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# Impacts of the Spotted Spiny Lobster (*Panulirus guttatus*) on the Long-Spined Sea Urchin (*Diadema antillarum*) and Patch Reef Communities in the Florida Keys

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# THE LONG-SPINED SEA URCHIN (*DIADEMA ANTILLARUM*) AND PATCH

# REEF COMMUNITIES IN THE FLORIDA KEYS

by

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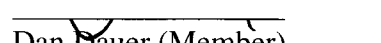
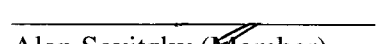DOCTOR OF PHILOSOPHY

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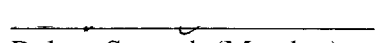
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# ABSTRACT

IMPACTS OF THE SPOTTED SPINY LOBSTER (*PANULIRUS GUTTATUS*) ON THE
LONG-SPINED SEA URCHIN (*DIADEMA ANTILLARUM*) AND PATCH REEF
COMMUNITIES IN THE FLORIDA KEYS

Meredith D. Kintzing
Old Dominion University, 2010
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Caribbean coral reefs have undergone a phase shift from a system dominated by corals to one where algae are pervasive. This shift was precipitated by the loss of herbivores, including the mass mortality of the long spined sea urchin (*Diadema antillarum*), coupled with disease and the recruitment failure of hermatypic corals. *Diadema* populations have recovered in some areas of the Caribbean, but are still below historical levels in the Florida Keys, likely due to low larval supply coupled with predation on juveniles. Lobsters are sea urchin predators in other systems and the spotted spiny lobster (*Panulirus guttatus*) is abundant on coral reefs in the Florida Keys, where I investigated their role as nocturnal, philopatric carnivores on patch reef communities, with particular emphasis on their density and trait mediated impacts on *Diadema*. Additionally, I examined the importance of predation threat and intra-specific competition on habitat utilization by *Diadema*. I found that *P. guttatus* consumes small herbivorous reef invertebrates including sea urchins and crabs and its foraging activities destabilize rubble substrate, a disturbance more intense with smaller rubble, which may inhibit coral recruitment. In addition to density mediated impacts, *Diadema* increased its flight response and consumed significantly less algae in the presence of *P. guttatus*.

However, *Diadema* did not increase its flight response to *P. argus*, a known *Diadema* predator. *Panulirus guttatus* cues also mitigated the importance of intra-specific competition for shelter by *Diadema*, with *Diadema* selecting shelters with conspecific chemical cues over those with *P. guttatus* chemical cues. Through its negative impact on the abundance and behavior of herbivores such as *Diadema* and destabilization of rubble substrates, high densities of *P. guttatus* potentially contribute to coral-to-algae phase-shifts on coral reefs.

To my family, Meg, John, Elizabeth, Kelley, Patrick, Ashley, and Katie, without whose love and support this work would not have been possible.

To Dewey, the world's best boyfriend and field assistant. Thanks for not killing me on the night dives.

And finally to the world's best dog, Cota.

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To Cota and Teddy, thanks for being a diversion, for listening attentively and pretending to care about what I said during practice talks, and not asking difficult questions afterwards.

To Dewey, your love, support, and assistance were integral in helping me complete my degree. You were the best field assistant, boat captain, cheerleader, and boyfriend anybody could hope to have. You always seemed to know whether I needed words of encouragement or a kick in the butt. My time in the Keys would not have been as productive or enjoyable without you. You might be the only guy that is as cool as Cota. Getting to know you was truly the best part of my time in graduate school. I will love you forever and always and my heart breaks that you are not here to revel in this accomplishment that is as much yours as it is mine.

