

# Effects of predation upon the long-spined sea urchin *Diadema antillarum* by the spotted spiny lobster *Panulirus guttatus*

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**ABSTRACT:** Sea urchins, important herbivores in marine ecosystems, are strongly impacted by both the direct and indirect effects of predation, and the long-spined sea urchin *Diadema antillarum* is no exception. Once abundant on Caribbean coral reefs, *D. antillarum* populations were decimated by disease in the early 1980s, and only where their natural predators have been overfished has *D. antillarum* recovery been observed. Spiny lobsters (Palinuridae) are predators of sea urchins, and although there are several species of spiny lobster in the Caribbean, only the spotted spiny lobster *Panulirus guttatus* is restricted to coral reefs where *D. antillarum* dwells. We investigated the direct and indirect impacts of *P. guttatus* on *D. antillarum* mortality, foraging, and behavior in a series of laboratory experiments. We found that *P. guttatus* prey on *D. antillarum*, especially small urchins. *D. antillarum* also consumed significantly less algae in the presence of *P. guttatus* and fled when exposed to the odor of *P. guttatus* but apparently not the scent of the Caribbean spiny lobster *P. argus*. The altered foraging and avoidance behaviors displayed by *D. antillarum* are strong evidence that predation by *P. guttatus* has played an important, but underappreciated, role in the evolutionary history of *D. antillarum* and perhaps its recovery on Caribbean coral reefs.

**KEY WORDS:** *Diadema antillarum* · *Panulirus guttatus* · Florida Keys · Predation · Trait-mediated interactions · Coral reefs

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## INTRODUCTION

Predators unquestionably influence the composition of prey communities, and in some circumstances their trophic effects can cascade through the community (Paine 1966). So too can the indirect effects of predation, such as the alteration of prey behavior in response to predator cues (Trussell et al. 2003, Freeman 2006). In marine ecosystems, studies of sea urchins and their predators have provided compelling examples of the dual consequences of direct and indirect predation on community structure. For example, consumption of sea urchins by sea otters

(Estes & Palmisano 1974) and spiny lobsters (Tegner & Levin 1983) has positive cascading effects on kelp forests by reducing sea urchin grazing on kelp. Often the mere cue of a predator is enough to change prey behavior. Sea urchins cease feeding or flee an area when exposed to the odor of potential predators (Vadas & Elner 2003, Matassa 2010, Morishita & Barreto 2011), which potentially diminishes their foraging activities and impacts as herbivores.

The long-spined sea urchin *Diadema antillarum*, which inhabits Caribbean coral reefs and is the subject of our investigation, is consumed by a number of piscine and invertebrate predators (Randall et al.

1964), and its foraging is depressed on reefs where the threat of piscine predation is high (Carpenter 1984). Whether *D. antillarum* responds directly to predator odors is unknown, but they flee when exposed to the odor of an injured conspecific (Snyder & Snyder 1970). Therefore, predators impact *D. antillarum* on coral reefs directly through consumption while indirectly inhibiting their foraging and thus their functional significance as reef herbivores.

In the early 1980s, an unknown pathogen spread rapidly throughout the Caribbean sparking a catastrophic die-off of *Diadema antillarum* that resulted in greater than 95% mortality in the region (Carpenter 1988). Within weeks of the *D. antillarum* mass mortality, many reefs experienced rapid phase shifts from coral-dominated systems to those dominated by macroalgae (Carpenter 1988). Decades after the mass mortality of *D. antillarum* in the Caribbean, recovery has been slow and spatially inconsistent. Coral reefs in the Florida Keys (Florida, USA), where our study was conducted, have seen limited recovery of *D. antillarum* (Chiappone et al. 2002). Several mechanisms have been postulated to explain their continued absence, including limited larval supply, lack of appropriate settlement habitat, and high post-settlement mortality (Chiappone et al. 2002, Lee 2006, Miller et al. 2009). However, pulses of *D. antillarum* recruits are frequent (Chiappone et al. 2002), suggesting that post-settlement mortality plays an important role in determining *D. antillarum* abundance in Florida. Where urchins have recovered, macroalgal cover has decreased, resulting in a corresponding increase in coral recruitment (Carpenter & Edmunds 2006, Myhre & Acevedo-Gutiérrez 2007). Macroalgae not only compete with coral for space (Box & Mumby 2007) but also decrease coral fecundity (Foster et al. 2008) and recruitment (Birrell et al. 2008, Arnold et al. 2010). Thus, the maintenance of a healthy herbivore community and the recovery of important herbivores, such as *D. antillarum*, which have been diminished by disease or overfishing, is crucial to the reestablishment of coral dominance on reefs.

