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THE INFLUENCE OF SHELTER, CONSPECIFICS, AND THREAT OF PREDATION ON THE BEHAVIOR OF THE LONG-SPINED SEA URCHIN (*DIADEMA ANTILLARUM*)

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ABSTRACT The interplay of competition and predation often affects prey habitat use, which may concentrate prey in safer areas with indirect consequences on their foraging efficiency and the effects of their foraging on the community. Predation is intense on coral reefs where competition for limited space and food is severe. The sea urchin *Diadema antillarum*, an inhabitant of Caribbean coral reefs, uses crevice shelters and often aggregates with conspecifics for protection against predators, which appears to reflect a conflicting balance between group defense versus competition for limited shelter. A series of laboratory experiments was used to determine how the availability of shelter, conspecifics, and chemical odors from conspecifics and a predator—the spotted spiny lobster (*Panulirus guttatus*)—affect *D. antillarum* shelter use. The long-spined sea urchin *D. antillarum* responded strongly to the odor of conspecifics and the lobster predator. Absent the threat of predation, *D. antillarum* compete for shelter and avoid shelters bearing the scent of other urchins. But, *D. antillarum* readily shared shelters and preferred the scent of conspecifics when exposed to lobster odors. Thus, efforts to enhance the recovery of *D. antillarum* populations on degraded reefs must strike a balance between minimizing their mortality from predation and increasing habitat complexity, which not only increases shelter for *D. antillarum*, but also their predators.

KEY WORDS: sea urchin, *Diadema antillarum*, habitat complexity, ideal free distribution, predation threat, coral reefs

INTRODUCTION

Predators can shape the taxonomic structure of animal communities and control the abundance of prey (Hairston et al. 1960, Paine 1966). In turn, prey have evolved physical (Hoverman et al. 2005), chemical (Bolser & Hay 1996), and behavioral adaptations that limit their vulnerability to predation (Trussell et al. 2003, Smee & Weissburg 2008) and, in some cases, combine these strategies to reduce predation risk. For example, the sharp, sometimes toxic spines of sea urchins provide both physical and chemical deterrence to predation, but urchins have also evolved a number of defensive behaviors to avoid predators (Vadas & Elner 2003). Sea urchins have well developed olfactory senses, and many species flee or curtail feeding in response to chemical cues produced by predators and injured conspecifics (Snyder & Snyder 1970, Freeman 2006, Matassa 2010). Antipredatory adaptations such as these provide obvious evolutionary advantages to prey, but often come at a cost, such as reduced foraging or restriction to suboptimal habitats where their growth or fecundity is compromised by overcrowding (Katz & Dill 1998).

This Faustian dilemma—enhanced competition in resource-poor habitats versus greater risk of predation—is embodied in Fretwell's ideal free distribution theory (Fretwell & Lucas 1970), an outgrowth of optimal foraging theory first developed to explore how trade-offs in competitive ability and predation risk impact resource use (MacArthur & Pianka 1966). Although Fretwell's original theory examined how organism density, a proxy for competition, affects habitat quality, others have extended the idea to examine how the threat of predation concentrates prey in safer areas and thus indirectly impacts habitat quality (Grand & Dill 1999, Heithaus et al. 2007, Heithaus et al. 2009). Many of these studies confirm Connell's idea (Connell 1975) that the threat of predation usually trumps the disadvantages of increased interspecific competition in

mediating habitat selection and resource use (Heithaus et al. 2007, Heithaus et al. 2009). This ecological trade-off is common in tropical marine ecosystems.

Predation is intense in low-latitude, high-diversity ecosystems such as coral reefs (Bertness et al. 1981, Menge & Lubchenco 1981, Bolser & Hay 1996,) where competition for limited space and food is also severe (Jackson & Buss 1975, Williams 1981, Connell et al. 2004). The sea urchin *Diadema antillarum*, which inhabits the coral reefs of the tropical Caribbean, offers a case in point. It uses crevice shelters and often aggregates with conspecifics for protection against predators (Carpenter 1984, Lee 2006, Miller et al. 2007). This may reflect the conflicting balance between group defense for protection versus competition for limited quality habitats. The sea urchin *D. antillarum* was used as a model organism in a series of laboratory experiments to examine how the availability of shelter and conspecifics affect *D. antillarum* behavior in the presence and absence of a common predator, the spotted spiny lobster (*Panulirus guttatus*).

