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Mark J. Butler & Angela M. Mojica

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Mark J. Butler IV · Angela M. Mojica

Abstract Caribbean coral reefs are increasingly dominated by macroalgae instead of corals due to several factors, including the decline of herbivores. Yet, virtually unknown is the role of crustacean macrograzers on coral reef macroalgae. We examined the effect of grazing by the Caribbean king crab (*Mithrax spinosissimus*) on coral patch reef algal communities in the Florida Keys, Florida (USA), by: (1) measuring crab selectivity and consumption of macroalgae, (2) estimating crab density, and (3) comparing the effect of crab herbivory to that of fishes. *Mithrax* prefers fleshy macroalgae, but it also consumes relatively unpalatable calcareous algae. Per capita grazing rates by *Mithrax* exceed those of most herbivorous fish, but *Mithrax* often occurs at low densities on reefs and its foraging activities are reduced in predator-rich environments. Therefore, the effects of grazing by *Mithrax* tend to be localized and when at low density contribute primarily to spatial heterogeneity in coral reef macroalgal communities.

Introduction

Many coral reefs worldwide are undergoing an ecological phase shift from coral dominance to reefs overgrown by macroalgae (Wilkinson 1996; McCook 1999; Bruno et al. 2007). Chronic stressors such as eutrophication, coral disease, climate change, and overfishing in combination with acute disturbances (e.g., hurricanes) degrade reef

M. J. Butler IV (✉) · A. M. Mojica
Department of Biological Sciences, Old Dominion
University, Norfolk, VA 23529, USA
e-mail: mbutler@odu.edu

resilience, promote phase shifts, and threaten the persistence of coral reefs (Carpenter et al. 2008). The problems are particularly acute in the Caribbean where the loss of important herbivores has contributed greatly to this change (Hughes 1994; Aronson and Precht 2001; Gardner et al. 2003). Herbivores such as the sea urchin *Diadema antillarum*, whose populations were decimated by an unidentified pathogen (Lessios et al. 1984; Lessios 1988), and herbivorous fishes that have declined due to overfishing (Mumby 2006) are crucial for the control of macroalgae (Ogden and Lobel 1977; Lewis 1986; Hay 1997) that are superior competitors for space on coral reefs (Hughes 1994; Aronson and Precht 2006). On healthy reefs, macroalgal dominance is prevented by a diverse group of herbivores (Hughes et al. 1987; Klumpp and Pulfrich 1989; Mumby et al. 2007). The effects of fish and urchin herbivory on coral reefs are well known (Hatcher and Larkum 1983; Carpenter 1988; Hay and Steinberg 1992; Hay 1997; Hay et al. 2004), but less known are the effects of herbivory by other reef-dwelling invertebrates such as crabs (Stachowicz and Hay 1996), chitons (Littler et al. 1995), and limpets (Steneck 1982).

The Caribbean king crab (*Mithrax spinosissimus*) (Crustacea; Decapoda; Majidae), also known as the West Indian spider crab and the channel clinging crab, is a common nocturnal herbivore (Adey 1987; Tunberg and Creswell 1991) throughout the Caribbean on coral and rocky reefs from just a few meters depth to depths approaching 200 m (Rathbun 1925; Williams 1965; Provenzano and Brownell 1977). It is the largest spider crab in the Caribbean; large males can weigh more than 3 kg with carapace lengths of 170 mm or more (Winfree and Weinstein 1989). *Mithrax* is a candidate for large-scale mariculture because of its short larval duration, large size, rapid growth, and palatability (Bohnsack 1976;

Brownell et al. 1977), and it supports small, artisanal fisheries in the Caribbean (Hartnoll 1963; Provenzano and Brownell 1977; Guzman and Tewfik 2004). Considered herbivorous by some (Bohnsack 1976; Adey 1987; Coen 1988; Stachowicz and Hay 1996) and omnivorous by others (Hartnoll 1963; Hazlett and Rittschof 1975; Winfree and Weinstein 1989; Guzman and Tewfik 2004), it is a cryptic, solitary crab whose dependence on crevice shelters limits its dispersal (Hazlett and Rittschof 1975). Little else is known about its ecology, including its feeding habits in the wild or the impact of its foraging on macroalgal community structure.

Our goal was to study the effect of herbivory by *M. spinosissimus* on coral patch reef macroalgal communities in the Florida Keys (USA). Algal selectivity and consumption by *M. spinosissimus* was measured in laboratory experiments in which the potential influence of crab size, gender, and time of the day was examined. We also estimated macroalgal consumption by *M. spinosissimus* and herbivorous fishes in field experiments to compare the relative magnitude of herbivory by both types of herbivores.