Spiny lobsters are important predators of echinoderms and mollusks worldwide, and their predatory activities sometimes result in trophic cascades (Tegner & Dayton 1981, Robles 1987, Mayfield et al. 2000, Shears & Babcock 2002). The Caribbean spiny lobster *Panulirus argus* is the most numerous lobster species in the Caribbean and, although adults shelter on coral reefs by day, at night they primarily feed off the reef in seagrass meadows and rubble zones (Cox et al. 1997). In contrast, the spotted spiny lobster *P. guttatus* is an obligate inhabitant of coral reefs where it is nu-

merous but often overlooked because it is a small species, retreats deep into the reef by day, and emerges only at night to forage on the reef. Although there are fisheries for *P. guttatus* in some areas of the Caribbean (Wynne & Côté 2007), none exists in the Florida Keys where high densities of *P. guttatus* correspond with documented poor sea urchin population recovery (Sharp et al. 1997, Chiappone et al. 2002, Robertson & Butler 2003, Miller et al. 2009). Thus, we examined whether *P. guttatus* preys on *Diadema antillarum*, whether *D. antillarum* can attain a size-specific refuge from *P. guttatus* predation, and whether trait-mediated interactions occur between these species that alter *D. antillarum* foraging.

## MATERIALS AND METHODS

### Lobster selectivity for *Diadema antillarum* size

*Panulirus guttatus* is a diminutive species of lobster whose maximum size is less than half that of its common Caribbean congener, *P. argus* (Robertson & Butler 2003). Prey consumption by lobsters is often size-specific (Butler et al. 2006) and it is likely that the size of prey consumed by *P. guttatus* is limited by lobster size. Thus, we determined in laboratory experiments if this potential anatomical constraint impacts *P. guttatus* consumption of *Diadema antillarum*. Lobsters and urchins used in this trial were collected by divers from coral reefs in the Florida Keys and maintained in the laboratory for <1 wk prior to the start of the experiment. To begin a trial, the size (carapace length [CL]; 36.5 to 53.7 mm) and sex of a *P. guttatus* that had been starved for 24 h prior to the experiment was recorded, and the lobster was then placed in a 100 l flow-through saltwater tank. *D. antillarum* were grouped into size categories based on test diameter, where every 5 mm increase in test diameter represented a different size group. Three *D. antillarum* differing in test diameter (5.0 to 30.2 mm) were selected haphazardly from different size categories, measured with calipers to the nearest 0.1 mm, and then added to the tank, and their survival was recorded after 24 h. The experiment was replicated 13 times, each with a separate lobster. For analysis, percent consumption of each size class was determined by dividing the number of *D. antillarum* consumed in a given size class by the total number of *D. antillarum* offered in that size class. Additionally, *D. antillarum* were regrouped into 2 larger size categories: small (<15 mm test diameter) and large (>15 mm test diameter), and a repeated measures

Mantel-Haenszel test was run to determine if consumption of urchins by *P. guttatus* was independent of urchin size. This test accounts for the lack of independence in the data as more than one urchin was consumed in several trials.

### ***Diadema antillarum* feeding in response to the presence of lobster**

To determine if the threat of predation by *Panulirus guttatus* alters the foraging behavior of *Diadema antillarum*, the consumption of macroalgae by a single urchin in laboratory trials was measured with or without a lobster present. *D. antillarum* were starved for 24 h prior to the experiment, then placed in a 100 l flow-through saltwater tank containing 2 shelters (each shelter consisted of 3 bricks arranged to create a den) and a known quantity of 2 types of macroalgae (*Halimeda* spp. and *Dictyota* spp.) collected from nearby coral reefs. Before addition to the experimental tanks, the macroalgae were spun for 30 revolutions in a salad spinner, weighed on a top-loading balance (nearest 0.01 g), and inserted into small, square (25 cm<sup>2</sup>) pieces of rubber bath mat attached to the bottom of the tank to keep the algae stationary. The *D. antillarum* was given 24 h to graze, then the remaining algae was removed, spun, and reweighed. *D. antillarum* were tested either alone or in the presence of a *P. guttatus* that we constrained near one shelter with an 8 cm long monofilament tether attached to its carapace by a monofilament harness. Each trial was replicated 19 times; thus, there were 38 total trials, with different urchins and lobsters. To determine if there was a difference in consumption of either *Halimeda* spp. or *Dictyota* spp. due to the presence of the *P. guttatus*, a 1-factor model I multivariate analysis of variance (MANOVA) was performed with lobster presence/absence as the factor and consumption of the 2 algal species as the response variables.