MATERIALS AND METHODS

All the experiments described were conducted at the Goshen College Marine Laboratory on Long Key, Florida, from July 2008 through October 2009. Unless otherwise noted, experiments were conducted in 200-L flow-through seawater tanks and ran for approximately 24 h under natural photoperiod and ambient seawater temperatures (range, 27–31°C) and salinity (range, 32–36 ppt). Experimental setups that included head tanks had natural, sand-filtered seawater flowing to a 20-L head tank. Seawater then flowed from each head tank at approximately 1 L/min through plastic airline tubing to a shelter below. All experimental shelters were constructed with 3 stacked masonry bricks soaked previously in seawater. Sea urchins (*Diadema antillarum*) and lobsters (*Panulirus guttatus*) used in the experiments were collected from nearby reef habitats by divers and returned to those reefs at the conclusion of these studies.

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Effect of Conspecifics on *Diadema* Shelter Choice

Three separate experiments were conducted to investigate the effects of conspecifics on shelter use by *Diadema antillarum*; specifically, shelter choice was tested with (1) conspecifics present and shelter not limited, (2) conspecific odors present and shelter not limited, and (3) conspecific odors present and shelter limited. To determine whether the presence of a conspecific affects shelter selection by *D. antillarum*, 2 *D. antillarum* were added to an experimental tank containing 2 shelters. The choice of the *D. antillarum* to shelter together or apart was recorded after 24 h ($n = 26$) and was tested using Fisher's exact test.

Also tested was whether the choice, by *Diadema antillarum*, of a shelter with or without a conspecific was controlled by conspecific odors. To do so, a single *D. antillarum* was placed in an experimental tank with two shelters. Seawater from 2 head tanks—1 empty head tank (i.e., the seawater control) and 1 containing a single *D. antillarum* (test diameter, 30–50 mm)—flowed to separate shelters. At the conclusion of the experiment 24 h later, the shelter selected by *D. antillarum* was recorded ($n = 21$). Fisher's exact test was used to determine whether *D. antillarum* was attracted to 1 shelter over the other.

To determine whether shelter limitation influences whether *Diadema antillarum* will co-occupy a shelter with a conspecific, a single *D. antillarum* was added to a tank with a single shelter. Water from a head tank containing a single *D. antillarum* (test diameter, 30–50 mm) flowed to the shelter. Whether the *D. antillarum* used the shelter ($n = 21$) was recorded and tested with Fisher's exact test.

Diadema Shelter Choice in the Presence of Predator Odor

The sea urchin *Diadema* co-occur on coral reefs with predatory lobsters, so the importance of urchin shelter use in the presence of a predatory odor was examined. A single *D. antillarum* was added to an experimental tank with 1 shelter into which water flowed from a head tank containing a single lobster (*Panulirus guttatus*; carapace length, 45–55 mm). After 24 h, whether the *D. antillarum* used the shelter ($n = 18$) was tested with a Fisher's exact test.

Effect of Predator and Conspecific Odors on *Diadema* Shelter Choice

Last, shelter choice by *Diadema antillarum* when given the preference between 2 shelters from which flowed either a conspecific or a predator chemical cue was tested. Each of the 2 shelters received seawater from 1 of 2 head tanks—1 containing a single *Panulirus guttatus* (carapace length, 45–55 mm) and the other containing a single 30–50-mm (test diameter) *D. antillarum*. One *D. antillarum* was then added to the experimental tank. At the conclusion of the experiment, which shelter the urchin selected was recorded ($n = 19$) and Fisher's exact test was used to examine the results.

RESULTS

Effect of Conspecifics on *Diadema* Shelter Choice

When 2 *Diadema antillarum* were given the choice to shelter together or separately with no threat of predation and when shelter was not limiting, they occupied separate shelters more frequently than together ($n = 26$, $P = 0.002$; Fig. 1A).

The sea urchin *Diadema antillarum* also avoided shelters from which flowed a conspecific odor only ($n = 21$, $P = 0.034$; Fig. 1B). The size of *D. antillarum* did not affect these results; the 5 individuals that chose the shelter with a conspecific odor spanned the size range of the *D. antillarum* tested. This result is consistent with the outcome of the previous experiment (see Fig. 1A) and demonstrates that *D. antillarum* use olfaction to detect and avoid conspecifics.