Materials and methods

Study area and general methodology

The Florida Keys barrier reef tract extends about 8 km offshore of the Florida Keys archipelago, which lies off the southern tip of the Florida peninsula (USA). Shoreward of the barrier reef, an intricate network of over 3,000 patch reefs occurs within 4 km of shore (Porter and Meier 1992; Jaap et al. 2003). These patch reefs possess coral formations and species very similar to those found elsewhere in the Caribbean (Vaughan 1914), and they harbor a high diversity of stony corals dominated by *Montastraea annularis*, *Colpophyllia natans,* and *Siderastrea siderea*. Our field studies were conducted during the summer (May–August) of 2006, 2007, and 2008 on 17 inshore patch reefs (size range, 53–840 m^2) situated 1.6 km offshore (depth range, 1.5–6.6 m) of Lower Matecumbe Key (24°50′N; 80°43′W). For all of our experiments, crabs were collected from this area by divers, and the carapace length (CL; maximum distance between posterior and anterior margins of the carapace), carapace width (CW; maximum distance between lateral margins of the carapace), presence of injuries (e.g., lost legs or claws), and sex of each crab were determined prior to inclusion in our experiments. Crabs were released back into the field after experimentation.

Mithrax diet preference and consumption rates in the laboratory

We designed two laboratory experiments to examine *Mithrax* preference for and consumption of macroalgae common on patch reefs in the Florida Keys. The first experiment tested whether crabs preferred specific common algal taxa. Therefore, each type of macroalgae was carefully separated into single-taxon clumps from the mixed macroalgae matrix that one typically finds on the reef. In the second experiment, natural clumps of macroalgae comprised a mixture of algae species were collected from the reef and used to examine crab consumption of algae.

Diet preference

Crabs were placed individually in seawater-filled, aerated aquaria (8 L) and starved for 48 h prior to the start of this experiment conducted in 2007. Crabs ($n = 33$) were offered a choice of four pre-weighed pieces of the most common macroalgae on patch reefs in the Florida Keys: *Ulva* sp. (a fleshy, green algae, 10–15 g), *Halimeda* sp. (a calcareous green algae, ∼10 g), *Laurencia* sp. (a fleshy red algae, 10–15 g), and *Dictyota* sp. (a fleshy brown algae, ∼20 g). We controlled for algal volume in each experiment rather than mass, which differed among algal species used in the experiment because of morphological differences among taxa (e.g., degree of calcification, tightly packed vs. open branching, etc.). After 24 h, the remaining pieces of algae were collected, sorted, wet-dried in a salad spinner, and reweighed. A control trial ran prior to this experiment confirmed that in the absence of herbivory, there is virtually no change (mean = 1.8 % change; range, 0.5–2.9 % per species) in algal mass over 24 h (the length of our experiments) for any of the species of algae we tested. Thus, in crab consumption trials, we considered a loss in algal mass >2 % as being due to herbivory.

Total consumption (T_c) of each type of macroalgae by each crab was determined at the end of the trial [initial weight (W_i) − final weight (W_f) = T_c], and differences between crab sexes were evaluated using Manly's $\acute{\alpha}$ for variable prey populations calculated as:

$$\acute{\alpha}_i = \log p_i / \Sigma p_j$$

where p_i and p_j are the proportions of prey i or j (respectively) remaining at the end of the experiment (Manly 1974; Krebs 1999). This index is appropriate when initial quantities of the items offered (algae species in this case) are not constantly replenished during the experiment. An index of 1.0 indicates that consumers are highly selective and only a single prey type comprises the entire diet. In this

case, a $\acute{\alpha}$ value of 0.25 indicates no preference if all four types were selected equally; therefore, values above and below 0.25 indicate preference or avoidance, respectively. Differences in diet preference (Manly's $\acute{\alpha}$) among algal types and between crab genders were tested using a two-factor split-plot ANOVA (fixed whole plot factor = sex; fixed subplot factor = algae; block = crab). One of the algal types (*Dictyota* sp.) whose consumption by crabs varied little between sexes was not included in the statistical analysis, so that consumption of the other three types could vary independently and thus be tested in this analysis.

Consumption rates

Mithrax consumption of mixed aggregations of macroalgae was measured by placing natural clumps of macroalgae (mostly *Halimeda* sp. and *Dictyota* sp.) collected from the reef into individual aquaria (8 L) where each crab ($n = 60$; 30 male and 30 female) was fed for two consecutive 12-h periods (12-h day; 12-h night) to test for differences in feeding behavior day and night. Consumption rates (g of algae h^{-1}) were measured as the T_c of algae at the end of each 12-h observation period ($W_i - W_f = T_c$). Results were analyzed using a two-factor split-plot ANOVA (fixed whole plot factor = sex; repeated subplot factor = time of day; block = individual crab). Data were transformed as necessary prior to analysis to meet assumptions of normality and homogeneity of variance. Crab size was not included in this evaluation because regression analyses showed that crab size did not significantly impact consumption rates by male or female crabs (Mojica 2009).