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# CHAPTER I

## GENERAL INTRODUCTION

Coral reefs world-wide are in a state of decline due to a number of factors including: global climate change, eutrophication, bleaching, disease, overfishing, and ocean acidification (Hughes et al. 1999, Lapointe 1997, Jackson et al. 2001, Bellwood et al. 2004, McManus and Polsenberg 2004, Valentine and Heck 2005, Pandolfi et al. 2005, Aronson, and Precht 2006, Carpenter et al. 2008, Hoegh-Guldberg et al. 2007). The reefs of the Caribbean have experienced some of the most dramatic changes, having largely undergone a phase shift from a system dominated by corals, to a system where algae and sponges are pervasive (Hill 1998, Gardner et al. 2003, Aronson and Precht 2006). This phase shift was precipitated by the loss of herbivores, including the mass mortality of the long-spined sea urchin (*Diadema antillarum*) over two decades ago (Carpenter 1988, Lesios 1988, Aronson and Precht 2000), coupled with disease-induced mortality (Hughes 1994, Aronson and Precht 2001, Aronson and Precht 2006) and the recruitment failure of hermatypic corals (Hughes and Tanner 2000, Miller and Szmant 2006, Quinn and Kojis 2006, Williams et al. 2008). While *Diadema* populations have rebounded in some areas of the Caribbean, with an associated decline in algal cover and recovery of coral recruitment (Woodley 1999, Edmunds and Carpenter 2001, Carpenter and Edmunds 2006, Myhre and Acevedo-Gutiérrez 2007, Idjadi et al. 2010), *Diadema* populations in other regions including the Florida Keys are still well below historical densities (Chiappone et al. 2002, Miller et al. 2009).

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The journal model for this dissertation is Coral Reefs

The key factors hypothesized to be responsible for the heterogeneous recovery of

*Diadema* populations are lack of suitable habitat, recruitment limitation, and predation

(Lee 2005, Miller et al. 2009, Chiappone et al. 2002 Harborne et al. 2009).

Predation directly and indirectly regulates sea urchin populations in several

ecosystems (Tegner and Dayton 1981, Carpenter 1984, Estes et al. 1998, Lafferty 2004,

Freeman 2005) and is likely an important factor regulating the recovery of *Diadema*

populations (Chiappone et al. 2002). Lobsters are important consumers of sea urchins in

temperate systems (Tegner and Dayton 1981, Shears and Babcock 2002, Langlois et al.

2005) and can shape some temperate communities via the cascading effects of their

predatory activities (Tegner and Dayton 1981, Robles 1987, Shears and Babcock 2002,

Langlois et al. 2005a, Langlois et al. 2005b, Branch 2008). Yet, the predatory role of

lobsters on the structure of tropical ecosystems is less well studied. Of the lobster species

common in the Caribbean, the cryptic, reef dwelling, and philopatric spotted spiny lobster

(*Panulirus guttatus*) is most likely to strongly impact shallow reef communities because

it lives and forages exclusively on shallow reefs.

I examined the effects of the spotted spiny lobster (*P. guttatus*) on the patch reef

communities of the Florida Keys, Florida (USA), with particular attention to impacts on

*D. antillarum*. Additionally, I explored how habitat availability, presence of a

conspecific, and the threat of predation influenced the behavior of *D. antillarum*. In

Chapter II, I examined how predation by *P. guttatus* impacts patch reef prey

communities. Chapter III focuses on the direct and indirect effects of *P. guttatus* on *D.*

*antillarum*. Chapter IV examines how shelter, presence of a conspecific, and predation

threat influences the behavior of individual *D. antillarum*. In Chapter V, I summarize my findings and discuss the potential importance of *P. guttatus* to patch reef communities.

# CHAPTER II

## IMPACTS OF *PANULIRUS GUTTATUS* ON PATCH REEF COMMUNITIES IN THE FLORIDA KEYS

**Introduction**

Trophic cascades are important in structuring marine benthic communities (Paine 1966, Estes 1998, Pinnegar et al. 2000, Dulvy et al. 2004, Heck and Valentine 2007), in contrast to their debatable importance for other animal communities, especially in terrestrial systems (Strong 1992, Pace et al. 1999, Shurin et al. 2002, Chase 2003). The dramatic effects of keystone species can trigger trophic cascades (Paine 1966, Power et al. 1996), however, cascades are sometimes caused by predators via more subtle means, such as apparent competition and trait-mediated changes in prey behavior (Holt 1977, Strauss 1991, Bonsall and Hassell 1997, Pace et al. 1999 Trussell et al. 2003, Schmitz et al. 2004 Matassa 2010). Lobsters, for example, can be keystone predators in temperate benthic marine communities and cause trophic cascades by consuming prey, modifying prey behavior (Tegner and Dayton 1981, Robles 1987, Shears and Babcock 2002, Langlois et al. 2005a, Langlois et al. 2005b, Branch 2008, Matassa 2010), and even by altering prey disease dynamics (Lafferty 2004).

