Original Research Article

Invertebrate herbivores: Overlooked allies in the recovery of degraded coral reefs?

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A B S T R A C T

A key question for coral reef conservation is whether reefs dominated by macroalgae can recover. Since the near-disappearance of the herbivorous urchin *Diadema antillarum* in the Caribbean, a prevalent management paradigm has focused on protecting herbivorous fishes to trigger shifts back to a coral-rich state. However, in the absence of *D. antillarum*, the contribution of other large macroinvertebrates to herbivory intensity has been largely overlooked. We used day and night field surveys and behavioural observations at 16 degraded reef patches in the Bahamas to measure the abundance of large herbivorous macroinvertebrates and their consumption of fleshy macroalgae. *Tripneustes* sea urchins and *Maguimithrax* crabs were the main herbivorous macroinvertebrates on our sites and were active mainly at night, with 97% of urchins and 45% of crabs observed consuming fleshy macroalgae. By comparison, < 5% of herbivorous fishes observed ate macroalgae. In the laboratory, *Tripneustes* sea urchins and *Maguimithrax* crabs readily consumed macroalgae (at rates of $0.19 \, \text{g h}^{-1}$ and $0.38 \, \text{g h}^{-1}$, respectively), but their low abundance on patch reefs (4 crabs and 2.3 urchins per reef, on average) translated into low overall rates of macroalgal removal. Perhaps for this reason, there was no relationship between the density of these large macroinvertebrates or their grazing rate and macroalgal cover on patch reefs. Nevertheless, we calculated that macroalgal consumption by *Maguimithrax* crabs alone could exceed macroalgae production with a doubling of their current low abundance; a 2.6-fold increase in *Tripneustes* urchin abundance would achieve the same result. Our results suggest that large herbivorous macroinvertebrates, some of which are currently the target of artisanal fishing in many Caribbean countries, could contribute greatly to the recovery of coral reefs with established macroalgal communities, at least in patch reef habitats.

1. Introduction

An increased abundance of fleshy macroalgae is an acknowledged sign of coral reef degradation (Jackson et al., 2014; Mumby et al., 2007). In the Caribbean, some reefs (e.g., in Jamaica) have shown rapid and persistent losses in coral cover and large increases in macroalgal abundance (Gardner et al., 2003; Hughes, 1994) in the wake of historical overfishing of herbivorous fishes (Jackson et al., 2001), severe hurricanes in the early 1980s (Gardner et al., 2005), the loss to disease of

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branching *Acropora* corals (Alvarez-Filip et al., 2009) and the herbivorous sea urchin *Diadema antillarum* (Lessios et al., 1984), and increasingly frequent and strong ocean warming events (Donner et al., 2007). The response of Caribbean reefs to this perfect storm of multiple stressors has not been even across the region and the extent to which Caribbean coral reefs have shifted from a coral-rich to a macroalgal-dominated state is contentious (Bruno et al., 2009). Overall, average macroalgal cover has hovered around 15–20% since the mid-1980s (Jackson et al., 2014; Schutte et al., 2010; Côté et al., 2013; Suchley et al., 2016). Nevertheless, there is regional disparity among locations in reef substrate composition, with some Caribbean reefs becoming truly dominated by macroalgae (Jackson et al., 2014). Macroalgal proliferation is cause for concern because macroalgae interfere with coral growth, fecundity, and recruitment, with cascading effects on reef complexity, reef-associated fauna, and the myriad services provided by these ecosystems (Mumby and Steneck, 2008; Perry et al., 2015).

A key question for coral reef conservation is whether degraded reefs dominated by macroalgae can recover. In the absence of *D. antillarum,* attention has focused on the role of herbivorous fishes as grazers of macroalgae (Bellwood et al., 2004; Mumby, 2006). This interest seems justified. Highly fished reefs with low herbivore abundance were among the first to shift to macroalgal dominance after *D. antillarum* died (e.g., Jamaica; Jackson et al., 2001). Moreover, multiple studies have documented a negative relationship between algal biomass and the abundance of herbivorous fishes (Burkepile et al., 2013; Mora, 2008; Newman et al., 2006; Williams and Polunin, 2001). As a result, there have been calls to protect herbivorous fishes to increase grazing intensity on reefs and trigger shifts back to a coral-rich state (Bozec et al., 2016; Hughes et al., 2010; Jackson et al., 2014; Mumby and Steneck, 2008; Cinner et al., 2009; Edwards et al., 2014; Kramer et al., 2015). However, there is increasing evidence that increases in fish biomass are not always associated with reductions in algal abundance (Ilves et al., 2011; Loh et al., 2015; Suchley et al., 2016). In addition, empirical evidence for coral recovery on reefs with abundant herbivorous fishes (e.g., within marine protected areas) is mixed (positive evidence: Mumby and Harborne, 2010; Selig and Bruno, 2010; no evidence: Cox et al., 2017; Guarderas et al., 2011; Kramer and Heck, 2007; McClanahan, 2008; Newman et al., 2006; Toth et al., 2014; Bruno et al., 2019). The role of herbivorous fishes on coral reefs might therefore be context-dependent (reviewed by Adam et al., 2015; Bruno et al., 2019) and vary, for example, with the extent of macroalgal defenses (e.g., Rasher et al., 2013; Briggs et al., 2018) and macroalgal abundance. Reefs that are heavily degraded may have crossed a threshold where feedback mechanisms that reinforce macroalgal dominance make recovery driven by fish herbivory difficult (Williams and Polunin, 2001; Williams et al., 2001; Mumby et al., 2007).

To date, the herbivory narrative for the Caribbean region has focused largely on fishes and, by comparison, the contribution of other grazers, such as nocturnal macroinvertebrates, has been relatively overlooked, especially in the post-*Diadema* era. Yet, in addition to *Diadema,* macroinvertebrates such as *Tripneustes* sea urchins and *Maguimithrax* herbivorous crabs are known to consume fleshy macroalgae (e.g., Butler and Mojica, 2012; Tertschnig, 1989), including species from the family Dictyotacea, which most often proliferate on degraded Caribbean reefs. Adults of these macroalgal species (*Dictyota* sp., *Padina* sp., *Lobophora* sp.) (McClanahan et al., 1999; Nugues and Bak, 2008) have chemical defenses such as polyphenolics and nonpolar metabolites (terpenes, acetogenins, and compounds of mixed terpenoid-aromatic biosynthesis) that deter most fish grazers (Briggs et al., 2018; Maschek and Baker, 2008). Moreover, when herbivorous invertebrates increase in abundance, as *Diadema* has done very patchily across Caribbean reefs (Rogers and Lorenzen, 2016), coral recruitment improves and algal cover declines (Edmunds and Carpenter, 2001; Carpenter and Edmunds, 2006; Myhre and Acevedo-Gutiérrez, 2007; Idjadi et al., 2010). Macroinvertebrate herbivores such as *Maguimithrax* crabs have received attention from a mariculture perspective (Creswell et al., 1989; Tunberg and Creswell, 1988), but the role of these invertebrates in driving algal dynamics remains unclear. The current picture of herbivory on Caribbean coral reefs is therefore incomplete, and conservation measures focused on enhancing herbivory might be more effective with an additional consideration of herbivorous invertebrates.