Macroalgal consumption on patch reefs

Consumption of macroalgae on patch reefs by different sizes of *Mithrax* was compared to that by all grazers in a field experiment where changes in macroalgal height were determined after 15 days on replicated plots where: (a) a single medium-sized *Mithrax* was constrained in a cage, (b) a single large *Mithrax* was constrained in a cage, (c) an empty cage excluded herbivory by large grazers (control cage), and (d) a partial-cage control plot permitted access to all herbivores. Cages were built of PVC tubing (25 cm × 25 cm × 32 cm) enclosed by plastic mesh (1.5-mm-dia mesh). Ten experimental plots were haphazardly distributed on each of five patch reefs. On each patch reef, three cages contained a single medium-sized crab (41–60 mm CL), three cages contained a single large crab (61–90 mm CL), two cages served as controls (empty cage), and two partial cages were open to all grazers. Macroalgae consumption was assessed by monitoring the mean change in the canopy height (cm) measured at 12

random locations within each cage or partial cage. This permitted us to calculate on each patch reef the net macroalgal consumption by *Mithrax* and other grazers as the difference between the expected algal growth (based on changes in macroalgae height in control cages inaccessible to grazers) and the change in macroalgal height measured at the end of the trial in *Mithrax* inclusion cages and in partial cages accessible to all grazers. The cages were cleaned and maintained every 5 days to reduce fouling. Changes in mean macroalgal canopy height among cages containing *Mithrax* and partial-cage treatments were analyzed using a two-factor mixed model ANOVA (fixed factor = cage treatment; random factor = patch reef). Additionally, a one-factor ANOVA was used to compare *Mithrax* consumption of macroalgae *in situ* (this experiment) and in the laboratory (data from laboratory consumption experiment). Data were transformed as necessary prior to these analyses to meet assumptions of normality and homogeneity of variance. A REGW *F* test multiple comparison procedure was used to identify specific differences among treatments.

Foraging by *M. spinosissimus* and fishes on patch reefs

Crab density surveys

Mithrax spinosissimus is a nocturnal grazer and dwells deep within reef crevices during the day, so field surveys to determine crab density on individual patches were carried out at night on 17 patch reefs during May–August 2007 and 2008. During each survey, two divers recorded the size (CL, CW), sex, and injuries of crabs observed and captured during each 20-min survey per reef. Sex and size were estimated for crabs that escaped capture. The total area (m^2), depth (m), and rugosity (estimated as the difference between the length of a taught line and a chain laid on the reef) of each patch reef were estimated during separate daytime surveys. A comparison between crab densities and patch reefs physical parameters was assessed using multiple linear regression.

Additionally, surveys to estimate the benthic composition (% cover of various taxa) of patch reefs were carried out during the day at five reef patches. Surveys were completed by two divers using a point intercept method (Paddack et al. 2006) wherein different taxa were identified and recorded every 25 cm along each of four 25-m-long transects (100 points per transect). The relationship between *Mithrax* density and algal cover on these reefs was assessed using a correlation analysis.

Fish surveys

Counts of herbivorous fishes and estimates of their bite rates were conducted during the day in the summer of 2008

on the same 17 patch reefs as described above. On each patch reef, the number, size, and species of all fishes observed by stationary divers at five haphazardly selected locations per patch reef were recorded. Diver observations at each stationary location (each location = 20 m^2 area) were made for a 5-min period, preceded by a 3-min acclimation period to minimize disturbance to fishes between observation periods. Fork length (FL; distance from the tip of the longest jaw to the center of the fork in the caudal fin) was estimated for each fish using a measured 1-m PVC tube. Observations of fish were made at stationary locations rather than along belt transects because of the small size of the patch reefs and our desire to minimize disturbance to the fish. Fish densities were compared to patch reef area using a Pearson correlation analysis.

After estimating fish abundance at each location, divers then counted the bite rates of the major herbivorous fishes (families: Acanthuridae, Scaridae, and Pomacentridae) of all size classes to estimate fish macroalgal consumption on each patch reef. At each location, five fishes were haphazardly selected by the diver who counted the number of bites the fish took while the diver followed it for 1 min. The species and FL of each fish were also recorded.