### ***Diadema antillarum* response to lobster chemical cues**

We investigated in the laboratory whether *Diadema antillarum* flees in response to the odor of 2 species of spiny lobster: *Panulirus guttatus* and *P. argus*. Our methodology is similar, although not identical, to that of Morishita & Barreto (2011). To initiate a trial, we added a single *D. antillarum* of known size (test diameter; measured to the nearest 0.1 mm) to an aquarium marked along the bottom

with a 5 × 5 cm grid, and filled with approximately 45 l of water. The *D. antillarum* was given 15 min to acclimatize before approximately 7.5 l of seawater was slowly added to the aquarium. The additional seawater added was one of 2 types: an untreated seawater (control; n = 20), or seawater obtained from an aerated 19 l aquarium in which a single 45 to 65 mm CL *P. guttatus* had been held for approximately 24 h (n = 20). The movement of the *D. antillarum* in response to the added water was then observed for 5 min and the total distance moved (cm) during this 5 min period was recorded. A year later, we performed an identical experiment with 15 *D. antillarum* that we exposed to either untreated seawater or seawater containing odors produced by the Caribbean spiny lobster *P. argus*. The results of these 2 separate experiments permitted us to investigate the behavioral response of *D. antillarum* to conspecific lobsters that both inhabit coral reefs, but whose foraging behaviors and thus risk to *D. antillarum* differ. Despite their procedural similarity and the similar range of urchin sizes tested, the experiments with *P. guttatus* and *P. argus* conducted a year apart involved separate sampling events and potential confounding factors. Thus, for both experiments, we compared the distance moved by urchins in each lobster predator treatment and its corresponding control using 2-sample *t*-tests with unequal variance rather than ANOVA. A post-hoc power analysis was run on the *P. argus* experimental results.

## **RESULTS**

### **Lobster selectivity for *Diadema antillarum* size**

*Panulirus guttatus* preferred smaller *Diadema antillarum*: 88% of the *D. antillarum* in the smallest size class (5 to 10 mm test diameter) were eaten, whereas only 21% of the *D. antillarum* of intermediate sizes (10 to 15 mm test diameter) were consumed, and no urchins with test diameters >26 mm were eaten. Results of a repeated measures Mantel-Haenszel (MH) test confirmed that significantly more small *D. antillarum* (test diameter of 15 mm or less) were eaten than large ones ( $\chi^2_{MH} = 11.6364$ ; df = 1; p = 0.0006).

### ***Diadema antillarum* feeding in response to the presence of a lobster**

A 1-factor Model I MANOVA revealed that *Diadema antillarum* consumed significantly less algae in

the presence of *Panulirus guttatus* compared to a seawater control ( $F = 5.45$ ;  $df = 2, 35$ ;  $p = 0.009$ ). *D. antillarum* consumed more *Dictyota* than *Halimeda*, but both types of algae were consumed in greater abundance in the control trials where *P. guttatus* was not present (*Dictyota*  $p = 0.012$  and *Halimeda*  $p = 0.038$ ) (Fig. 1).

### *Diadema antillarum* response to lobster chemical cues

*Diadema antillarum* moved significantly more in response to the odor of the reef-dwelling lobster *Panulirus guttatus* compared to a seawater control ( $t = 2.65$ ;  $df = 18$ ;  $p = 0.016$ ) but did not move more in response to another lobster (*P. argus*) cue compared to the seawater control ( $t = 1.84$ ;  $df = 18$ ;  $p = 0.083$ ). There was also a significant difference in *D. antillarum* movement when the results of the 2 lobster cues were compared, with *D. antillarum* moving significantly more when exposed to the *P. guttatus* cue ( $t = 2.268$ ;  $df = 21$ ;  $p = 0.034$ ) (Fig. 2). A post-hoc power analysis of the non-significant *P. argus* results yielded a low power of 45%; a sample size >34 ind. would be required to achieve a power of 80% for this experiment. Thus, even if the sample sizes for the *P. argus* and *P. guttatus* trials had been equal ( $n = 20$ ), our results would likely remain unchanged.