When only 1 shelter was available, *Diadema antillarum* sometimes sheltered in dens from which flowed a chemical cue of a conspecific. However, they were just as often found alone outside the shelter ($n = 21$, $P > 0.99$; Fig. 1C).

Shelter Choice by *Diadema* in the Presence of Predator Odor

When shelter was limited and the only available shelter contained a waterborne predator cue, *Diadema antillarum* just as often remained in the open outside a shelter as entered a shelter producing the scent of the predator *Panulirus guttatus* ($n = 18$, $P > 0.99$; Fig. 1D).

Shelter Choice by *Diadema* with Both Predator and Conspecific Odors

When given the choice between using a shelter with either a conspecific odor or that of a potential predator, *Diadema antillarum* more often selected the shelter with the conspecific odor than the predatory cue ($n = 19$, $P = 0.011$; Fig. 1E).

DISCUSSION

Several studies have examined the independent effects of shelter and reef complexity, predators, and conspecifics on *Diadema antillarum* behavior (Carpenter 1984, Lee 2006, Miller et al. 2007, Clemente & Hernández 2008,), but this is the first to examine all 3 concurrently. Laboratory results indicate that *D. antillarum* are, first and foremost, attracted to shelter, although chemically mediated responses to conspecifics and predators also strongly influences *D. antillarum* shelter use. The presence of conspecifics deters aggregation among *D. antillarum*, but when the threat of predation occurs, *D. antillarum* aggregate within available shelter, indicating a trade-off between reduced predation risk and competition.

The laboratory results are consistent with field observations of decreased movement and foraging by *Diadema antillarum* in predator-rich environments (Carpenter 1984), and they support the theory that reduced predation risk comes at the cost of lost foraging opportunities. The sea urchin *D. antillarum* often aggregate in crevices on reefs and, after they locate a suitable shelter, they move only at night and only short distances from that "home shelter," which appears to enhance their survival—especially that of juveniles (Randall et al. 1964, Miller et al. 2007). But this behavior, which prioritizes protection from day-active predators over food acquisition, impacts their growth, fecundity, and survivorship negatively (Levitan 1988, Levitan 1989). The results indicate that interactions with conspecifics and at least 1 confirmed predator, the spotted lobster *Panulirus guttatus*, are driven by chemical cues. Thus, even the threat of predation acquired via olfaction is sufficient to decrease the fitness of *D. antillarum*.