For example, in Southern California the spiny lobster *Panulirus interruptus* preys on mussels, (Robles 1987) and exerts community control similar to that of the sea star *Pisaster orchracues*, as described in Paine's (1966) seminal study on keystone predation. Macroalgal-dominated systems persist in New Zealand and South Africa because of

predation by spiny lobsters (*Jasus edwardsii* and *Jasus lalandii*, respectively) on sea

urchins that otherwise become so numerous that they can convert kelp beds to rocky

barrens (Shears and Babcock 2002, Branch 2008). Overfishing of spiny lobsters in South

Africa has even led to a bizarre predator-prey reversal, where carnivorous whelks

normally eaten by lobsters become so numerous that they mob and consume lobsters,

preventing the reestablishment of lobsters as a regulatory agent (Barkai and McQuaid

1988). Changes in spiny lobster abundance in southern California due to fishing have

also been implicated in controlling density-dependent disease dynamics in temperate sea

urchins (Lafferty 2004). Despite their demonstrated importance in shifting community

structure in temperate systems, the relevance of lobsters in controlling prey communities

in tropical systems is unknown (Behringer and Butler 2006). The few studies that have

examined lobster foraging in tropical systems have generally addressed lobster diets with

no documented effects on associated prey communities (Cox et al. 1997, Nizinski 2007).

Such is the case in the Caribbean where two abundant species of spiny lobster, the

Caribbean spiny lobster (*Panulirus argus*) and the spotted spiny lobster (*Panulirus

guttatus*), co-occur on coral reef ecosystems from Brazil to Bermuda (Sutcliffe 1953,

Caillouet et al. 1971, Moe 1991), but whose trophic effects on coral reefs are

undocumented.

 *Panulirus argus* is the larger and more numerous species, and it supports

economically important fisheries throughout Florida and the Caribbean (Ehrhardt et al.

2010, Hunt 2000, FAO 2000), and thus has been the focus of most research (Butler et al.

2006). However, only adult *P. argus* live on coral reefs and then only while sheltering

during the day; at night, they forage off the reef in adjacent seagrass beds and rubble

zones (Cox et al. 1997). Thus, the impact of *P. argus* foraging on reef communities is probably minimal. In contrast, *P. guttatus* is an obligate inhabitant of coral reefs from the time they settle as postlarvae (Sharp et al. 1997, Robertson and Butler 2009), through adulthood. Moreover, *P. guttatus* demonstrates high site fidelity, residing on coral reefs day and night (Sharp et al. 1997, Robertson and Butler 2009, Lozano- Álvarez et al. 2002), and generally remain on patch reefs when transplanted (Kintzing personal observation). Most studies of *P. guttatus* have focused on population demographics and dynamics associated with fisheries (Evans and Lockwood 1994, Losada-Tosteson et al. 2001, Negrete-Soto et al. 2002), or behavioral comparisons with the congeneric *P. argus* (Lozano- Álvarez and Briones-Fourzán 2001, Lozano- Álvarez et al. 2007, Acosta and Robertson 2003). Few studies have examined the ecology of *P. guttatus* (Robertson and Butler 2003, Wynne and Côté 2007, Robertson and Butler 2009) and none have examined the potential trophic impacts of *P. guttatus* predation on Caribbean coral reef communities.

Via a series of laboratory and field experiments, I examined the trophic dynamics of *P. guttatus* and the potentially cascading impact of these abundant predators on coral patch reef communities. Specifically, I determined what organisms *P. guttatus* consumed in the field and, in laboratory experiments, tested their preference among common prey taxa. I also manipulated *P. guttatus* density on patch reefs to assess their impact on patch reef invertebrate communities. Finally, I examined *P. guttatus* foraging and its potential as a bioturbation mechanism in reef rubble zones.

**Methods**

Lobster collections and experimental field manipulations were conducted approximately 1 km south of Lower Matucumbe Key in the middle Florida Keys, Florida (USA) (Appendix A), where approximately 40 patch reefs occur in waters less than 5 m deep. Laboratory experiments were conducted at the Goshen College Marine Laboratory on Long Key, Florida (USA).