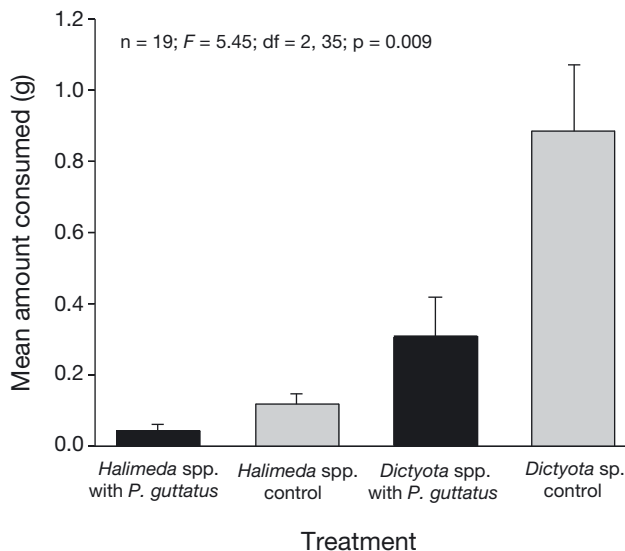


Fig. 1. *Diadema antillarum* response to *Panulirus guttatus*. Mean amount (g) of *Halimeda* spp. and *Dictyota* spp. consumed (dark bars) in the presence of a *P. guttatus* versus (light bars) a control without *P. guttatus*. Error bars represent 1 SE

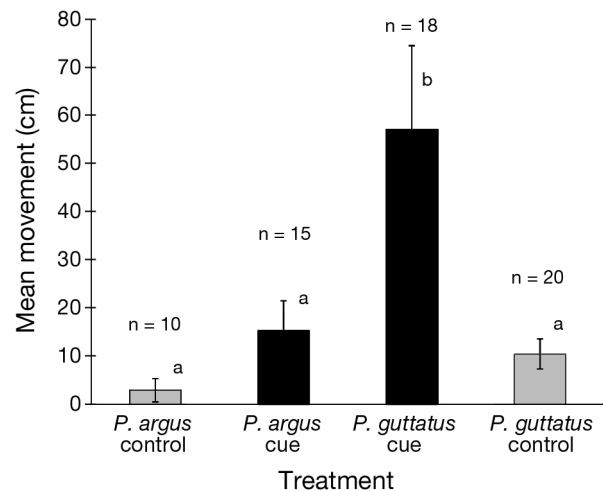


Fig. 2. *Diadema antillarum* response to *Panulirus argus* and *P. guttatus*. Movement (cm) in response to waterborne cues of (dark bars) *P. argus* and *P. guttatus*, and (light bars) their respective seawater controls. Error bars represent 1 SE. Different letters correspond to significant differences between treatments

## DISCUSSION

*Diadema antillarum* are important drivers of macroalgal abundance and thus community structure on Caribbean coral reefs, but our results suggest that their effectiveness as herbivores may be diminished by high juvenile mortality and chemically mediated reductions in foraging activity when the spotted spiny lobster *Panulirus guttatus* is present. *D. antillarum* consume both *Halimeda* and *Dictyota*, the 2 dominant species of macroalgae on patch reefs in the Florida Keys, but they prefer *Dictyota*. However, the foraging of *D. antillarum* on both species of algae is reduced in the presence of *P. guttatus*. This inhibitory behavior appears specific to *P. guttatus* and is absent or weak in response to its Caribbean congener, *P. argus*. Although *P. argus* consumes *D. antillarum* (Randall et al. 1964), this is the first demonstration of the direct and indirect effects of *P. guttatus* predation on *D. antillarum*. Yet, *P. guttatus* is a diminutive species and consumes mostly small *D. antillarum*, resulting in a size refuge from predation for large *D. antillarum*.

Our analysis of algal preference by *Diadema antillarum* focused on 2 types of macroalgae, *Dictyota* spp. (consisting mostly of *D. pulchella* and *D. menstrualis*) and *Halimeda* spp. (mainly *H. opuntia* but also *H. tuna*), that dominate the biomass of forereef (Beach et al. 2006) and patch reef habitats in the Florida Keys (Lirman & Biber 2000, Paddock et al.