In this study, we ask whether large macroinvertebrate herbivores have the potential to exert sufficient herbivory pressure to recover degraded coral reef patches. We use field surveys and behavioural observations at 16 patch reefs in the Bahamas, conducted during the day and at night, as well as laboratory feeding assays, to quantify the abundance of large herbivorous macroinvertebrates and their consumption of macroalgae. We place these numbers in context by providing qualitative comparisons with the abundance and foraging targets of reef fishes on the same patch reefs, by estimating the daily production of macroalgae removed by invertebrate herbivores, and by relating the density and grazing rate of herbivorous macroinvertebrates to current benthic composition of patch reefs. Identifying additional species, beyond fishes, that can consume macroalgae on Caribbean reefs could lead to important insights to help guide conservation management action.

2. Methods

2.1. Study area

We studied 16 patch reefs in Rock Sound, a large, shallow (maximum depth: 7 m) basin at the southern end of Eleuthera Island, The Bahamas (Fig. S1). These reefs ranged in area from 8 to 212 m^2, in depth from 3 to 3.5 m, and were separated by at least 200 m of sand (mean distance to nearest reef = 512 m ± 265 m SD), which restricted inter-patch movement by all but the largest herbivores. The patch reefs had highly variable cover of Dictyotacea (1.4–69.2%), relatively low architectural complexity (rugosity 1.9 to 2.5; see Benthic Cover section), and variable coral cover (9.3–66.2%) (Table S1), characteristics that are representative of other patch reefs in the area (IMC, unpublished data) and within the range of what is observed on Caribbean reefs more generally (Schutte et al., 2010).

2.2. Invertebrate and fish surveys

We conducted two sets of diel surveys of macroinvertebrates and fishes at each site in May and June 2016. During each set, we visited each site twice during a 24-h period: once between 12:00 and 17:00 (day) and once between 22:00 and 03:00 (night). We estimated the abundance of all herbivorous and omnivorous fishes at each site using a 12–15 min roving snorkel survey during which each of two observers examined the entire reef area, starting at the periphery and moving to the top of the patch reef, and counted, sized, and identified fishes to species (Table S2). Fish size was estimated visually to the nearest cm, after observers were trained to correctly determine the lengths of plastic PVC pipes underwater. The numbers and locations of large herbivorous macroinvertebrates (in our area, this included only two species: the white urchin *Tripneustes ventricosus* and the West Indian spider (also known as king) crab *Maguimithrax spinosissimus*), predatory macroinvertebrates (i.e., the Caribbean spiny lobster *Panulirus argus*), and carnivorous fishes were recorded in a second 12–15 min roving snorkel survey, immediately following the first. In the second survey, the two observers thoroughly searched the periphery of the patch as well as crevices and overhangs to count and estimate the size (carapace width in the case of macroinvertebrates) to the nearest cm of all individuals (Table S2). Herbivorous macroinvertebrates were limited to larger species (>2–3 cm long) that divers could reliably identify and count during snorkel surveys. Note that more cryptic invertebrates such as buried crustaceans or echinoids were not observed in surveys, but may have been overlooked with this survey method. If the two independent observers differed in their counts for a given species, they discussed and reconciled these discrepancies post survey by comparing locations and sizes, and usually recorded the higher of the two counts. The trophic guilds of species were determined *a priori* from field guides (e.g., Humann and DeLoach, 2014), published literature (e.g., Butler and Mojica, 2012; Paddack et al., 2009; Tertschnig, 1989) and personal experience.

To quantify the diet of *T. ventricosus* and *M. spinosissimus,* the two species of herbivorous macroinvertebrates observed in the field, we recorded the type of any algae (mainly *Lobophora variegata* or *Laurencia* sp.) we saw crabs consume and we overturned each urchin to record the presence and type of algae or seagrass *Thalassia testudinum* in or around their mouth during day and night surveys. The algal fragments on the oral surface of urchins were always large enough to make species identification easy. We estimated grazing rates of invertebrates using ex situ feeding assays (see below).

To gain comparative insight into the diet of herbivorous and omnivorous fishes, we conducted daytime behavioural observations of 16 species of herbivorous fishes and 7 species of omnivorous fishes (107 individuals; mean 6.7 ± 8.2 SD individuals per species). Surveys were conducted at a minimum distance of 2–3 m from a focal individual and were abandoned if the presence of the observer appeared to influence fish behaviour. For each fish we recorded the number of bites and the substrate bitten (sponge, turf algae (including filamentous turfs, epilithic algae and branching coralline algae), macroalgae (as above), seagrass) in a 5-min period. We used a general turf algae category because fishes would often bite dead coral overgrown with epilithic algae, making it hard to determine which species they were consuming. Similarly, bites on *T. testudinum* might have included consumption of epiphytic organisms in addition to, or instead of, seagrass. We focused on *L. variegata* and *Laurencia* sp. because they were the only macroalgae species consumed by fishes and invertebrates during our observations, and together they comprised 91% of total macroalgal cover. Fish focal observations were evenly distributed across our 16 sites.

Finally, we classified the activity level of each herbivorous fish, urchin, and crab observed during day and night surveys as either active, if it was moving, defending territory, and/or consuming algae, or inactive if it was not moving or was hiding.

