shown at these sites in McClanahan (1997). Teasing apart these environmental drivers of algal production would help us to better understand factors other than herbivory that may control these algal communities.

Some small fleshy macroalgae (i.e., *Padina*) developed on the experimental plates in the caged treatments of this study. These established within the first 100 d but rarely covered more than 25% of the plates. This resembles some reefs from the Caribbean in the sense that macroalgae settled quickly to the substratum, or within the first few months (e.g., Morrison 1988, Sotka and Hay 2009, Ferrari et al. 2012). However, it differs from these Caribbean studies in that the macroalgae did not proliferate to reach levels of 60–100% cover. Instead, macroalgae and resulting algal production stabilized at similar values as those found in Fiji, Hawaii, and the Great Barrier Reef (Scott and Russ 1987; Hixon and Brostoff 1996; Rasher et al. 2012; Kelly et al. 2017). So, while settlement of macroalgae was quick on these reefs in the absence of herbivory, settled algae did not continue to proliferate and increase as in many Caribbean reefs. Seasonality did not play a significant role in these findings as there is only a calm and windy season that does not affect daylength or other environmental variables significantly (McClanahan 1988). There is, however, the possibility that micrograzers such as damselfishes influenced the maximum algal biomass observed as it was not possible to avoid or exclude them completely even when care is taken not to place cages in their territories (Russ 1987).

Spatial differences in the intensity of grazing may also dictate whether herbivores are able to suppress algal production effectively. For instance, herbivore communities may aggregate in areas and increase their foraging rates in response to increases in algal production and water temperature, thus creating patches of ungrazed areas (Horn and Gibson 1990; Ferreira et al. 1998a; Russ 2003). Understanding these fluctuations and responses is critical for reef management and avoiding macroalgal phase shifts, but parsing out the various mechanisms has proven difficult (van Nes and Scheffer 2005). In fact, one of the more significant oversimplifications in the rapid ecological transition models is that ecosystems are spatially homogeneous (Scheffer and Carpenter 2003). Nonetheless, over the 390-d period of this experiment, our results were relatively steady across spatial scales after the initial ~ 100 d, and no disturbances significantly influenced algal biomass at the caged treatments where there was no herbivory.

Exploitation of herbivorous fishes has the ability to reduce grazing intensity and ecosystem functioning on reefs drastically if other species cannot fill their niche (Bellwood et al. 2004). Here, sea urchins appear to be capable of effectively replacing fishes in terms of algal turf removal on the two fished reefs. This transition, however, was not linear and consumption was not strong enough to avoid algal accumulation at reefs in the community-managed fisheries closures. Consequently, management and the recovery dynamics of fishes that are associated with the interaction of the age (and size) of marine protected areas may be especially important in this system if one is to achieve the desired grazing levels that prevent macroalgal phase shifts (Claudet et al. 2008). Findings from other studies indicate this is especially critical for scraping parrotfishes greater than 20 cm in length, which tend to require more than 10 yr of protection to recover and have a large grazing impact on reefs (McClanahan et al. 2007; Lokrantz et al. 2008). Furthermore, sea urchins are bioeroders that have been shown to significantly reduce reef accretion and prevent settlement of crustose coralline algae aside from algal turf consumption (Mokady et al. 1996, O'Leary and McClanahan 2010). Therefore, the replacement of grazing fishes with sea urchins on heavily fished reefs does not mean the reefs are functionally equivalent. These differences in influencing organic versus inorganic reef production may influence their desirability to managers.