Estimation of the amount of macroalgae consumed per bite for each size and species of fish was beyond the scope of this study, so like other researchers (Paddack et al. 2006), we used data from one well-known species (*Sparisoma viride*, a dominant grazer in the Caribbean) to estimate algal consumption for other fish species. Daily consumption of macroalgae for *S. viride* was obtained by combining observed bite rates with algal yield per bite from Bruggeman et al. (1994a). Fish guild consumption rates were then extrapolated from the *S. viride* results following the method used by Paddack et al. (2006), a protocol based on the premise that algal consumption by herbivorous fishes is a function of fish biomass (van Rooij et al. 1998). Herbivorous fish biomass was obtained using the length-to-weight formulae:

$$\text{Log weight (g)} = \log a + b \times \log \text{FL (mm)}$$

where a and b are constants. Weight–length relationships for the species recorded were obtained from Bohnsack and Harper (1988) and Paddack et al. (2006) (see Mojica 2009 for details). Consumption rates by *S. viride* and the entire herbivorous fish guild were then compared to reef area using a Pearson correlation analysis. Differences in the mean consumption of macroalgae by *M. spinosissimus* obtained in the laboratory and the field were compared to those for *S. viride* in different developmental (i.e., size) stages were analyzed using a one-factor ANOVA.

Results

Mithrax spinosissimus diet preference and consumption rates in the laboratory

Diet preference

Mithrax spinosissimus preferred fleshy macroalgae over calcareous algae and consumed more *Dictyota* sp. than *Laurencia* sp. or *Ulva* sp. *Halimeda* sp. was by far the least preferred, but was nonetheless consumed by Mithrax even when portions of the other species remained (Table 1; Fig. 1). Male and female *Mithrax* did not differ in their preference for macroalgae among the three species of algae that we tested (Table 2).

Consumption rates

Consumption of mixed clumps of macroalgae by *Mithrax* under laboratory conditions was higher at night than during day (7.98 and 5.2 g day^{-1}, respectively; Table 2). Total consumption of macroalgae did not differ significantly between sexes (mean for males = 14.28 g; mean for females = 12.07 g; Table 2).

Macroalgal consumption on patch reefs

The effects of grazing by *M. spinosissimus* inside experimental cages surpassed the macroalgal consumption by all grazers combined observed in the partial-cage controls ($F_{(2,30)} = 3.326$, $P = 0.050$; Fig. 2). Although the mean change in the height of the macroalgae within experimental

Table 1 Manly's alpha index of preference for four common macroalgae consumed by male and female *M. spinosissimus* in simultaneous-choice laboratory experiments

| Sex	Algae species			
	Halimeda sp.	*Laurencia* sp.	*Ulva* sp.	*Dictyota* sp.
Male	0.04	0.31	0.2	0.45
Female	0.07	0.2	0.36	0.44

Alpha index values range from 0 to 1; in this experiment, values above and below 0.25 indicate preference or avoidance of a food item, respectively

plots varied severalfold among treatments, the difference was only of borderline significance because of variability in macroalgal consumption among individual patch reefs rather than differences in macroalgal growth among patch reefs. *Mithrax* also consumed almost three times more macroalgae in the laboratory than in the field (13.1 and 4.37 g day^{-1}, respectively) ($F_{(4,156)} = 35.283$, $P < 0.0005$).

Foraging by *M. spinosissimus* and fishes on patch reef

Crab density surveys

Thirty-six crabs (30–90 mm CL; mean = 53.63 mm) were seen during night surveys on 17 patch reefs; most were foraging on macroalgae within a half meter of a crevice. Females were five times more abundant than males. Large
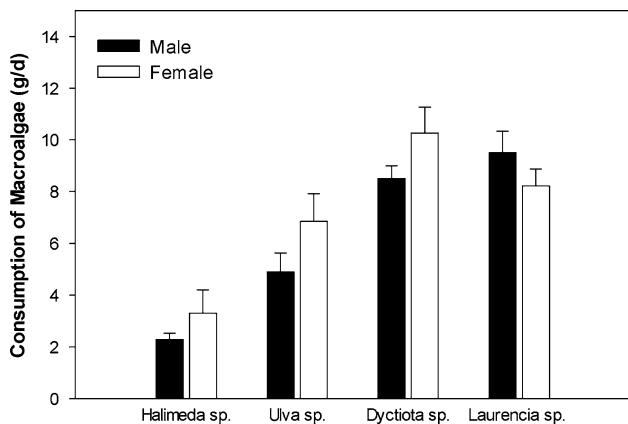
Fig. 1 Mean consumption (g/day) of four types of macroalgae (±SE) by *M. spinosissimus* in a laboratory feeding experiment where macroalgae (*x* axis) were offered simultaneously to individual crabs during a 24-h period

(61–90 mm CL)- and medium (41–60 mm CL)-sized crabs were the most abundant size classes (47.2 and 38.9 %, respectively); small crabs (<40 mm CL) only accounted for 11.1 % of those observed. Estimated densities of *Mithrax* were low (0.01 and 0.005 crabs/m^2 during 2007 and 2008, respectively), with an average density of 0.007 crabs/m^2.