2.3. Benthic cover and physical factors

To estimate benthic community composition, we placed $0.25 \, m^2$ quadrats haphazardly around the periphery and across the top of each patch reef. The number of quadrats sampled per site varied with reef area; it was determined by calculating the number of quadrats needed to cover 90% of the area of our largest patch and downscaling this number for smaller sites ($<50 \, m^2 = 20$ quadrats, $50–100 \, m^2 = 25$ quadrats, and $>100 \, m^2 = 30$ quadrats, with total quadrat area covering 75–90% of the patch area). Each quadrat was photographed and benthic cover was obtained using the Excel-based program CPCe (Kohler and Gill, 2006), adding *Laurencia* sp. to the default substrate categories. We identified substrate type under 25 spatially random points per image to determine percent cover of coral, turf algae, dead coral with turf algae, sponge, *L. variegata*, *Laurencia* sp. and other macroalgae. A similarity analysis using 16 images (1 randomly selected image per reef) showed that selecting more than 25 points did not significantly increase accuracy of percent coral and algal cover estimates (Fig. S2).

We also measured rugosity, total hard bottom area, and maximum height of each patch reef. To measure rugosity we laid a 10-m chain on the reef patch following the reef contour, 4–10 times depending on reef area, and measured the linear distance between the ends of the chain. We calculated rugosity as the ratio of the chain length divided by linear distance between the chain ends, with higher values indicating a more rugose reef (Alvarez et al., 2009). Total hard bottom area was approximated by multiplying the lengths of the two widest perpendicular cross-sections of a patch. Maximum height was measured as the distance from the seafloor to the highest point on the patch.

2.4. Invertebrate herbivory rates

We determined daytime and nocturnal grazing rates of the two main herbivorous macroinvertebrate species: crabs (n = 9; mean carapace width: $124.4 \, mm \pm 20.5 \, mm$ SD) and urchins (n = 18; mean test diameter: $9.7 \, mm \pm 0.7 \, mm$ SD), using

feeding trials in outdoor flow-through seawater tanks (see Supplementary Material). All invertebrates were adults (i.e., >70 mm carapace width for *M. spinosissimus*, Baeza et al., 2012; >60−80 mm for *T. ventricosus*, Pena et al., 2010), collected from patch reefs in our study area within 24 h of the feeding trials. We provided either *L. variegata* (to urchins and crabs) or *Laurencia* sp. (to urchins only) to captive invertebrates and measured the total wet weight of algae immediately before and after each trial. Trials lasted 8 h, running from 09:00 to 17:00 for day trials or from 22:00 to 06:00 for night trials. Each individual crab or urchin was used in one day trial and one night trial, with only one algal species at a time. During each trial we also monitored autogenic changes in algal mass in control tanks containing only *L. variegata* or *Laurencia* sp.

To estimate overall invertebrate grazing rates on *T. testudinum, L. variegata*, and *Laurencia* sp., we combined hourly grazing rates for each species of invertebrate with their respective abundance data to calculate a total hourly grazing rate during the day (TGR_{DAY}) and night (TGR_{NIGHT}), at each reef site. We then extrapolated these values for each reef to a 24-h period (TGR_{24}), assuming that day and night each last 12 h.

2.5. Algal production

To estimate biomass of *L. variegata* per unit area on our patch reefs, we used razor blades to scrape off all *L. variegata* (adults and juveniles) in each of 10 circular quadrats (area: $0.078 \, m^2$) placed haphazardly on reef patches. Algae from each quadrat were collected in separate plastic bags, blotted dry at the surface, and weighed. We averaged these 10 biomass measures to obtain mean *L. variegata* biomass per unit area (wet weight g m^{-2}) and combined this estimate with the total grazing rate (TGR_{24}, g per 24 h) on *L. variegata* at each site to obtain the mean area grazed (in m^2) per 24 h.

Finally, we converted our biomass per unit area (wet weight g m^{-2}) measurements to g carbon per unit area using 0.0023% inorganic content for *L. variegata* (Thennarasan and Murugesan, 2015). We then compared daily consumption of *L. variegata* (g C m^{-2} d^{-1}) to average daily production rates of this species across the Caribbean (2.07 ± 0.51 g C m^{-2} d^{-1}; Table 5 in Paddack et al. (2006)).

2.6. Analyses

We evaluated the similarity of herbivore assemblages (herbivorous fishes, urchins, and crabs) across the two sets of surveys by correlating total counts of active herbivorous fishes, urchins and crabs during day and night between the two surveys. Total herbivore counts per reef were highly correlated across the two survey sets (Pearson's r = 0.79, n = 16, p < 0.001). We therefore averaged daytime counts and, separately, nighttime counts from the two surveys for each reef.

We estimated algal consumption rates (in g h^{-1}) from the feeding trials by calculating the difference in algal wet weight between the start and end of each trial. In trials without urchins or crabs, changes in algal weight were not significantly different from zero (*L. variegata* with crab: $t_5 = 0.18$, p = 0.86; *L. variegata* with urchin: $t_5 = 0.99$, p = 0.37; *Laurencia* sp. with urchin: $t_5 = 0.61$, p = 0.57), hence we did not correct for autogenic changes in algal mass. Consumption rates of urchins were analysed using a two-way ANOVA (fixed factor Time: day and night; fixed factor Diet: *L. variegata* and *Laurencia* sp.). We compared consumption rates of crabs during day and night trials using a Student's *t*-test.

Finally, we used linear models to test for relationships between macroinvertebrate density and total daily grazing rate (TGR_{24}) (response variables) and coral, turf algae and macroalgal cover as well as reef rugosity and height (explanatory variables).

3. Results

3.1. Abundance of reef herbivores

Fishes were the most abundant active herbivores on patch reefs, comprising 91% of the total herbivore abundance across all sites (Fig. 1). Parrotfishes occurred at the highest densities (Fig. 1) and made up 73% of all herbivorous fishes. Parrotfishes ranged in size from 2 to 50 cm total length (TL), with the majority (86%) being < 15 cm TL. Other groups of herbivorous fishes present on the patches were damselfishes (Pomacentridae) and surgeonfishes (Acanthuridae) (Fig. 1). The most abundant omnivorous fish were sharpnose puffers (*Canthigaster rostrata*; Tetraodontidae), angelfishes (Pomacanthidae), and planktivorous damselfishes (Pomacentridae; Table S2). Omnivorous fishes were rarely observed grazing algae, and were therefore omitted from further analyses. *Maguimithrax spinosissimus* crabs and *Tripneustes ventricosus* urchins were the only herbivorous macroinvertebrates observed in our surveys and occurred at low average densities across reef sites (Fig. 1). A total of 66 *M. spinosissimus* and 36 *T. ventricosus* were observed across the 16 reef sites. No *Diadema antillarum* urchins were observed at reef sites during the study.