2006). We found that *D. antillarum* preferred *Dictyota* and consumed little *Halimeda*. Other investigators have examined algal preference in different species of sea urchin in the genus *Diadema* (Ogden & Lobel 1978, Solandt & Campbell 2001), but their conclusions with respect to algal preference are conflicting. Several studies (Maciá et al. 2007, Myhre & Acevedo-Gutiérrez 2007) indicate that *D. antillarum* prefers non-calcareous macroalgae, which is consistent with our findings. Other studies have shown that *D. antillarum* consumes even heavily calcified algae (Morrison 1988, Solandt & Campbell 2001). Although *Dictyota* and *Halimeda* are both chemically defended, which deters grazing by most fishes (Lewis 1985, Paul & Hay 1986), only *Halimeda* is heavily calcified. Populations of herbivorous fish are by far the most abundant reef herbivores in the Florida Keys (Paddack et al. 2006, Butler & Mojica 2012), but they alone are unlikely to reverse the algal dominance on coral reefs that are populated largely by chemically defended and calcified algae such as *Dictyota* and *Halimeda*. *D. antillarum* readily consumes uncalcified algae such as *Dictyota*, but its corresponding effect on *Halimeda* is less certain.

Others have demonstrated that tropical sea urchins flee in response to predatory cues (Vadas & Elner 2003), that *Diadema antillarum* flees in response to cues from injured conspecifics (Snyder & Snyder 1970), and that *D. antillarum* has smaller home feeding scars on reefs with high predator densities (Carpenter 1984). However, the evidence we present here is the first direct demonstration of flight response and a trait-mediated reduction in algal consumption by *D. antillarum* in response to odor of a specific predator: *Panulirus guttatus*. We also show that foraging by *D. antillarum* on *Dictyota* and *Halimeda* was significantly reduced in the presence of *P. guttatus*. These results have important implications for Caribbean coral reefs where *P. guttatus* is abundant, such as the Florida Keys.

Nevertheless, the recovery of *Diadema antillarum* alone is unlikely to reverse the algal dominance now occurring on many Caribbean coral reefs. There are attempts, for example, to enhance *D. antillarum* populations via transplantation of both natural and hatchery-reared sea urchins (Burdick 2008, Rogers & Lorenzen 2008). However, lobsters restrict *D. antillarum* foraging close to shelters, so if *Panulirus guttatus* is abundant on reefs, they will minimize the impact of urchins on algal communities. Whether *D. antillarum* respond similarly to other predators that dwell on coral reefs is unknown, but our results suggest that they will respond differently to different

predators. Although the larger Caribbean spiny lobster *P. argus* will consume *D. antillarum* (Randall et al. 1964), it forages much less on the reef than the philopatric *P. guttatus*, which spends its entire benthic existence on the reef (Sharp et al. 1997, Robertson & Butler 2003, 2009) and appears to be a more important predator of *D. antillarum* than *P. argus*.

*Panulirus guttatus* clearly preferred smaller *Diadema antillarum*, providing the urchin with a size-specific refuge from predation, a finding consistent with studies of sea urchin predation by other species of lobster (Tegner & Levin 1983). Some suggest that the return of *D. antillarum* populations to historically high densities (Knowlton 2001, Maciá et al. 2007) may be the best method for releasing Caribbean reefs from algal dominance, prompting their return to coral dominance. Even in areas like the Florida Keys with relatively intact herbivorous fish guilds, rates of piscine herbivory are insufficient to decrease the standing algal biomass (Paddack et al. 2006), especially when dominated by chemically defended algae (Paul & Hay 1986, Lirman & Biber 2000). Fish, sea urchins, and herbivorous crabs graze differently; sea urchins are generally less selective grazers than fish and perhaps crabs (Ogden & Lobel 1978, Morrison 1988, Butler & Mojica 2012). Thus, sea urchins, when abundant, tend to have a greater impact on algal quantity and species composition in shallow reef communities (Morrison 1988). *D. antillarum* has been associated with reversal of the coral-to-macroalgae phase shift in areas of the Caribbean where *D. antillarum* populations have recovered (Carpenter & Edmunds 2006, Myhre & Acevedo-Gutiérrez 2007). Efforts to jump-start the recovery of *D. antillarum* are underway in several areas of the Caribbean and rely on stock-enhancement via transplantation of existing recruits or out-planting of hatchery-reared urchins (Burdick 2008, Rogers & Lorenzen 2008). Thus far, transplantation of *D. antillarum* has met with mixed results (Maciá et al. 2007, Burdick 2008, Kintzing 2010), and the poor recovery of transplanted populations is likely a result of intense predation, high emigration, or both. Our results suggest that simply out-planting *D. antillarum*, especially juveniles, will be unsuccessful if the size and abundance of potential predators, such as *P. guttatus*, on the managed site are not taken into account. The likelihood of *D. antillarum* recovery and their effectiveness as agents of change on Caribbean coral reefs appear intimately tied to the status of their predators, especially *P. guttatus*. Predation is an important factor that influences the density and foraging behavior of many species of sea urchins (Carpenter 1984, Vadas & Elner 2003,