Stomach content analysis

To determine the natural diet of *P. guttatus,* lobsters were caught by divers using nets or spears while the lobsters foraged on reefs at night. The lobsters were immediately placed on ice and transported back to the laboratory where the size, sex, and molt condition of the lobster were recorded prior to removing the stomachs, which were preserved in 70% ethanol (EtOH). Only stomachs from lobsters in the inter-molt condition were used, because lobsters generally do not forage when in the pre- and post-molt conditions (Lipcius and Herrnkind 1982). The stomachs were later opened and the contents rinsed into a glass dish divided by 1 $cm^2$ gridlines. Using a dissecting microscope, I then randomly selected thirty grids in which I identified the stomach contents to the lowest taxonomic grouping and also recorded the percent contribution of those taxa in the diet of *P. guttatus* (Castañeda-Fernández-de Lara et al. 2005).

Lobster Density Manipulation

To determine the effect of *P. guttatus* density on coral patch reef communities, twelve patches were selected based on degree of isolation and size from those available

off the coast of Lower Matecumbe Key. Relatively small, (68-295 m$^2$) isolated

(surrounded by sand and/or seagrass to create distinct experimental units) patches were

chosen to enable experimental density manipulations. Patches were then randomly

assigned to either a high (equal to or greater than reported natural densities; Sharp et al.

1997, Robertson 2001), or low (near zero) *P. guttatus* density treatment (Appendix A).

High and low density treatments, rather than specific static densities, were selected

because: (a) *P. guttatus* densities naturally vary (Robertson and Butler 2009) and

variability in predator densities influences community structure (Butler 1989, Abrams

1995, Navarrete 1996, Griffen and Williamson 2008, Griffin et al. 2008, Eitam and

Blaustein 2010), (b) I wanted to maximize differences between treatments so

experimental effects of lobster density could be easily detected, and (c) specific densities

are difficult to maintain on patch reefs.  I originally also assigned patches to either a high

or low *Diadema* density treatment in a fully crossed two factor design.  However, I was

unable to maintain the *Diadema* treatments due to high mortality, thus I abandoned that

portion of the study.  To account for differences between experimental patches I

measured the area, rugosity, and benthic cover of each reef prior to the start of

experimental manipulations.  I estimated the area of each patch reef from underwater

measurements of cross-reef dimensions.  To estimate rugosity I strung a 10 m straight

line transect over the reef and compared that length to the distance covered by a 10 m

long chain inserted into crevices to obtain a unitless measure of vertical relief for each

reef (Risk 1972).  Benthic cover on reefs was estimated by divers who used 10 m long

point intercept belt transects and 0.0625 m$^2$ quadrats.  Lobster density manipulations

were initiated in the summer of 2006 with monthly maintenance of the high and low

density treatments by lobster removal or addition to reefs during the summers (May -

August) of 2006 and 2007. For logistical reasons, I was unable to visit and actively

maintain lobster density on reefs each month during the remainder of the year in 2006

and 2007, so I instead monitored lobster density every 3-5 months. However, beginning

in May 2008 I again monitored and maintained lobster density treatments each month

until the termination of the experiment in the summer of 2009. To examine the overall

treatment effect, a 2-sample t-test on the square root transformed mean *P. guttatus*

density was run and confirmed that the high and low lobster density treatments indeed

differed significantly as expected ($t = 10.76$, $df = 83$, $p < 0.0005$). To examine the

success of the treatments over time, a 1-factor repeated measures ANOVA was run. This

confirmed the overall result that the high and low lobster density treatments were

significantly different ($F = 305.52$; $df = 8, 7$; $p < 0.001$).

Concurrent with the lobster density manipulations, natural densities of the

herbivorous West Indian spider crab, *Mithrax spinosissimus*, were monitored during the

summers of 2007 and 2008 on the twelve experimental patches for a separate study (see

Mojica 2009). As *Mithrax* density and functional significance are negatively impacted

by predation (Mojica 2009) and as spiny lobsters tend to be generalist carnivores known

to consume crabs (Joll and Philips 1984, Jernakoff 1987, Edgar 1990, Cox et al. 1997,

Mayfield et al. 2000, Castaneda-Fernadez et al. 2005, Guest et al. 2009), a correlation

analysis was run to determine if there was a relationship between *P. guttatus* and *M.*

*spinosissimus* densities.