Herbivorous fishes were active and observed feeding only in the daytime, in contrast to herbivorous macroinvertebrates, which were predominantly active at night (Fig. 2). Any observations of actively swimming fishes at night appeared to be the result of disturbance from observers. Active crabs and urchins were occasionally observed during the day (Fig. 2), but these individuals were usually hidden within the reef and rarely observed feeding. At night, both invertebrate species were observed moving and feeding on the reef patches. This was particularly dramatic for crabs, which were typically found atop dense patches of *Lobophora variegata,* pulling off large fragments of algae with their claws and consuming them.
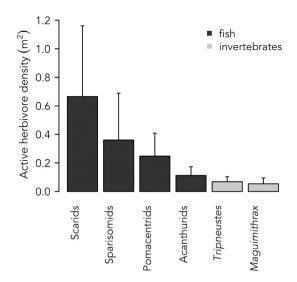
Fig. 1. Average density of active individuals (mean ± SD) in six herbivore groups on 16 coral reef patches in Eleuthera, The Bahamas. Groups are herbivorous fishes (scarid parrotfishes, sparisomid parrotfishes, pomacentrids, acanthurids), *Tripneustes ventricosus* urchins, and *Maguimithrax spinosissimus* crabs. Density estimates were derived from daytime and nighttime surveys.
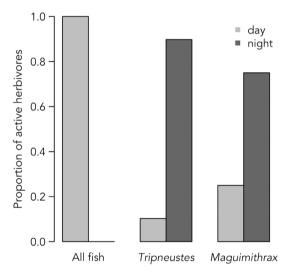

Fig. 2. Proportion of herbivores that were active during the day and at night for all herbivorous fishes (scarids, sparisomids, pomacentrids, acanthurids), *Tripneustes ventricosus* urchins, and *Maguimithrax spinosissimus* crabs on 16 coral reef patches in Eleuthera, The Bahamas.

3.2. Diet of reef herbivores

Field observations. There were large differences in food type use between herbivore groups. Herbivorous fishes fed predominantly on turf algae and on seagrass *Thalassia testudinum* (or epiphytes on seagrass) adjacent to the reefs. Macro-invertebrates fed primarily on the fleshy macroalga *L. variegata*. Of 107 focal fish observations, we only recorded five individual fish feeding on *L. variegata,* including two instances where the focal fish rejected the macroalga after biting it. Collectively, the 107 fishes observed took 7829 bites during our observations, and only 122 of these bites (<2%) were taken on macroalgae. None of the fishes consumed *L. variegata* as their primary food source; the highest consumption rate was 8% of bites by one stoplight parrotfish (*Sparisoma viride*). In contrast, 45% of *M. spinosissimus* crabs and 97% of *T. ventricosus* urchins observed were consuming *L. variegata*.

Ex situ feeding trials. *T. ventricosus* urchins and *M. spinosissimus* crabs consumed macroalgae during both day and night feeding trials, resulting in algal mass losses (Fig. 3). Average per capita algal consumption rate over 24 h by crabs ($0.38 \pm 0.10\,\mathrm{g\,h^{-1}}$) was twice as high as that by urchins ($0.19\,\mathrm{g\,h^{-1}} \pm 0.06\,\mathrm{g\,h^{-1}}$). There was no effect of algal species ($F_{1,32} = 1.15$, $P = 0.29$) or time of day (i.e., day vs night; $F_{1,32} = 2.06$, $P = 0.16$), and no interaction between the two ($F_{1,32} = 1.05$,
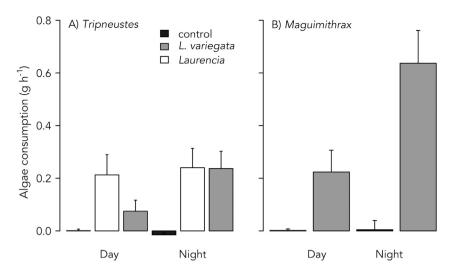
Fig. 3. Daytime and nighttime average consumption rates per hour of the macroalgae *Lobophora variegata* and *Laurencia* sp. by A) *Tripneustes ventricosus* urchins and B) *Maguimithrax spinosissimus* crabs in laboratory feeding trials. Means are shown + 1SD. Control trials contained algae without an invertebrate herbivore. N = 6 in all cases.

$P = 0.31$), on the consumption rate of urchins (Fig. 3a), indicating that *T. ventricosus* foraged equally on both algal species by day and night. In contrast, there was a significant effect of time of day on feeding rates of *M. spinosissimus*, with crabs consuming more *L. variegata* at night than during the day ($t_{16} = -2.76$, $P = 0.011$; Fig. 3b).

3.3. Daily algal removal rates by reef macroinvertebrates

The average biomass to area ratio of *L. variegata* was $0.29 \pm 0.17 \, \text{kg m}^{-2}$. Estimated daily consumption rates of standing *L. variegata* biomass by *M. spinosissimus* and *T. ventricosus*, derived from the ex situ feeding trials, were almost all below estimated daily algal production rates for each reef (Fig. 4). Consumption greatly exceeded production on only one reef, which had very low *L. variegata* abundance (1.36% cover; Fig. 4). Excluding this reef, the average consumption rate of *L. variegata* by macroinvertebrates was $45 \pm 31\%$ of estimated daily production of *L. variegata*. This was equivalent to an average of $5.1 \pm 4.0\%$ of the total cover and $0.3 \pm 0.2\%$ of the current biomass of *L. variegata* on each reef.
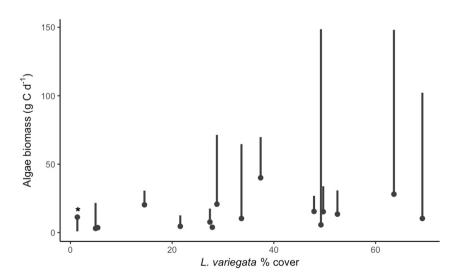

Fig. 4. Daily biomass (g C) of *Lobophora variegata* consumed by invertebrate herbivores in relation to the percent cover of *L. variegata* at each of 16 patch reef sites in Eleuthera, The Bahamas. Vertical lines show the direction and magnitude of additional consumption rates needed to equal algal production rates based on a growth rate of *L. variegata* of $2.07 \, \text{g C m}^{-2}$ per day (Paddack et al. 2006). The asterisk denotes the only reef where current algal consumption by invertebrate herbivores exceeds algal production.