Fish surveys

Seventeen families and 49 species of fish were recorded during fish surveys on the patch reefs that we studied (Mojica 2009). Fish densities (no. of fish/m^2) varied greatly among patch reefs and feeding guilds, and patch reef size had no effect on total fish density ($r_{(17)} = -0.006$, $P = 0.981$), the density of herbivorous fish ($r_{(17)} = 0.361$, $P = 0.154$), or the density of non-herbivorous fish ($r_{(17)} = -0.062$, $P = 0.814$). The herbivorous fish guild consisted primarily of 13 species from three families (Acanthuridae, Pomacentridae, and Scaridae) whose abundances varied appreciably among species and size classes (Mojica 2009). The most abundant herbivorous fish were scarids and acanthurids between 10 and 25 cm FL, but some parrotfish exceeded 40 cm in total length.

Total estimated consumption of macroalgae by *S. viride* was significantly greater on large patch reefs ($r_{(17)} = 0.614$, $P = 0.009$); however, this relationship was not significant for other herbivorous fishes ($r_{(17)} = 0.344$, $P = 0.177$). Total macroalgal consumption on patch reefs estimated for all herbivorous fishes combined (0.42 g C m^{-2} day^{-1}) and *S. viride* alone (0.06 g C m^{-2} day^{-1}) greatly surpassed that by *Mithrax* (0.002 g m^{-2} day^{-1}) (Fig. 3). However, per capita consumption of macroalgae by *Mithrax*, in both the laboratory and field, differed significantly from *S. viride* of different developmental phases ($F_{(4,156)} = 35.283$,

Table 2 Split-plot ANOVA results testing *M. spinosissimus* diet preference (A) and consumption rates (B) of macroalgae in the laboratory

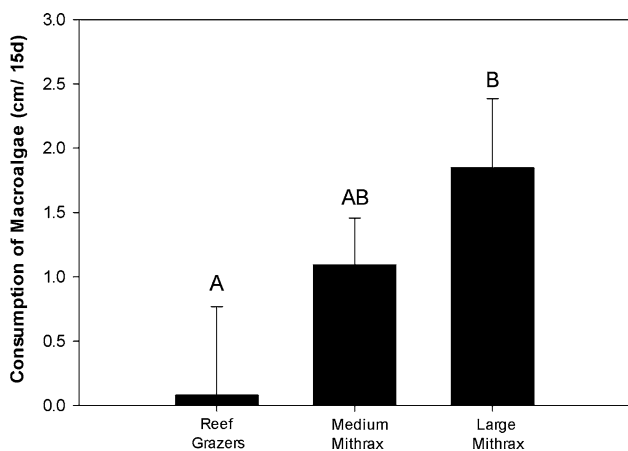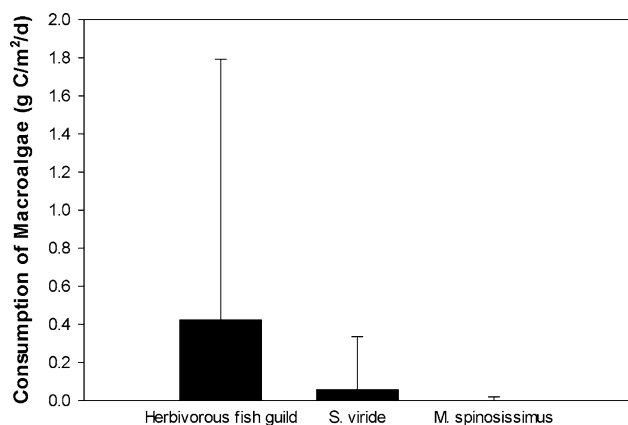| Source	df	SS (type III)	MS	F	P
(A) Diet preference					
Sex	1	25.615	25.615	1.916	0.176
Crab (sex)	31	414.35	13.366	2.215	0.002
Algae sp.	3	881.236	293.745	48.686	<0.0005
Sex × algae sp.	3	54.64	18.213	3.019	0.34
Error	93	561.115	6.033		
Total	131				
(B) Consumption rates					
Sex	1	54.448	54.448	0.972	0.328
Crab (sex)	57	3,194.046	56.036	3.878	<0.0005
Time	1	214.021	214.021	14.812	<0.0005
Sex × time	1	2.205	2.205	0.153	0.697
Error	59	852.525	14.45		
Total	119				