In this study system, marine-protected areas mediated interactions between sea urchins and parrotfishes and prevented them from co-occurring in high densities. This could be due to a combination of factors, one being the recovery of the orange-lined triggerfish (*Balistapus undulatus*), a major sea urchin predator (McClanahan and Muthiga 2016). Populations of this fish tend to recover fully after approximately 10 yr following the establishment of a of marine-protected area at which point it drives sea urchin wet weight down to values less than 10 kg/ha on reefs (McClanahan 2000). Another factor preventing sea urchins and parrotfishes from co-occurring on these reefs might be competition for shared algal resources. Food quality and availability have been shown to limit parrotfish feeding (Targett and Targett 1990), and parrotfish quickly occupies reefs where sea urchins have been removed (Hay and Taylor 1985). Thus, the functional redundancy of algal turf grazers in this ecosystem is low and competitive interactions between species occupying a similar niche, as well as predator–prey dynamics, shape these relationships. The transition between urchin-dominated reefs and parrotfish-dominated reefs might be expedited by the removal of sea urchins upon designation of a marine protected area to free up substratum and allow parrotfish to occupy reefs more quickly. Similar management and urchin-parrotfish interactions occurred on reefs across the Caribbean in the 1970s and 80s (Hay 1984), making heavily fished reefs more vulnerable to macroalgal phase shifts during the *Diadema* die-off in the 1990s (Hughes 1994).

This study shows how marine-protected areas can increase the biomass of fish that graze algal turf, leading to high consumption rates that prevent algal buildup on experimental substrata. Reefs that were heavily fished were able to do the same but through the medium of sea urchins. The previous work in this system shows that parrotfish takes approximately 10 yr to recover, as do urchin predators (McClanahan et al. 2007). The community fisheries closures in this study were less than 10 yr old, and therefore, the algal turf grazing niche was in the process of transitioning from urchin-dominated to parrotfish-dominated control (McClanahan 2000, McClanahan et al. 2007, Humphries et al. 2014). During this transition period, algal turf herbivory is not high enough to prevent the development of significant algal biomass, thus putting reefs in a vulnerable state through phase shifts due to environmental shocks such coral bleaching that might free up additional substrata for algae proliferation (McClanahan et al. 2002; Adam et al. 2015). Overall, our findings highlight the transition from fished to protected areas as a period of particularly high vulnerability to algal dominance. Consequently, it is not simply the cessation of fishing that is important, but also the replacement of urchins by fishes as the dominant algal turf grazers.

Compliance with ethical standards

References

Adam TC, Burkepile DE, Ruttenberg BI, Paddack MJ (2015) Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. Mar Ecol Prog Ser 520:1–20

Adey WH, Adey P, Burke R, Kaufman L (1977) Holocene reef systems of eastern Martinique. Atoll Research Bulletin 218:1–40

Afeworki Y, Bruggemann JH, Videler JJ (2011) Limited flexibility in resource use in a coral reef grazer foraging on seasonally changing algal communities. Coral Reefs 30:109–122

Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proceedings of the Royal Society B: Biological Sciences 279(1733):1621–1629

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecology letters 6(4):281–285

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827

Bonaldo RM, Bellwood DR (2008) Size-dependent variation in the functional role of the parrotfish Scarus rivulatus on the Great Barrier Reef, Australia. Mar Ecol Prog Ser 360:237–244

Bozec Y-M, O'Farrell S, Bruggemann JH, Luckhurst BE, Mumby PJ (2016) Tradeoffs between fisheries harvest and the resilience of coral reefs. Proc Natl Acad Sci 113:4536–4541

Bruggemann JH, Begeman J, Bosma EM, Verburg P, Breeman AM (1994a) Foraging by the stoplight parrotfish Sparisoma viride. II. Intake and assimilation of food, protein and energy. Mar Ecol Ser 106:57

Bruggemann JH, Kuyper MWM, Breeman AM (1994b) Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish Scarus vetula and Sparisoma viride (Scaridae). Mar Ecol Prog Ser 112:51–66

Bruggemann JH, Van Kessel AM, Van Rooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the Caribbean parrotfish Scarus vetula and Sparisoma viride: implications of fish size, feeding mode and habitat use. Mar Ecol Prog Ser 134:59–71

Bruggemann JH, Van Oppen MJH, Breeman AM (1994c) Foraging by the stoplight parrotfish Sparisoma viride. I. Food selection in different, socially determined habitats. Mar Ecol Ser 106:41