3.4. Benthic composition

Description of benthic composition. Reef patches were mainly covered in fleshy macroalgae (36.6% ± 21.4% SD) and turf algae (17.1% ± 13.2), and had lower coral (25.7% ± 18.9% SD) and sponge cover (11.3% ± 9.1% SD). *L. variegata* was the dominant macroalga, covering over one-third of the total substrate. Other macroalgae included *Laurencia* sp., *Avrainvillea* sp., and *Batophora* sp., which collectively covered 2.8% of the reef patches.

Herbivory and benthic composition. We found no relationship between our estimate of herbivory intensity by macroinvertebrates and the benthic composition of reefs. The percent cover of turf algae, *L. variegata*, and hard coral at each site was not related to estimated daily rates of algal consumption by macroinvertebrates (Pearson's r < 0.23, p > 0.31 in all cases) (Fig. S3). We also found no relationship between benthic composition and macroinvertebrate density or benthic composition and herbivorous fish density (Pearson's r < 0.32, p > 0.21 in all cases) (Fig. S4). Similarly, there was no relationship between macroinvertebrate density and reef rugosity (Pearson's r = −0.02, p = 0.93) or reef height (Pearson's r = −0.36, p = 0.18).

4. Discussion

Bahamian patch reefs host several groups of macroherbivores. As expected, fishes, especially parrotfishes, dominated in terms of abundance, but they were active only by day and fed primarily on turf algae and seagrass and/or their epiphytes. Macroinvertebrates − the herbivorous crab *Maguimithrax spinosissimus* and the white urchin *Tripneustes ventricosus* − were less abundant and foraged mainly at night, but were the main consumers of the dominant fleshy macroalga *Lobophora variegata*. As a result of the low abundance of the two main species of herbivorous macroinvertebrates on our reef sites, only ~45% of the daily production of *L. variegata* on our patch reefs is estimated to be removed by herbivore grazers. Perhaps because of this low overall rate of macroalgal removal, we found no relationship between our estimates of macroinvertebrate herbivory (in terms of density or grazing rate) and benthic composition of reef patches, including coral and macroalgal cover. However, the identification of large macroinvertebrates as effective consumers of fleshy macroalgae suggests that efforts to recover degraded reefs might benefit from targeting herbivorous macroinvertebrate populations.

4.1. Who consumes macroalgae?

Herbivorous fishes on our patch reefs are clearly not filling the role of consumers of established fleshy macroalgae. Fishes almost exclusively grazed on turf algae and the seagrass *T. testudinum* and/or its epiphytes. This may be partly due to small sizes of fishes on our patch reefs in our study area. However, although large sparisomid parrotfishes do browse on erect macroalgae (e.g., Adam et al., 2015), multiple studies have shown that most Caribbean herbivorous fish species target mainly palatable algae, such as turf, juveniles of macroalgae, and epilithic algae, and avoid large unpalatable macroalgae (Adam et al., 2015; Briggs et al., 2018; Burkepile and Hay, 2010; Carpenter, 1986). For example, on Curaçao reefs, parrotfishes and surgeonfishes grazed almost exclusively on turf algae (Vermeij et al., 2010), as they did in the present study. Moreover, close examination of a seminal study of stoplight parrotfish (*Sparisoma viride*) foraging, which is widely used to extrapolate macroalgal removal rates, reveals that fleshy brown macroalgae (e.g., *Dictyota* spp., *L. variegata*) were exceedingly rare among the 'large turfs' consumed, and in fact *S. viride* at all life stages targeted mainly sparse turf (<3.5 mm high) (Bruggemannn et al., 1994). These findings are difficult to reconcile with the important role ascribed to herbivorous fishes, especially parrotfishes, as effective grazers of fleshy macroalgae in models of Caribbean coral reef dynamics (e.g., Bozec et al., 2016; Mumby, 2006; Mumby et al., 2006).

Two nocturnal macroinvertebrates were responsible for virtually all removal of fleshy macroalgae on our patch reefs. In captivity, the large herbivorous crab *M. spinosissimus* consumed *Lobophora variegata* at a rate of ~0.64 g h^{-1} at night. An even higher macroalgal consumption rate was measured for captive *D. spinosissimus* in the Florida Keys (day: 5.2 g h^{-1}, night: 8.0 g h^{-1}) (Butler and Mojica, 2012). The white urchin *T. ventricosus* also contributed to nocturnal herbivory on our patch reefs, at a lower rate (~0.24 g h^{-1} in captivity) but on both *L. variegata* and *Laurencia* sp. Both species therefore have the potential to exert top-down pressure on macroalgae if these consumption rates are realized in the wild.

The finding that invertebrates are potentially important consumers of macroalgae should not be surprising. *Diadema antillarium* was one of the most ecologically important herbivores in Caribbean. Its disappearance triggered the overgrowth of macroalgae on many coral reefs (Jackson et al., 2001), and its recovery in some locations has been accompanied by declines in macroalgal cover (Edmunds and Carpenter, 2001; Carpenter and Edmunds, 2006; Myhre and Acevedo-Gutiérrez, 2007; Idjadi et al., 2010; see also Macia et al., 2007 for an experimental demonstration). The mismatch between the timing of invertebrate activity − both *Tripneustes* urchins and *Maguimithrax* crabs were less active and less visible during the day − and usual researcher observations might explain why these other invertebrate species are rarely, if ever, considered in discussions of macroalgae dynamics. Indeed, a Web of Science search for ("coral reef" OR "coral reefs") AND herbivor* NOT (night OR nocturnal OR crepuscular OR twilight) returned 1077 studies compared to only 21 when the keywords related to nighttime were included. Our results suggest that overlooking the activity of nocturnal reef organisms can lead to a biased understanding of herbivory on coral reefs.

4.2. Herbivores and benthic composition

Benthic composition of reef patches did not covary with any measure of herbivory pressure by macroinvertebrates. The lack of expected negative relationships between macroalgae cover and the abundance of macroalgae consumers or rate of macroalgae consumption by invertebrates is most likely due to the very low densities of herbivorous crabs and urchins. At almost all sites, the estimated consumption rates of *L. variegata* by *Maguimithrax* crabs and *Tripneustes* urchins were not enough to outpace estimated growth rates of this macroalga. A single site had higher macroalgal consumption than production and two other reefs had nearly equal macroalgal production and consumption (Fig. 4). These three sites had high coral and sponge cover and very low macroalgal cover, suggesting some form of effective control on macroalgal growth.