*Panulirus guttatus* forages in a variety of benthic substrates on patch reefs

including reef rubble and macroalgae (Kintzing personal observation), thus I used two

methods to estimate the effect of the *P. guttatus* density manipulation on patch reef prey

communities. To measure *P. guttatus* predation on rubble-dwelling invertebrates, I

placed 3 - 5 plastic mesh (0.49 $cm^2$ mesh) trays filled with rock and coral rubble on each

experimental patch reef. The trays were sampled once during both the summers of 2008

and 2009 and during the winter of 2008 to account for seasonal and temporal variation.

Sampling involved the removal and placement of into 250 $\mu$m mesh bags by divers,

transportation of trays back to the laboratory, rinsing of the tray contents through a 500

$\mu$m sieve, and storage of sample organisms in 70% EtOH for later identification. After

the trays were sampled, the tray and the rubble were rinsed with fresh water and allowed

to dry for approximately 24 hours before being reconstructed and returned to a patch reef.

A 1-factor repeated measures MANOVA was used to analyze difference in the mean

number of five different invertebrate taxa (crustaceans, mollusks, echinoderms,

polychaetes, and other soft tissue invertebrates) between treatments.

To estimate the effect of *P. guttatus* predation on prey dwelling within reef

macroalgae, I plucked clumps of macroalgae from six replicate 0.01 $m^2$ quadrats from

each patch reef and placed the samples in plastic ziploc bags. Upon returning to the

laboratory, the macroinvertebrates within each quadrat were rinsed from the algae with

freshwater through a 500$\mu$m sieve; all organisms were collected and stored in 70% EtOH

for later identification under a dissecting microscope. Again, a 1-factor repeated

measures MANOVA was used to analyze difference in the mean number of five different

algal-dwelling invertebrate taxa (crustaceans, mollusks, echinoderms, polychaetes, and other soft tissue invertebrates) between the treatments.

## Lobster Prey Selection Experiment

To determine if *P. guttatus* prefer certain prey, I conducted a standard cafeteria-style prey selection experiment in the laboratory (Peterson and Renaud 1989, Krebs 1999). A single *P. guttatus* was starved for 24 hours prior to the experiment then placed in a flow-through saltwater tank (100 L) along with a small (1.5 - 2 g) crab (*Mithrax sculptus*), gastropod (*Cerithium* sp.), and sea urchin (*Echinometra lucunter*); three numerically dominant taxa found on patch reefs and also abundant in *P. guttatus* gut contents. The lobster was allowed to feed for 24 hours, and then the presence/absence of the three taxa was recorded (n = 21 replicates). The data were analyzed using a log-linear goodness of fit test to ascertain if *P. guttatus* preferred any of the taxa offered them.

## Rubble Disturbance Experiment

To determine whether *P. guttatus* displaces coral rubble while foraging, I placed plastic mesh trays (0.49 cm$^2$ mesh) filled with painted coral rubble in a 100 L flow-through saltwater tank. Rubble size and weight likely impact the foraging success of *P. guttatus* as they overturn rubble to search for buried prey, so trays were filled with pieces of either large (mean size 90.3 g, s.e. = 3.71) or small (mean size 12.1 g, s.e. = 0.406) coral rubble. I weighed 25 haphazardly selected pieces of rubble from each tray to confirm the validity of the treatments. A Kruskal-Wallis test confirmed that the rubble

pieces in the large rubble treatments were significantly heavier, approximately five times heavier, than those in the small rubble treatments ($\chi^2 = 74.45$; df = 3; p < 0.0005). A piece of bait shrimp was placed in each tray under the rubble to provide a foraging cue and a *P. guttatus* that had been starved for 24 hours preceding the experiment was then added to the tank. After 24 hours, the lobster was removed and the presence or absence of the shrimp piece was recorded (n = 18 replicates). A photograph of the painted rubble was taken before the lobster was added and again at the termination of the experiment to assess how much of the rubble had been overturned. The photographs were analyzed using Coral Point Count with Excel Extensions (CPCe) (Kohler and Gill 2006) by overlaying each photograph with a five by five grid and recording the percentage of painted rubble visible.

A 2 x 2 contingency table was used to determine whether *P. guttatus* were equally successful in acquiring the shrimp bait buried under large versus small rubble. Differences in the amount of large and small rubble displaced by *P. guttatus* while foraging was determined using a repeated-measures ANOVA that compared between treatments the amount of painted rubble visible in photographs before and after each foraging trial.