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–3139

Burkepile DE, Allgeier JE, Shantz AA, Pritchard CE, Lemoine NP, Bhatti LH, Layman CA (2013) Nutrient supply from fishes

facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. Sci Rep-UK 3:1493

Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. Ecol Monogr 56:345–364

Carpenter RC (1988) Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. Proc Natl Acad Sci 85:511–514

Cheal AJ, MacNeil MA, Cripps E, Emslie MJ, Jonker M, Schaffelke B, Sweatman H (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

Choat JH, Bellwood DR (1985) Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. Mar Biol 89:221–234

Claudet J, Osenberg CW, Benedetti-Cecchi L, Domenici P, García-Charton J, Pérez-Ruzafa Á, Badalamenti F, Bayle-Sempere J, Brito A, Bulleri F (2008) Marine reserves: size and age do matter. Ecol Lett 11:481–489

Connor J, Adey WH (1977) The benthic algal composition, standing crop and productivity of a Caribbean algal ridge. Atoll Research Bulletin. https://doi.org/10.5479/si.00775630.211.1

Doropoulos C, Hyndes GA, Abecasis D, Vergés A (2013) Herbivores strongly influence algal recruitment in both coral-and algal-dominated coral reef habitats. Marine Ecology Progress Series 486:153–164

Enochs IC, Manzello DP, Donham EM, Kolodziej G, Okano R, Johnston L, Young C, Iguel J, Edwards CB, Fox MD (2015) Shift from coral to macroalgae dominance on a volcanically acidified reef. Nat Clim Chang 5:1083

Ferreira CEL, Gonçalves JEA, Coutinho R, Peret AC (1998a) Herbivory by the dusky damselfish Stegastes fuscus (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. J Exp Mar Bio Ecol 229:241–264

Ferreira DEL, Peret AC, Coutinho R (1998b) Seasonal grazing rates and food processing by tropical herbivorous fishes. J Fish Biol 53:222–235

Ferrari R, Gonzalez-Rivero M, Ortiz JC, Mumby PJ (2012) Interaction of herbivory and seasonality on the dynamics of Caribbean macroalgae. Coral Reefs 31:683–692

Froese R, Pauly D (2006) Fishbase. http://www.fishbase.org. Accessed 20 June 2018

Green AL, Bellwood DR, Choat H (2009) Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience. A Pract Guid coral reef Manag Asia Pacific Reg IUCN, Gland Switzerland Available online http://cmsdata iucn org/downloads/resilience_herbivorous_monitoring.pdf

Hatcher BG (1981) The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. 2:515–524

Hawkins JP, Roberts CM (2004) Effects of fishing on sex-changing Caribbean parrotfishes. Biol Conserv 115:213–226

Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65:446–454

Hay ME, Taylor PR (1985) Competition between herbivourous fishes and urchins on Caribbean reefs. Oecologia 65:591–598

Heck KL, Valentine JF (2007) The primacy of top-down effects in shallow benthic ecosystems. Estuaries and Coasts 30:371–381

Hixon MA, Brostoff WN (1996) Succession and herbivory: Effects of differential fish grazing on Hawaiian coral-reef algae. Ecol Monogr 66:67–90

Holbrook SJ, Schmitt RJ, Adam TC, Brooks AJ (2016) Coral reef resilience, tipping points and the strength of herbivory. Sci Rep 6:35817

Horn MH, Gibson RN (1990) Effects of temperature on the food processing of three species of seaweed-eating fishes from European coastal waters. J Fish Biol 37:237–247

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

Hughes TP, Bellwood DR, Folke CS, McCook LJ, Pandolfi JM (2007) No-take areas, herbivory and coral reef resilience. Trends Ecol Evol 22:1–3

Humphries AT, McClanahan TR, McQuaid CD (2014) Differential impacts of coral reef herbivores on algal succession in Kenya. Mar Ecol Prog Ser 504:119–132

Kelly ELA, Eynaud Y, Clements SM, Gleason M, Sparks RT, Williams ID, Smith JE (2016) Investigating functional redundancy versus complementarity in Hawaiian herbivorous coral reef fishes. Oecologia 182:1151–1163