We also found no relationship between herbivorous fish density and either macroalgal, turf or coral cover (Fig. S4). The latter is not surprising, given the growing empirical evidence that abundant herbivorous fishes seldom lead to coral recovery in the Caribbean (e.g., Cox et al., 2017; Guarderas et al., 2011; McClanahan, 2008; Suchley et al., 2016; Toth et al., 2014; Bruno et al., 2019). In contrast, many have reported a negative association between herbivorous fish biomass and macroalgal cover (Burkepile et al., 2013; Mora, 2008; Newman et al., 2006; Williams and Polunin, 2001). There are several potential explanations for the absence of such a relationship in our system. First, the cover of fleshy macroalgae was relatively high (~37% on average), which might have exceeded the threshold beyond which the herbivorous fish community can keep the substrate cropped (Williams and Polunin, 2001; Williams et al., 2001). Second, variation in feeding preferences of herbivorous fishes might have opposing effects on macroalgal abundance. For example, in enclosure experiments in Florida, grazing by redband parrotfish *Sparisoma aurofrenatum* reduced upright macroalgal cover, while grazing by ocean surgeon *Acanthurus bahianus* and princess parrotfish *Scarus taeniopterus* increased it (Burkepile and Hay, 2010). Redband parrotfish were moderately common on our study patches, but *Scarus* species and stoplight parrotfish *Sparisoma viride*, which forages more like a turf-grazing scarid than a macroalgal-browsing sparisomid (Adam et al., 2015), were far more abundant (Table S2). Third, a large proportion of herbivorous fishes on our patch reefs were small (<15 cm), and it has been argued that juvenile herbivorous fishes might have a minor impact on the benthos and do not target macroalgae compared to large herbivorous fishes (Bruggemann et al., 1994). Finally, there are important abiotic factors (e.g., episodic thermal stress and bleaching) that can drive coral mortality and/or algal growth more strongly than herbivory.

4.3. Implications for coral reef management

Our results suggest that management efforts to promote coral reef recovery, at least on reefs such as those we studied, should perhaps aim to increase large herbivorous invertebrates. In particular, our results highlight the potential importance of targeting crab and urchin macroinvertebrate species that still occur on degraded reefs, but have been overlooked in the past. As an initial exploration of this strategy, we estimated how many additional *Maguimithrax* crabs would be required to outpace macroalgal production on each reef by taking each reef-specific shortfall in macroalgal consumption (Fig. 4) and dividing it by the daily consumption rate of crabs calculated from our feeding trials (10.3 g d^{-1} crab^{-1}; Fig. 3). Increases in crab density on the order of 0.06 crabs m^{-2} (i.e., a doubling of the average density observed), or on average 4.7 ± 4.6 (SD) crabs per patch reef (range: 0.1–9.7 crabs per reef), should be enough to control macroalgae on many of the reefs. Due to their much lower per capita consumption rates of *L. variegata* (3.7 g d^{-1} urchin^{-1}; Fig. 3), a larger increase in *Tripneustes* urchin density, on the order of 0.18 urchins m^{-2} or 260% over the average density observed, would be necessary to outpace macroalgal production. These calculations obviously assume that the algal consumption rates measured in captivity can be extrapolated to the wild, and we do not know whether this is the case. Feeding rates in mesocosms could be overestimated because search time for food is reduced in a confined space, or underestimated if the stress associated with capture and confinement leads to decreased willingness to feed. Our calculations could also be biased if *L. variegata* production rates are higher or lower than the average value we considered. Nevertheless, it seems safe to conclude that increases in herbivorous macroinvertebrate numbers would help to curb the proliferation of macroalgae.

How can herbivorous macroinvertebrate populations be increased? The density of *M. spinosissimus* in our study area is 5–7 times higher than it was in other areas of the Caribbean a decade ago, but similar to the only available contemporary estimate (i.e., 0.06 crabs m^{-2}; reeflifesurvey.com, Table S3). This low abundance in absolute terms might be in part due to habitat changes and to current and past fishing pressure, although data on historical population trends of this species are too limited to tell. Coral loss to disease and bleaching and the concomitant reduction in structural complexity and refuge availability (Alvarez-Filip et al., 2009) might contribute to maintaining low densities of these large herbivorous macroinvertebrates. Moreover, in the Bahamas, as elsewhere in the Caribbean, *M. spinosissimus* is the target of unregulated artisanal harvesting (personal observations). Similarly, populations of *T. ventricosus* have experienced heavy fishing pressure in some areas of The Bahamas and many other Caribbean islands (e.g., Scheibling and Mladenov, 1987). For example, adult urchin densities on unfished reefs in Barbados were once as high as 3.8 individuals m^{-2} (Scheibling and Mladenov, 1987; Table S3). Such densities, which are nearly 40 times higher than those we observed, would be sufficient to make macroalgal consumption by invertebrates surpass macroalgae production on all of our study reefs. However, again, lack of historical data make it difficult to determine if these densities could be supported on our study patch reefs. Regardless, restricting the artisanal fisheries targeting these invertebrates may be one conservation intervention that could lead to higher densities, although it would likely have impacts on local communities. Alternatively, the potential for captive culture of *M. spinosissimus* (Tunberg and Creswell, 1988; Creswell et al., 1989; Spadaro, 2014) and the strong potential for aquaculture of *T. ventricosus* (Lawrence and Bazhin,

1998) might offer an attractive option from both community and conservation viewpoints. Manipulative studies looking at the impacts of varying densities of these grazers (e.g., increased bioerosion of reefs from urchin grazing) would be necessary prior to any attempts at increasing reef-wide densities using these strategies.

Are herbivorous fishes still important in coral reef conservation? Although our results suggest that herbivorous fishes might not be the key to shifting macroalgal-rich reefs to a macroalgal-poor state in our study system, they are likely to be important for preventing the initial phase shift (Burkepile and Hay, 2010). Algal settlers are more palatable and less chemically defended than upright macroalgae and are readily consumed by most herbivorous fishes (Briggs et al., 2018; Bruggemannn et al., 1994). Multiple grazer-exclusion experiments show that excluding herbivorous fishes from an area of reef can result in rapid recruitment and/or growth of macroalgae on bare or cropped substrates (e.g., Diaz-Pulido and McCook, 2003; Suchley and Alvarez-Filip, 2017; Vermeij et al., 2010). In contrast, once fleshy macroalgae are established, fishes do not appear to control them with grazing, and might even facilitate growth (e.g., Burkepile et al., 2013). In other words, the ability of herbivorous fishes to control macroalgae cover might depend on the stage of a phase shift, because the herbivores that inhibit the initial growth of macroalgae are different than those that can remove established macroalgae (see also Chong-Seng et al., 2014). Increasing herbivorous fish densities should therefore be an effective solution to prevent phase shifts on coral reefs, but a less effective strategy to reverse them.