**Results**

Stomach content analysis

A total of 66 *P. guttatus* (32 female, 34 males) ranging in size from 26.8 - 62.8 mm carapace length (CL) were collected and analyzed. Five taxa accounted for more than 80% percent of the diet of *P. guttatus*: crabs (48%), bivalves (14%), gastropods (8%), sea

urchins (8%), and polychaetes (7%); about 9% of their diet was unidentifiable soft tissue.

Shrimp (2%), algae (2%), peanut worms (1%), and brittlestars (1%) were all also

observed in the guts of *P. guttatus* (Figure1). A 2 factor fully crossed MANOVA

revealed no significant differences in *P. guttatus* gut content based on either lobster size

(F = 1.114, df = 5, p = 0.365) or sex (F = 0.311, df = 5, p = 0.904), nor was there an

interaction between the factors (F = 0.847, df = 5, p = 0.523).
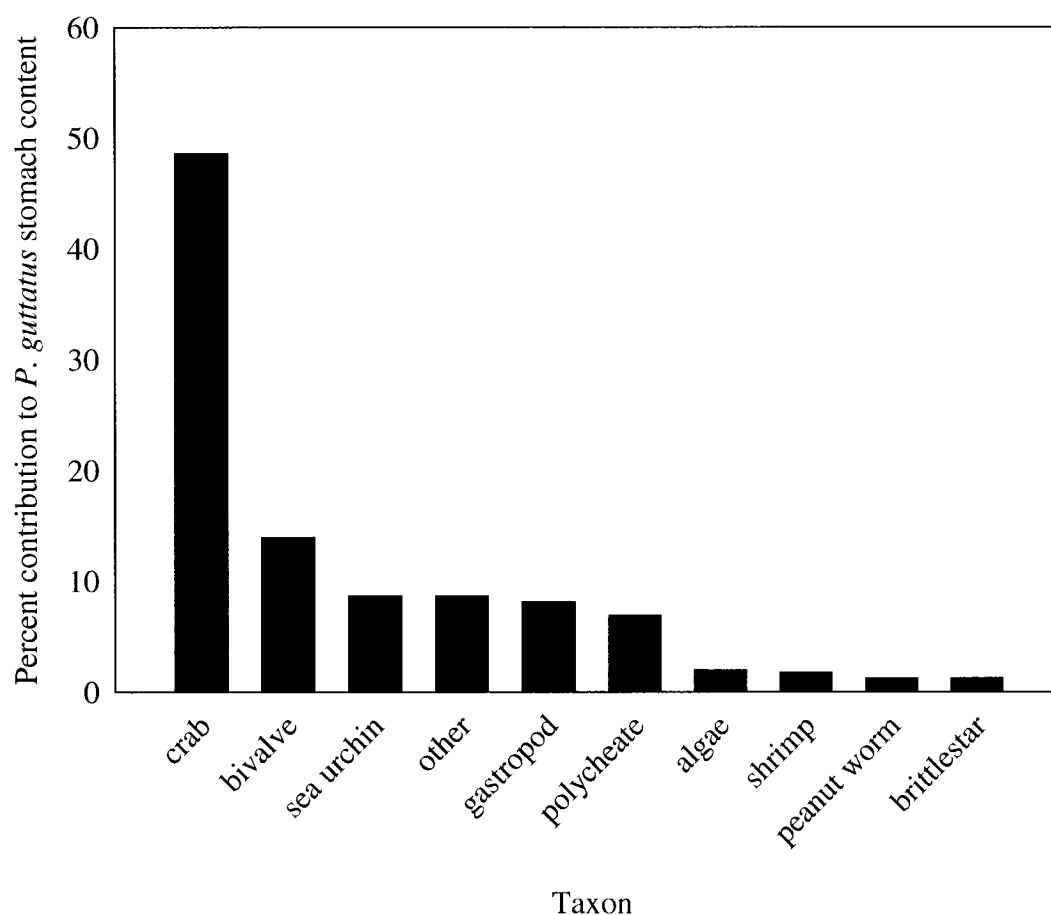


Figure 1: The percent contribution of various taxa to the diet of *P. guttatus* collected in the wild, as based on gut content analysis (n = 66 lobsters).