Kelly ELA, Eynaud Y, Williams ID, Sparks RT, Dailer ML, Sandin SA, Smith JE (2017) A budget of algal production and consumption by herbivorous fish in an herbivore fisheries management area, Maui. Hawaii, Ecosphere, p 8

Klumpp DW, McKinnon AD (1989) Temporal and spatial patterns in primary production of a coral-reef epilithic algal community. J Exp Mar Bio Ecol 131:1–22

Kopp D, Bouchon-Navaro Y, Louis M, Mouillot D, Bouchon C (2010) Herbivorous fishes and the potential of Caribbean marine reserves to preserve coral reef ecosystems. Aquat Conserv Mar Freshw Ecosyst. https://doi.org/10.1002/aqc.1118

Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Poluni NV, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs 26:641–653

Letourneur Y, Kulbicki M, Labrosse P (1998) Length-weight relationship of fishes from coral reefs and lagoons of New Caledonia: an update. Naga, ICLARM Q 21:39–46

Lokrantz J, Nyström M, Thyresson M, Johansson C (2008) The non-linear relationship between body size and function in parrotfishes. Coral Reefs 27:967–974

Marshell A, Mumby PJ (2012) Revisiting the functional roles of the surgeonfish Acanthurus nigrofuscus and Ctenochaetus striatus. Coral Reefs 31:1093–1101

Marshell A, Mumby PJ (2015) The role of surgeonfish (Acanthuridae) in maintaining algal turf biomass on coral reefs. J Exp Mar Bio Ecol 473:152–160

McClanahan TR (1988) Seasonality in East Africa's coastal waters. Marine Ecology Prog Series 44:191–199

McClanahan TR (1995) A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. Ecol Modell 80:1–19

McClanahan TR (1997) Primary succession of coral-reef algae: differing patterns on fished versus unfished reefs. J Exp Mar Bio Ecol 218:77–102

McClanahan TR (2000) Recovery of a coral reef keystone predator, Balistapus undulatus, in East African marine parks. Biol Conserv 94:191–198

McClanahan TR (2019) Coral reef fish communities, diversity, and their fisheries and biodiversity status in East Africa. Mar Ecol Prog Ser 632:175–191

McClanahan TR, Allison EH, Cinner JE (2013) Managing marine resources for food and human security. Food Secur Sociopolitical Stab 142–168

McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA (2007) Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecol Appl 17:1055–1067

McClanahan TR, Humphries AT (2012) Differential and slow life-history responses of fishes to coral reef closures. Mar Ecol Prog Ser 469:121–131

McClanahan TR, Mangi S (2001) The effect of a closed area and beach seine exclusion on coral reef fish catches. Fish Manag Ecol 8:107–121

McClanahan TR, Muthiga NA (2016) Geographic extent and variation of a coral reef trophic cascade. Ecol 97:1862–1872

McClanahan T, Polunin N, Done T (2002) Ecological states and the resilience of coral reefs. Conserv Ecol 6:18

McClanahan TR, Shafir SH (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia 83:362–370

McManus JW, Polsenberg JF (2004) Coral–algal phase shifts on coral reefs: ecological and environmental aspects. Prog Oceanogr 60:263–279

Mokady O, Lazar B, Loya Y (1996) Echinoid bioerosion as a major structuring force of Red Sea coral reefs. Biol Bull 190:367–372

Montgomery WL, Myrberg AA Jr, Fishelson L (1989) Feeding ecology of surgeonfishes (Acanthuridae) in the northern Red Sea, with particular reference to Acanthurus nigrofuscus (Forsskål). J Exp Mar Bio Ecol 132:179–207

Morrison D (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 69:1367–1382

Mumby PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecol Appl 16:747–769

Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. Science 80(311):98–101

Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. Nature 450:98

van Nes EH, Scheffer M (2005) Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. Ecology 86:1797–1807