Fig. 2 Mean consumption (±SE) of macroalgae by various reef grazers (i.e., open cages) and by medium and large *M. spinosissimus* constrained within cages deployed on patch reefs. Consumption is expressed as the change in the mean height of macroalgae (cm) in experimental plots over the 15-day experiment. Treatments that were not significantly different from one another share the *same letter* above the *histogram* as determined using a REGWF test
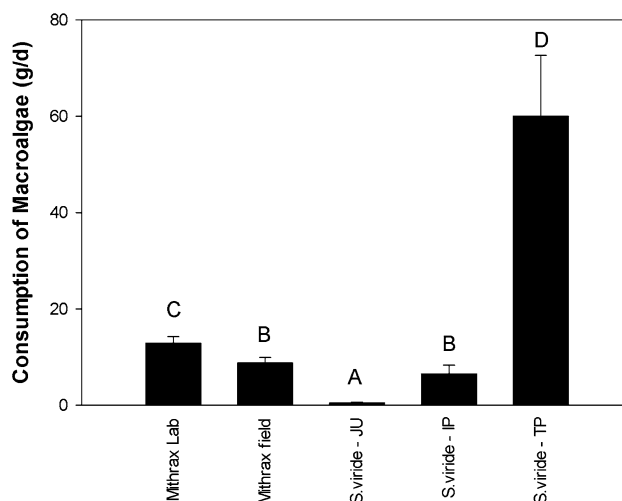

Fig. 4 Comparison of the mean (±SE) daily consumption of macroalgae (g/day) by *M. spinosissimus* in the laboratory and the field and by the parrotfish *S. viride* in different developmental phases (i.e., sizes). *Histograms* sharing *letters* were not significantly different in the amount of macroalgae consumed as determined using REGWF test

Fig. 3 Comparison of the daily total consumption (g C/m^2/day; mean ± 1 SE) of macroalgae on patch reefs during the summer in the Florida Keys, Florida (USA), by the entire herbivorous fish guild compared to that by the parrotfish *S. viride* and *M. spinosissimus* alone

$P < 0.001$; Fig. 4). Per capita macroalgal consumption by medium (2.97 g day^{-1}) and large (5.77 g day^{-1}) crabs was similar to or greater than those estimated for other fishes including juvenile (0.50 g day^{-1})- and intermediate (6.53 g day^{-1})-phase *S. viride,* respectively. However, adult-phase *S. viride* consumed more macroalgae per day (59.99 g^{-1}) than *Mithrax* or any herbivorous fish observed in this study.

Discussion

Many contend that restoration of coral reefs and enhancement of their resilience might best be accomplished by

promoting the reestablishment of functional groups capable of reversing the phase shift from coral to macroalgae dominance (Bellwood et al. 2006). Herbivores are one such functional group and major drivers of coral reef algal community structure (Lewis 1986; Hay 1997; Mumby et al. 2007). Yet, studies of herbivory on coral reefs have focused nearly entirely on reef fishes and echinoderms (Carpenter 1988; Lessios 1988; Klumpp and Pulfrich 1989). This is the first study to examine the feeding ecology of the herbivorous crab *M. spinosissimus* with respect to its potential role in regulating reef macroalgae in the Caribbean.

Mithrax prefers fleshy macroalgae, but it also consumes relatively unpalatable calcareous algae, sometimes in large quantities. Its per capita consumption of macroalgae rivals or surpasses that of all but the largest herbivorous reef fish in the Caribbean. When we caged *Mithrax* on patch reefs to estimate their grazing effects, we found that they can indeed graze macroalgae to levels significantly lower than that in open-cage controls exposed to the typical suite of mobile grazers present on Florida patch reefs. Yet, the collective effect of *Mithrax* on macroalgal abundance or community structure is minimized by the crab's natural rarity on coral reefs. Poor recruitment or high post-settlement mortality is obvious factor that might account for its low natural abundance, but virtually nothing is known of these processes. Similar studies of *M. spinosissimus* herbivory in other habitats or regions of the Caribbean are nonexistent, so the generality of our results to other regions of the Caribbean is unknown.

Mithrax spinosissimus diet preference

Our laboratory diet preference experiments indicate that *M. spinosissimus* preferred fleshy brown macroalgae over red and green macroalgae, but crabs also consumed large quantities of calcareous green macroalgae, which often dominate the macroalgae on highly stressed reefs. Most herbivorous reef fish consume minimal if any calcareous macroalgae (Polunin et al. 1995; Bruggeman et al. 1994a, b; Choat et al. 2002; Paddack et al. 2006), concentrating instead on filamentous algal turf (Lewis 1986; Paddack et al. 2006). Studies in the Florida Keys (Aronson et al. 1994), the Caribbean (Williams et al. 2001; Mumby 2006), and Australia (Naeem 2002; Bellwood et al. 2006) have shown that even robust communities of herbivorous fish alone are incapable of excluding macroalgae, especially calcarious algae, once established in the system.