<u>Lobster Density Manipulation</u>

The observed mean densities of *P. guttatus* in my experimental high and low

density treatments were within the range of natural densities reported in the literature

(Robertson and Butler 2009). However, the manipulated density of *P. guttatus* differed

significantly between the high and low density lobster treatments (Figure 2) over the 36

months of the study and also varried signficantly across sampling periods (Table 1)

(Figure 3). As a consequence, the total number of macroinvertebrates present within

rubble trays placed on patch reefs with a low density of *P. guttatus* were significantly

greater than on patch reefs with high lobster density ($\lambda = 0.171$, $F = 5.823$; df = 5,6; p =

0.027) (Figure 2.4) (Table 2). Specifically, the abundance of crustaceans, mollusks, and

echinoderms in rubble differed significantly between high and low lobster density reef

sites and, in the case of mollusks, echinoderms, polychaetes, and other invertebrates also

differed among sampling periods (Appendix B). In contrast, the total number of

macroinvertebrates dwelling within macroalgae collected in quadrats on the reef did not

differ between lobster treatments or among sampling periods ($\lambda = 0.761$, $F = 0.376$; df =

5,6; p = 0.849) (Figure 5) (Table 3). Further, *P. guttatus* density did not impact the

abundance of any of the individual macroinvertebrate taxa collected in macroalgae

(Appendix C). Additionally, *P. guttatus* density had a significant negative correlation

with *M. spinossiumus* density ($r = -0.568$, $p = 0.0038$, $n = 24$) (Figure 6).
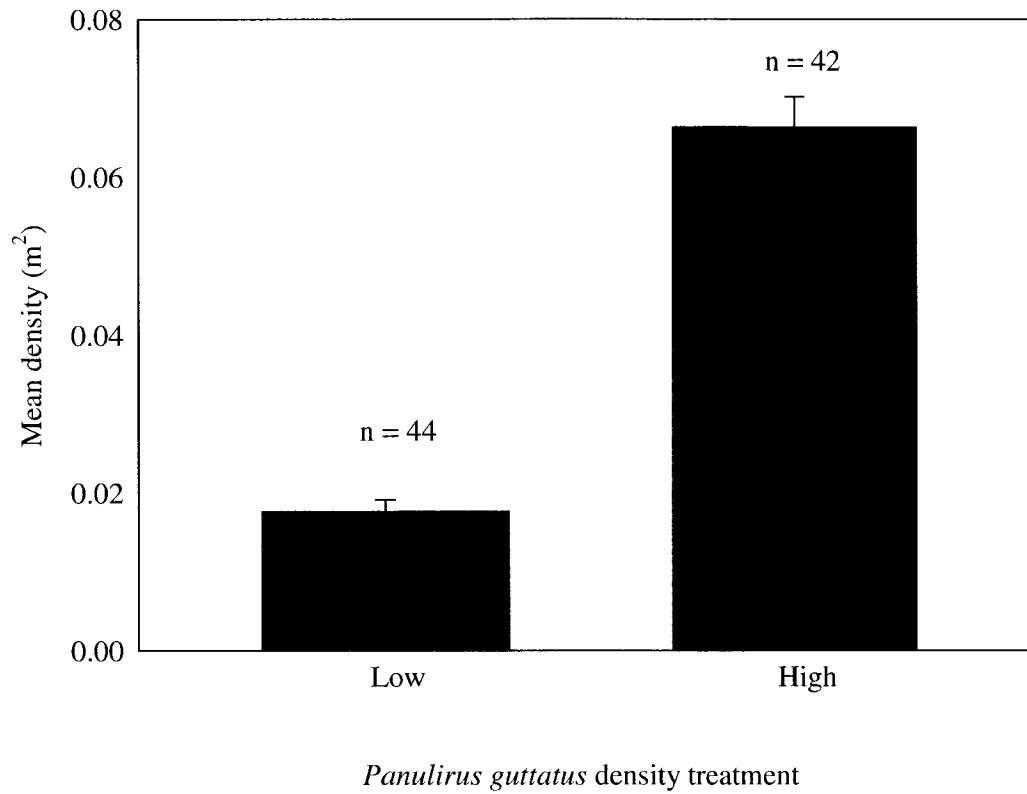
Figure 2: Mean *Panulirus guttatus* density on the six patch reefs in the Florida Keys used in this study. Error bars represent one standard error of the mean.