Hereu et al. 2005). Not surprisingly, the areas in the Caribbean where *D. antillarum* has rebounded tend to be severely overfished, especially with respect to predatory fish and lobster (Harborne et al. 2009). Whereas fish are clearly important predators of *D. antillarum* (Randall et al. 1964) and predation by diurnally active fishes likely influenced *D. antillarum* evolution into a nocturnal forager, our results suggest that predation by *P. guttatus* may have played an important, but underappreciated, role in the evolutionary history of *D. antillarum*.

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#### LITERATURE CITED

- Arnold SN, Steneck RS, Mumby PJ (2010) Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Mar Ecol Prog Ser* 414:91–105
- Beach KS, Walters LJ, Borgeas HB (2006) Irradiance and nutrient limitations of *Dictyota* spp. populations on Conch Reef, Florida Keys, USA. *J Exp Mar Biol Ecol* 329: 101–112
- Birrell CL, McCook LJ, Willis BL, Harrington L (2008) Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora*. *Mar Ecol Prog Ser* 362:129–137
- Box SJ, Mumby PJ (2007) Effects of macroalgal competition on growth and survival of juvenile Caribbean corals. *Mar Ecol Prog Ser* 342:139–149
- Burdick DR (2008) The effectiveness of macroalgal reduction and *Diadema antillarum* addition in limiting macroalgal growth and facilitating coral recovery. In: Proc 11th Int Coral Reef Symp, Ft. Lauderdale, FL, 7–11 July 2008, Vol 2, p 1210–1214
- Butler MJ IV, Steneck RS, Herrnkind WF (2006) Juvenile and adult ecology. In: Phillips BF (ed) *Lobsters: biology and management*. Blackwell Scientific Press, Oxford, p 263–309
- Butler MJ IV, Mojica AM (2012) Herbivory by the Caribbean king crab on coral reef patches. *Mar Biol* 159:2697–2706
- Carpenter RC (1984) Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. *Mar Biol* 82:101–108
- Carpenter RC (1988) Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. *Proc Natl Acad Sci USA* 85:511–514
- Carpenter RC, Edmunds PJ (2006) Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. *Ecol Lett* 9:271–280
- Chiappone M, Swanson DW, Miller SL, Smith SG (2002) Large-scale surveys of the Florida Reef Tract indicate poor recovery of the long-spined sea urchin *Diadema antillarum*. *Coral Reefs* 21:155–159
- Cox C, Hunt JH, Lyons WG, Davis GE (1997) Nocturnal foraging of the Caribbean spiny lobster (*Panulirus argus*) on offshore reefs of Florida, USA. *Mar Freshw Res* 48: 671–679
- Estes JA, Palmisano JF (1974) Sea otters: their role in structuring near-shore ecosystems. *Science* 185:1058–1060
- Foster NL, Box SJ, Mumby PJ (2008) Competitive effects of macroalgae on the fecundity of the reef-building coral *Montastraea annularis*. *Mar Ecol Prog Ser* 367:143–152
- Freeman A (2006) Size-dependent trait-mediated indirect interactions among sea urchin herbivores. *Behav Ecol* 17: 182–187
- Harborne AR, Renaud PG, Tyler EHM, Mumby PJ (2009) Reduced density of the herbivorous urchin *Diadema antillarum* inside a Caribbean marine reserve linked to increased predation pressure by fishes. *Coral Reefs* 28: 783–791
- Hereu B, Zabala M, Linares C, Sala E (2005) The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Mar Biol* 146:293–299
- Kintzing MD (2010) Impacts of the spotted spiny lobster (*Panulirus guttatus*) on the long-spined sea urchin (*Diadema antillarum*) and patch reef communities in the Florida Keys. PhD Dissertation, Old Dominion University, Norfolk, VA
- Knowlton N (2001) The future of coral reefs. *Proc Natl Acad Sci USA* 98:5419–5425
- Lee SC (2006) Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. *Oikos* 112: 442–447
- Lewis SM (1985) Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia* 65:370–375
- Lirman D, Biber P (2000) Seasonal dynamics of algal communities of the Northern Florida Reef Tract. *Bot Mar* 43: 305–314
- Maciá S, Robinson MP, 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
- Matassa CM (2010) Purple sea urchins *Strongylocentrotus purpuratus* reduce grazing rates in response to risk cues from the spiny lobster *Panulirus interruptus*. *Mar Ecol Prog Ser* 400:283–288
- Mayfield S, Branch GM, Cockcroft AC (2000) Relationships among diet, growth rate, and food availability for the South African rock lobster,  *Jasus lalandii* (Decapoda; Palinuridea). *Crustaceana* 73:815–834
- Miller MW, Kramer KL, Williams SM, Johnston L, Szmant AM (2009) Assessment of current rates of *Diadema antillarum* larval settlement. *Coral Reefs* 28:511–515
- Morishita VR, Barreto RE (2011) Black sea urchins evaluate predation risk using chemical signals from a predator and injured con- and heterospecific prey. *Mar Ecol Prog Ser* 435:173–181
- Morrison D (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* 69:1367–1382
- Myhre S, Acevedo-Gutiérrez A (2007) Recovery of sea urchin *Diadema antillarum* populations is correlated to increased coral and reduced macroalgal cover. *Mar Ecol Prog Ser* 329:205–210

- Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. *Environ Biol Fishes* 3:49–63
- Paddock MJ, Cowen RK, Sponaugle S (2006) Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* 25:461–472
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65–75
- Paul VJ, Hay ME (1986) Seaweed susceptibility to herbivory: chemical and morphological correlates. *Mar Ecol Prog Ser* 33:255–264
- Randall JE, Schroeder RE, Starck WAI (1964) Notes on the biology of the echinoid *Diadema antillarum*. *Caribb J Sci* 4:421–433
- Robertson DN, Butler MJ IV (2003) Growth and size at maturity in the spotted spiny lobster *Panulirus guttatus*. *J Crustac Biol* 23:265–272
- Robertson DR, Butler MJ IV (2009) Variable reproductive success in isolated populations of lobster. *J Exp Mar Biol Ecol* 377:84–92
- Robles C (1987) Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* 68:1502–1514
- Rogers A, Lorenzen K (2008) Recovery of *Diadema antillarum* and the potential for active rebuilding measures: modeling population dynamics. In: Proc 11th Int Coral Reef Symp, Ft. Lauderdale, FL, 7–11 July 2008, Vol 2, p 961–966
- Sharp WC, Hunt JH, Lyons WG (1997) Life history of the spotted spiny lobster, *Panulirus guttatus*, an obligate reef-dweller. *Mar Freshw Res* 48:687–698
- Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132:131–142
- Snyder N, Snyder H (1970) Alarm response of *Diadema antillarum*. *Science* 168:276–278
- Solandt J, Campbell AC (2001) Macroalgal feeding characteristics of the sea urchin *Diadema antillarum* Philippi at Discovery Bay, Jamaica. *Caribb J Sci* 37:227–238
- Tegner MJ, Dayton PK (1981) Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Mar Ecol Prog Ser* 5:255–268
- Tegner MJ, Levin LA (1983) Spiny lobsters and sea urchins: analysis of a predator–prey interaction. *J Exp Mar Biol Ecol* 73:125–150
- Trussell GC, Ewanchuk PJ, Bertness MD (2003) Trait-mediated effects in intertidal food chains: predator risk cues alter prey feeding rates. *Ecology* 84:629–640
- Vadas RL Sr, Elner RW (2003) Response to predation cues and food in two species of sympatric, tropical sea urchins. *Mar Ecol* 24:101–121
- Wynne SP, Côté IM (2007) Effects of habitat quality and fishing on the Caribbean spotted spiny lobster populations. *J Appl Ecol* 44:488–494

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