Food selectivity by herbivores is influenced by algal morphology, structure, chemical composition, nutritional value, and availability (Jensen 1983; Hay and Steinberg 1992; Kennish and Williams 1997), and it is likely that *Mithrax*'s preference for fleshy rather than calcareous macroalgae is similarly a result of species-specific differences in algal characteristics. Contrary to the avoidance that some marine herbivores display to brown algae rich in chemical defenses (Hay et al. 1988; Stachowicz and Hay 1999a), *Mithrax* preferred *Dictyota* spp. (a brown alga) over *Laurencia* spp. (a red alga) and the typically more palatable green algae, *Ulva* spp. The food preferences for *M. spinosissimus* are similar to those for conspecifics *M. sculptus* and *M. forceps* (Stachowicz and Hay 1996, 1999a), which are relatively resistant to algal chemical deterrents and exhibit compensatory feeding to meet intake requirements (Stachowicz and Hay 1999b). Such physiological adaptations have been associated with low mobility and high site fidelity in herbivores where high predation risk restricts them to physical refugia and, in turn, the quantity and quality of available food (Sih 1987)—all of which applies to *M. spinosissimus*.

Macroalgal consumption on patch reefs

The difference in the potential versus realized grazing effects of *M. spinosissimus* on coral reefs is attributable to the low natural abundance of crabs and their limited mobility compared to the herbivorous fish guild. Yet, given the crab's high per capita grazing rates and their ability to remove both fleshy and calcareous macroalgae, the effect of their grazing is dramatic if the crabs are aggregated or constrained, for example, near their daytime crevice shelters. We found that grazing by *Mithrax* significantly exceeded that of other grazers that foraged in partial-cage controls in our field experiment. Medium and large crabs

consumed between 65 and 100 % of the macroalgae inside experimental cages, respectively, but only about 5 % of macroalgal productivity was consumed by other macrograzers who freely moved in and out of our partial-cage controls. Laboratory estimates of macroalgal consumption by *M. spinosissimus* are even greater than the field estimates, in fact almost three times greater (13.1 and 4.37 g day^{-1}, respectively). Thus, a single crab can potentially consume essentially all of the net production of large, fleshy macroalgae on portions of the reef where *Mithrax* focus their foraging. The depressed consumption rates observed for *Mithrax* on the reef compared to laboratory estimates are presumably a consequence of predation pressure and crab vigilance in the wild. Anti-predator behavior and the availability of prey refuges are well-known factors that alter prey feeding ecology by reducing their mobility, foraging rates, and feeding preferences, and these non-lethal effects of predation in turn impact community structure (Koivula et al. 1995; Houtman et al. 1997; Stachowicz and Hay 1999b).

Holding crabs in cages undoubtedly constrains their foraging range and increases their estimated impact on macroalgae, but perhaps not as much as one might expect because *Mithrax* is a cryptic, relatively sedentary crab (Hazlett and Rittschof 1975). Our observations of *Mithrax* foraging at night on patch reefs confirms that they forage largely in the vicinity of crevices or coral heads to which they quickly return when threatened. This behavior clearly limits their grazing to localized areas of the reef near their dens.

Similar patterns of localized grazing in the presence of predators have been observed in another important Caribbean reef herbivore, the long-spined sea urchin *Diadema antillarium* (Ogden et al. 1973). In contrast to the sedentary foraging behavior of *Mithrax* and sea urchins, other large grazers in tropical systems (e.g., fish, turtles, manatees; Ogden et al. 1973; Jones and Andrew 2006) are more mobile and thus spread their grazing effects throughout the reef ecosystem. For example, coral reefs nearer mangroves experience higher grazing rates by parrotfish that move between those habitats (Mumby 2006). Consumption rates also vary among herbivorous fish species, depending on their diet preferences, digestive physiologies, life stage, and social status (Bruggeman et al. 1994a, 2004; Hay 1997), as well as with plant qualities (e.g., chemical feeding deterrents) and availability (Lewis 1986; Choat 1991; Hay 1996). Therefore, the local distribution and mobility of grazers in spatially heterogeneous habitats such as coral patch reefs can greatly impact the local intensity of grazing. Grazing rates are thus far from uniform on patch reefs, as demonstrated by the significant among-reef (block effect) variance we observed in the grazing of macroalgae within our partial-cage controls. Our estimates of

macroalgal growth absent herbivory (i.e., within cages that excluded herbivores) could also be underestimates if the potential confounding effect of cages (e.g., diminished flow or light) were large. We considered this and thus chose very thin mesh material for our cages and cleaned cages every 5 days to minimize shading and flow effects.

Our use of partial-cage controls was an attempt to estimate changes in macroalgal abundance (measured as height) in the presence of free-roaming grazers while also controlling for possible cage effects. Whereas that treatment may provide a reasonable control for cage-induced environmental effects (e.g., light, water flow) on macroalgal growth, it is also possible that the partial cages might have attracted or repelled grazers. We have other data that provide some insight into this. Just prior to the grazing study reported here, literally 1–2 weeks prior, we compared algal growth in caged versus uncaged controls on these same patch reefs (Mojica 2009). A comparison of macroalgal growth (i.e., change in height after 15 days) in the open plots versus those covered with partial cages suggests that macroalgae were about 30 % taller in the open plots than in partial cages. This can be attributed to either higher grazing rates within partial cages due to grazer attraction or inhibition of macroalgal growth. Either way, the consequences of this "cage effect" are that our estimates of the effect of caged *Mithrax* on macroalgal abundance are even greater than we estimated from partial-cage controls.