Author contributions

FTF, KFD and IMC conceived the ideas and designed the methodology; FTF, KFD, HFY and IMC collected the data; FTF and KFD analysed the data; FTF, KFD and IMC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Appendix A. Supplementary data

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References

Adam, T.C., Burkepile, D.E., Ruttenberg, B.I., Paddack, M.J., 2015. Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. Mar. Ecol. Prog. Ser. 520, 1–20.

Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., Watkinson, A.R., 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proc. Roy. Soc. Lond. B: Biol. Sci. 276, 3019–3025.

Baeza, J.A., Anderson, J.R., Spadaro, A.J., Behringer, D.C., 2012. Sexual dimorphism, allometry, and size at first maturity of the Caribbean king crab, *Mithrax spinosissimus*, in the Florida Keys. J. Shellfish Res. 31, 909–916.

Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. Nature 429, 827–833.

Bozec, Y.M., O'Farrell, S., Bruggemannn, J.H., Luckhurst, B.E., Mumby, P.J., 2016. Tradeoffs between fisheries harvest and the resilience of coral reefs. Proc. Natl. Acad. Sci. U.S.A. 113, 4536–4541.

Briggs, C.J., Adam, T.C., Holbrook, S.J., Schmitt, R.J., 2018. Macroalgae size refuge from herbivory promotes alternative stable states on coral reefs. PLoS One 13, e0202273.

Bruggemannn, J.H., Van Oppen, M.J., Breeman, A.M., 1994. Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. Mar. Ecol. Prog. Ser. 106, 41–55.

Bruno, J.F., Sweatman, H., Precht, W.F., Selig, E.R., Schutte, V.G.W., 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90, 1478–1484.

Bruno, J.F., Côté, I.M., Toth, L.T., 2019. Climate change, coral loss, and the curious case of the parrotfish paradigm: why don't Marine Protected Areas improve reef resilience? Annu. Rev. Mar. Sci. 11, 307–334.

Burkepile, D.E., Hay, M.E., 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. PLoS One 5, e8963.

Burkepile, D.E., Allgeier, J.E., Shantz, A.A., Pritchard, C.E., Lemoine, N.P., Bhatti, L.H., Layman, C.A., 2013. Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. Sci. Rep. 3, 1493.

Butler, M.J., Mojica, A.M., 2012. Herbivory by the Caribbean king crab on coral patch reefs. Mar. Biol. 159, 2697–2706.

Carpenter, R.C., 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecol. Monogr. 56, 345–364.

Carpenter, R.C., Edmunds, P.J., 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. Ecol. Lett. 9, 271–280.

Chong-Seng, K.M., Nash, K.L., Bellwood, D.R., Graham, N.A.J., 2014. Macroalgal herbivory on recovering versus degrading coral reefs. Coral Reefs 33, 409–419.

Cinner, J.E., McClanahan, T.R., Graham, N.A.J., Pratchett, M.S., Wilson, S.K., Raina, J.-B., 2009. Gear-based fisheries management as a potential adaptive response to climate change and coral mortality. J. Appl. Ecol. 46, 724–732.

Côté, I.M., Precht, W.F., Aronson, R.B., Gardner, T.A., 2013. Is Jamaica a good model for understanding Caribbean coral reef dynamics? Mar. Pollut. Bull. 76, 28–31.

Cox, C., Valdivia, A., McField, M., Castillo, K., Bruno, J.F., 2017. Establishment of marine protected areas alone does not restore coral reef communities in Belize. Mar. Ecol. Prog. Ser. 563, 65–79.

Creswell, R.L., Tunberg, B.G., Winfree, R.A., 1989. Mariculture of the Caribbean king crab, *Mithrax spinosissimus* (Lamarck), in the Caribbean region: progress and constraints. Proc. Gulf Caribb. Fish. Inst. 39, 469–476.

Diaz-Pulido, G., McCook, L.J., 2003. Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84, 2026–2033.

Donner, S.D., Knutson, T.R., Oppenheimer, M., 2007. Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. Proc. Natl. Acad. Sci. U.S.A. 104, 5483–5488.

Edmunds, P.J., Carpenter, R.C., 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proc. Natl. Acad. Sci. U.S.A. 98, 5067–5071.

Edwards, C.B., Friedlander, A.M., Green, A.G., Hardt, M.J., Sala, E., Sweatman, H.P., Williams, I.D., Zgliczynski, B., Sandin, S.A., Smith, J.E., 2014. Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. Proc. Roy. Soc. Lond. B 281, 20131835.

Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-term region-wide declines in Caribbean corals. Science 301, 958–960.

Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2005. Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. Ecology 86, 174–184.

Guarderas, A.P., Hacker, S.D., Lubchenco, J., 2011. Ecological effects of marine reserves in Latin America and the Caribbean. Mar. Ecol. Prog. Ser. 429, 219–225.

Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265, 1547–1551.

Hughes, T.P., Graham, N.A.J., Jackson, J.B., Mumby, P.J., Steneck, R.S., 2010. Rising to the challenge of sustaining coral reef resilience. Trends Ecol. Evol. 25, 633–642.

Humann, P., DeLoach, N., 2014. Reef Fish Identification: Florida, Caribbean, Bahamas, fourth ed. New World Publications, Jacksonville, FL.

Idjadi, J.A., Haring, R.N., Precht, W.F., 2010. Recovery of the sea urchin *Diadema antillarum* promotes scleractinian growth and survivorship on shallow Jamaican reefs. Mar. Ecol. Prog. Ser. 403, 91–100.

Ilves, K.L., Kellogg, L.L., Quattrini, A.M., Chaplin, G.W., Hertler, H., Lundberg, J.G., 2011. Assessing 50-year change in Bahamian reef fish assemblages: evidence for community response to recent disturbance? Bull. Mar. Sci. 87, 567–588.

Jackson, J., Donovan, M., Cramer, K., Lam, V., 2014. Status and Trends of Caribbean Coral Reefs: 1970–2012. ICUN Global Coral Reef Monitoring Network, Gland, Switzerland.

Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–637.

Kohler, K.E., Gill, S.M., 2006. Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comput. Geosci. 32, 1259–1269.

Kramer, K.L., Heck Jr., K.L., 2007. Top-down trophic shifts in Florida Keys patch reef marine protected areas. Mar. Ecol. Prog. Ser. 349, 111–123.