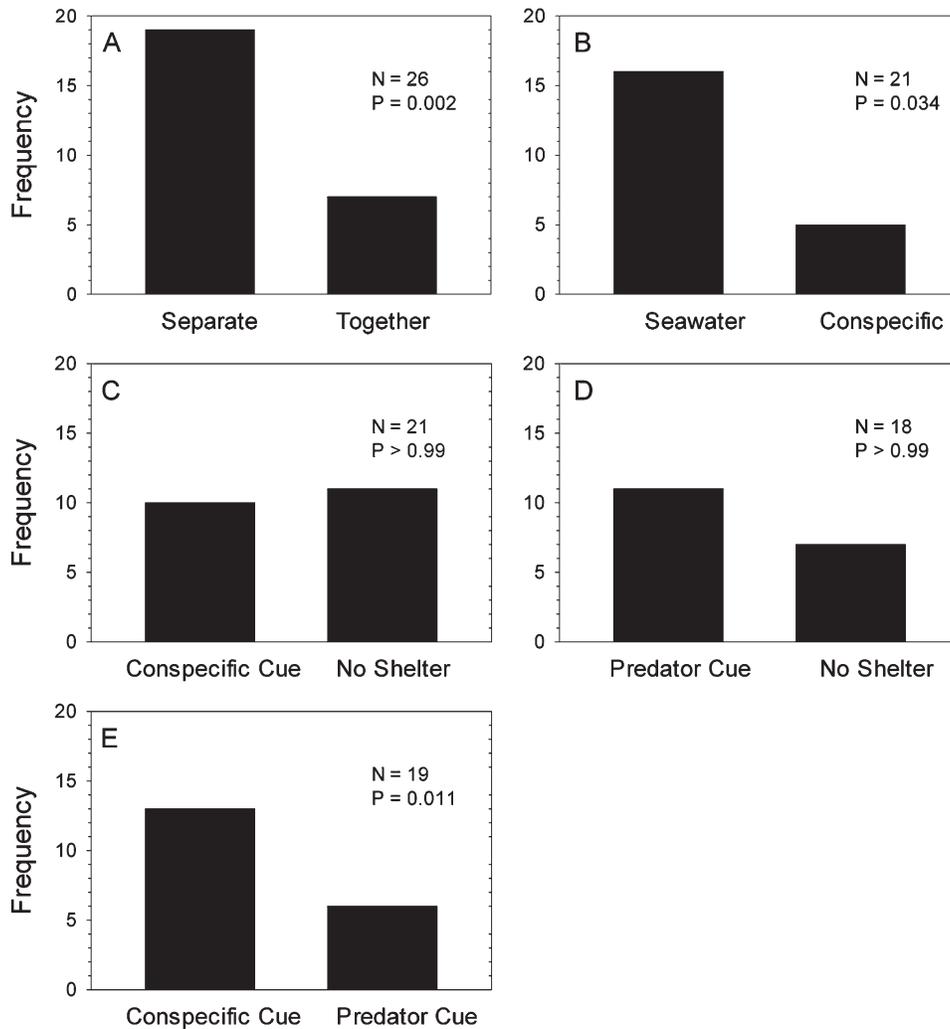


Figure 1. (A) Shelter use by 2 *Diadema antillarum* when offered 2 shelters and no predator odor. (B) Shelter choice by *D. antillarum* between shelters containing a seawater control cue or a conspecific waterborne chemical cue. (C) Shelter use by *D. antillarum* when a conspecific odor is present and shelter is limited. (D) Shelter use by *D. antillarum* when a predator odor is present and shelter is limited. (E) Shelter choice by *D. antillarum* when conspecific and predator odors are present.

Under natural circumstances, large fish and invertebrate predators of urchins are abundant on coral reefs and thus drive urchins to shelter with conspecifics. However, overfishing on Caribbean reefs is rampant (Dulvy et al. 2004, Aronson & Precht 2006). It may be no coincidence that *Diadema antillarum* populations have recovered from the massive die-off of the 1980s more quickly in areas where overfishing is particularly severe (Harborne et al. 2009) and on nearshore reefs where sea urchins often recruit and large predators are more easily accessed by fishermen.

Caribbean coral reefs are also becoming less structurally complex as a result of the loss of scleractinian corals from bleaching, disease, and algal overgrowth (Alvarez-Filip et al. 2009, Kennedy et al. 2013). Ocean acidification is expected to exacerbate this phenomenon (Hoegh-Guldberg et al. 2007). This “flattening” of coral reefs has serious implications for the recovery of *Diadema antillarum* populations in light of these results and those of other studies (Hereu et al. 2005, Lee 2006, Clemente & Hernández 2008), which demonstrate that

D. antillarum abundance is greatest in structurally complex environments (Lee 2006, Clemente & Hernández 2008)—a pattern shared with reef fishes (Gratwicke & Speight 2005, Ledlie et al. 2007, Alvarez-Filip et al. 2009). Populations of *D. antillarum* are already subject to intense predation pressure, and further loss of habitat structural complexity will likely exacerbate those losses (Chiappone et al. 2002, Miller et al. 2009, Harborne et al. 2009, Kintzing & Butler 2014). Therefore, recovery of *D. antillarum* populations and the associated recovery of algal-dominated reefs as a result of *D. antillarum* grazing (Edmunds & Carpenter 2001, Carpenter & Edmunds 2006, Idjadi et al. 2010) may require not only *D. antillarum* stock enhancement (Macía et al. 2007), but also supplementation of crevice shelters of various sizes (Lee 2006, Gratwicke & Speight 2005). Paradoxically, increased habitat complexity also often increases the abundance and diversity of urchin predators (Mattila et al. 2008), which in turn will constrain foraging by *D. antillarum* and limit their importance in reef recovery. It will thus be necessary to determine the right balance between

enhancement of coral reef structure and urchin stocks to achieve the hoped for gains in coral reef recovery.

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