O'Leary JK, McClanahan TR (2010) Trophic cascades result in large-scale coralline algae loss through differential grazer effects. Ecology 91:3584–3597

Paddack MJ, Cowen RK, Sponaugle S (2006) Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. Coral Reefs 25:461–472

Polunin NVC, Harmelin-Vivien M, Galzin R (1995) Contrasts in algal food processing among five herbivorous coral-reef fishes. J Fish Biol 47:455–465

Van Rooij JM, Videler JJ, Bruggemann JH (1998) High biomass and production but low energy transfer effciency of Caribbean parrotfish: implications for trophic models of coral reefs §. J Fish Biol 53:154–178

Rasher DB, Engel S, Bonito V, Fraser GJ, Montoya JP, Hay ME (2012) Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. Oecologia 169:187–198

Rasher DB, Hoey AS, Hay ME (2013) Consumer diversity interacts with prey defenses to drive ecosystem function. Ecology 94:1347–1358

Robinson JP, McDevitt-Irwin JM, Dajka JC, Hadj-Hammou J, Howlett S, Graba-Landry A, Hoey AS, Nash KL, Wilson SK, Graham NA (2019) Habitat and fishing control grazing potential on coral reefs. Functional Ecology. https://doi.org/10.1111/1365-2435.13457

Russ GR (1987) Is rate of removal of algae by grazers reduced inside territories of tropical damselfishes? J Exp Mar Biol Ecol 110:1–17

Russ GR (1991) Coral reef fisheries: effects and yields. In: Sale PF (ed) The ecology of fishes on coral reefs. Elsevier, Amsterdam, pp 601–635

Russ GR (2003) Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. Coral reefs 22:63–67

Russ GR, Questel SLA, Rizzari JR, Alcala AC (2015) The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. Mar Biol 162:2029–2045

Sammarco PW, Levinton JS, Ogden J (1974) Grazing and Control of Coral-Reef Community Structure by Diadema-Antillarum Philippi (Echinodermata-Echinoidea)-Preliminary Study. J Mar Res 32:47–53

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648–656

Schutte VGW, Selig ER, Bruno JF (2010) Regional spatio-temporal trends in Caribbean coral reef benthic communities. Mar Ecol Prog Ser 402:115–122

Scott FJ, Russ GR (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. Mar Ecol Prog Ser 39:293–304

Sebastián CR, McClanahan TR (2013) Description and validation of production processes in the coral reef ecosystem model CAFFEE (Coral–Algae–Fish-Fisheries Ecosystem Energetics) with a fisheries closure and climatic disturbance. Ecol Modell 263:326–348

Shin Y-J, Rochet M-J, Jennings S, Field JG, Gislason H (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. ICES J Mar Sci 62:384–396

Smith TB (2008) Temperature effects on herbivory for an Indo-Pacific parrotfish in Panamá: implications for coral–algal competition. Coral Reefs 27:397–405

Smith JE, Hunter CL, Smith CM (2010) The effects of top–down versus bottom–up control on benthic coral reef community structure. Oecologia 163(2):497–507

Sotka EE, Hay ME (2009) Effects of herbivores, nutrient enrichment, and their interactions on macroalgal proliferation and coral growth. Coral Reefs 28:555–568

Targett TE, Targett NM (1990) Energetics of food selection by the herbivorous parrotfish Sparisoma radians: roles of assimilation efficiency, gut evacuation rate, and algal secondary metabolites. Mar Ecol Prog Ser 66:13–21

Taylor BM, Lindfield SJ, Choat JH (2015) Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. Ecography 38(5):520–530

Tebbett SB, Goatley CHR, Bellwood DR (2017) Clarifying functional roles: algal removal by the surgeonfishes Ctenochaetus striatus and Acanthurus nigrofuscus. Coral Reefs 36:803–813

Webster FJ, Babcock RC, Van Keulen M, Loneragan NR (2015) Macroalgae inhibits larval settlement and increases recruit mortality at Ningaloo Reef, Western Australia. PloS one 10(4):e0124162

Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. Mar Ecol Prog Ser 222:187–196