Kramer, P., McField, M., Álvarez Filip, L., Drysdale, I., Rueda Flores, M., Giró, A., Pott, R., 2015. Report card for the Mesoamerican Reef. Health Reefs Initiative. Available at: http://www.healthyreefs.org.

Lawrence, J.M., Bazhin, A., 1998. Life-history strategies and the potential of sea urchins for aquaculture. J. Shellfish Res. 17, 1515–1522.

Lessios, H.A., Robertson, D.R., Cubit, J.D., 1984. Spread of *Diadema* mass mortality through the Caribbean. Science 226, 335–337.

Loh, T.-L., McMurray, S.E., Henkel, T.P., Vicente, J., Pawlik, J.R., 2015. Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. PeerJ 3, e901.

Macia, S., Robinson, M.O., Nalevanko, A., 2007. Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a coral reef. Mar. Ecol. Prog. Ser. 348, 173–182.

Maschek, J.A., Baker, B.J., 2008. The chemistry of algal secondary metabolism. In: Amsler, C.D. (Ed.), Algal Chemical Ecology. Springer, Berlin, pp. 1–24.

McClanahan, T.R., 2008. Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. Oecologia 155, 169–177.

McClanahan, T.R., Aronson, R.B., Precht, W.F., Muthiga, N.A., 1999. Fleshy algae dominate remote coral reefs of Belize. Coral Reefs 18, 61–62.

Mora, C., 2008. A clear human footprint in the coral reefs of the Caribbean. Proc. Roy. Soc. Lond. B: Biol. Sci. 275, 767–773.

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

Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W., Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311, 98–101.

Mumby, P.J., Hastings, A., Edwards, H.J., 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450, 98–101.

Mumby, P.J., Steneck, R.S., 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol. Evol. 23, 555–563.

Mumby, P.J., Harborne, A.R., 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS One 5, e8657.

Myrhe, S., Acevedo-Gutiérrez, A., 2007. Recovery of sea urchin *Diadema antillarum* populations is correlated with increased coral and reduced macroalgal cover. Mar. Ecol. Prog. Ser. 329, 205–210.

Newman, M.J., Paredes, G.A., Sala, E., Jackson, J.B., 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. Ecol. Lett. 9, 1216–1227.

Nugues, M.M., Bak, R.P.M., 2008. Long-term dynamics of the brown macroalga *Lobophora variegata* on deep reefs in Curaçao. Coral Reefs 27, 389–393.

Paddack, M.J., Cowen, R.K., Sponaugle, S., 2006. Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. Coral Reefs 25, 461–472.

Paddack, M.J., Reynolds, J.D., Aguilar, C., Appeldoorn, R.S., Beets, J., Burkett, E.W., Chittaro, P.M., Clarke, K., Esteves, R., Fonseca, A.C., Forrester, G.E., Friedlander, A.M., García-Saís, J., Gonzalez-Sanson, G., Jordan, L.K.B., McClellan, D.B., Miller, M.W., Molloy, P.P., Mumby, P.J., Nagelkerken, I., Nemeth, M., Navas-Camacho, R., Pitt, J., Polunin, N.V.C., Reyes-Nivía, M.C., Robertson, D.R., Rodriguez-Ramirez, A., Salas, E., Smith, S.R., Spieler, R.E., Steele, M.A., Williams, I.D., Wormald, C.L., Watkinson, A.R., Côté, I.M., 2009. Recent region-wide declines in Caribbean reef fish abundance. Curr. Biol. 19, 590–595.

Pena, M., Oxenford, H.A., Parker, C., Johnson, A., 2010. Biology and fishery management of the white sea urchin, Tripneustes ventricosus, in the eastern Caribbean. In: FAO Fisheries and Aquaculture Circular NO. 1056. FAO, Rome.

Perry, C.T., Steneck, R.S., Murphy, G.N., Kench, P.S., Edinger, E.N., Smithers, S.G., Mumby, P.J., 2015. Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. Glob. Chang. Biol. 21, 1153–1164.

Rasher, D.B., Hoey, A.S., Hay, M.E., 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. Ecology 94, 1347–1358.

Rogers, A., Lorenzen, K., 2016. Does slow and variable recovery of *Diadema antillarum* on Caribbean fore-reefs reflect density-dependent habitat selection? Front Mar. Sci. 3, 63.

Scheibling, R.E., Mladenov, P.V., 1987. The decline of the sea urchin, *Tripneustes ventricosus*, fishery of Barbados: a survey of fishermen and consumers. Mar. Fish. Rev. 49, 62–69.

Schutte, V.G., Selig, E.R., Bruno, J.F., 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. Mar. Ecol. Prog. Ser. 402, 115–122.

Selig, E.R., Bruno, J.F., 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. PLoS One 5, e9278.

Spadaro, A.J., 2014. Caribbean coral reef restoration: a brief review and concept proposal of a new method. Proc. Gulf Caribb. Fish. Inst. 67, 374–377.

Suchley, A., Alvarez-Filip, L., 2017. Herbivory facilitates growth of a key reef-building Caribbean coral. Ecol. Evol. 7, 11246–11256.

Suchley, A., McField, M.D., Alvarez-Filip, L., 2016. Rapidly increasing macroalgal cover not related to herbivorous fishes on Mesoamerican reefs. PeerJ 4, e2084.

Tertschnig, W.P., 1989. Diel activity patterns and foraging dynamics of the sea urchin *Tripneustes ventricosus* in a tropical seagrass community and a reef environment (Virgin Islands). Mar. Ecol. 10, 3–21.

Thennarasan, S., Murugesan, S., 2015. Biochemical composition of marine brown alga Lobophora variegata from Mandapam in the South East Coast of Tamil Nadu. Intl J. Phytopharm. 5, 25−29.

Toth, L.T., van Woesik, R., Murdoch, T.J.T., Smith, S.R., Ogden, J.C., Precht, W.F., Aronson, R.B., 2014. Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. Coral Reefs 33, 565−577.

Tunberg, B.G., Creswell, R.L., 1988. Early growth and mortality of the Caribbean king crab *Mithrax spinisissimus* reared in the laboratory. Mar. Biol. 98, 337−343.

Vermeij, M.J., Van Moorselaar, I., Engelhard, S., Hörnlein, C., Vonk, S.M., Visser, P.M., 2010. The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. PLoS One 5, e14312.

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

Williams, I.D., Polunin, N.V., Hendrick, V.J., 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.