Patterns of *M. spinosissimus* and fish abundance on patch reefs

Mithrax spinosissimus is considered a "common" species in the Caribbean, abundant enough to support small artisanal fisheries in some regions. However, few estimates of its natural abundance appear in the literature and nowhere is it reported to be locally abundant. Guzman and Tewfik (2004) reported *M. spinosissimus* densities on patch reefs in Panama (0.000041 crabs/m^2) that are an order of magnitude lower than the densities observed in this study. The only other studies of *M. spinosissimus* population structure in Florida were carried out in man-made canals (Hazlett and Rittschof 1975; Bohnsack 1976), but those density estimates were imprecise (i.e., Hazlett and Rittschof 1975; "8 crabs/100 m of canal," Bohnsack 1976) and not directly comparable to true density estimates.

The density of *Mithrax* no doubt differs among regions and habitats due to differences in shelter availability, competition, predation, recruitment, and fishing pressure. Previous studies found that *M. spinosissmus* density was directly related to the local abundance of crevices, for which they compete with other species such as spiny

lobsters (Hazlett and Rittschof 1975; Bohnsack 1976). We did not find a relationship between *M. spinosissimus* density and patch reef physical characteristics (e.g., reef size, rugosity, and depth) perhaps because of the seemingly limitless crevices and holes available on the rugose patch reefs that we studied.

The density of *M. spinosissimus* on patch reefs in the middle Florida Keys was also not correlated with carnivorous fish densities, although the natural predators of *M. spinosissimus* are poorly documented (Munro 1974). Several species of fish (e.g., groupers, snappers, wrasses, grunts, triggerfish, nurse sharks, and stingrays), as well as octopus and turtles feed on crustaceans (Randall 1965; Munro 1974), and all of these predators are common in our study area. Other studies conducted on the same patch reefs that we studied and during the same time period (Kintzing 2010) indicate that juvenile crab density, including *Mithrax*, is inversely related to the density of a reef-obligate spiny lobster (*P. guttatus*) whose main prey are small crabs, suggesting that early post-settlement mortality may limit *Mithrax* abundance on reefs. Patterns of *Mithrax* settlement in the wild are unknown, but are another obvious factor that potentially determines their local abundance. Regardless of the factors that dictate the abundance of *M. spinosissimus,* their density on the patch reefs that we studied was 2–3 orders of magnitude lower than those of herbivorous fish.

Total fish diversity and abundance observed on patch reefs in this study were somewhat lower than those reported from an extensive evaluation of reef fish communities from barrier and patch reefs throughout the Florida Keys from 1979 to 1998 (Bohnsack et al. 1999), but the density of herbivorous fish we observed was higher than those reported by Paddack et al. (2006) in the same region. Herbivorous fish in the families Achanturidae and Scaridae were the predominant herbivores in our study area, in terms of both density and mean size. By far the most abundant, large herbivorous fish that we observed was the stoplight parrotfish, *S. viride*, a large generalist herbivore (Bruggeman et al. 1994a). On shallow reefs like those we studied where fish density is high, adult *S. viridae* intermingle with large numbers of non-territorial initial phase and terminal phase fish and they forage together by day over large areas of the reef (Bruggeman et al. 1994a; van Rooij et al. 1996). Combined, the grazing impact on macroalgae by the abundant guild of herbivorous fishes in our study area far exceeded the intense, but localized impact exerted by *M. spinosissimus*.

Although herbivorous crabs may play a marginal role in removing macroalgae across the entire reef landscape because of their low abundance, qualitative differences in the impact of their grazing relative to fishes may be

important. Not only does *Mithrax* consume some unpalatable algae that fish avoid, they also clear patches of the reef of macroalgae because of their restricted foraging areas near shelter. Thus, like the long-spined sea urchin *D. antillarum*, herbivorous crabs may open up patches of the reef to recruitment or growth of corals, sponges, and other sessile taxa that compete with rapidly growing algae. On Caribbean reefs, a rebuilding of *D. antillarum* populations previously devastated by disease is thought by many to be key to the recovery of reefs overgrown by unpalatable macroalgae largely immune to fish grazers (Edmunds and Carpenter 2001). Despite their naturally low abundance, *M. spinosissimus* serve a similar function, consuming both fleshy and calcareous macroalgae from reefs at levels disproportionate to their size and density. However, if or where herbivorous crabs are sufficiently abundant, their ecological effects could be substantial and particularly relevant on degraded, algal-covered reefs.

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