Table 1: 1-factor Repeated Measures ANOVA table testing the effectiveness of *P. guttatus* density treatments across time.

| Source | df | Sum of Squares | Mean Square | F | p |
|--------|----|----|----|----|----|
| Treatment | 8 | 0.00140 | 0.000175 | | |
| Time | 1 | 0.00901 | 0.00901 | 211.554 | < 0.001 |
| Error | 7 | 0.000298 | 0.0000426 | | |
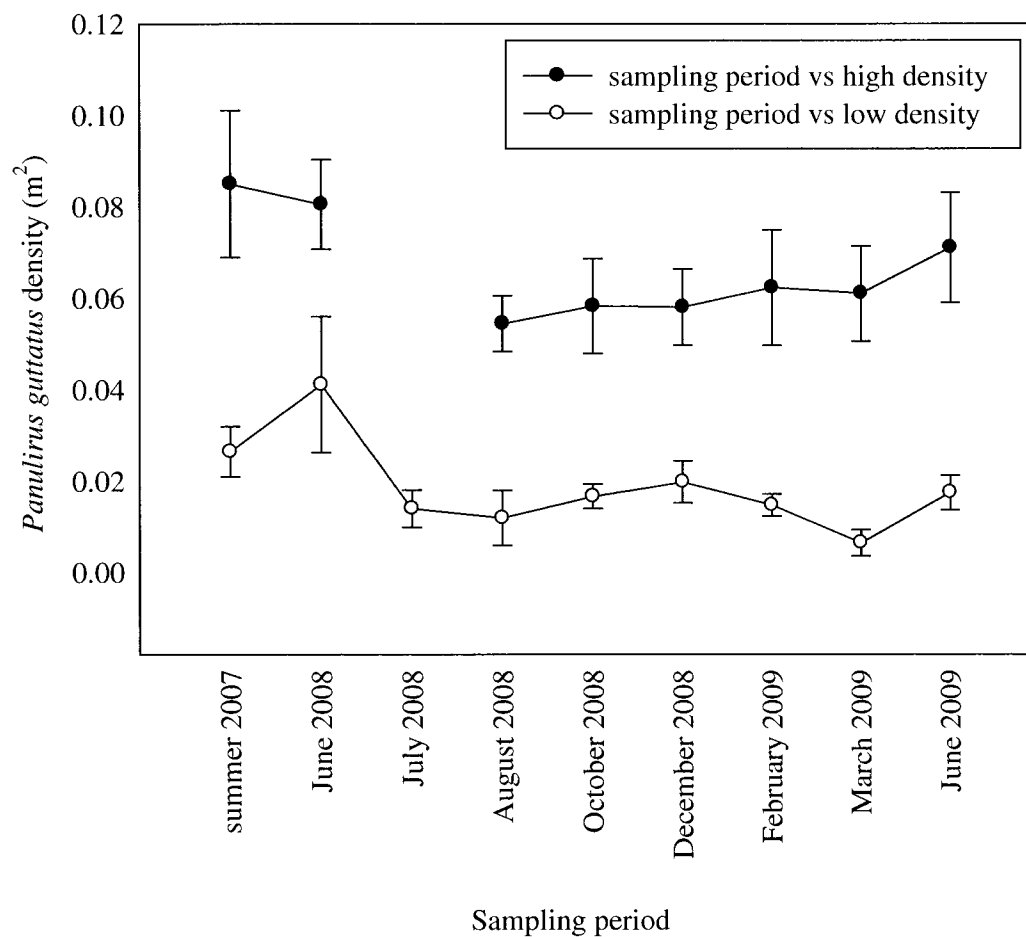
Figure 3: *Panulirus guttatus* density treatments across time. Error bars represent one standard error of the mean.

Table 2: Repeated Measures MANOVA table testing the effect of lobster density treatment and sampling time on the abundance of five macroinvertebrate taxa collected from rubble trays deployed on patch reefs.

| Source | Wilks' lambda | F | Hypothesis df | Error df | p |
|---|---|---|---|---|---|
| Treatment | 0.171 | 5.823 | 5 | 6 | 0.027 |
| Time | 0.003 | 37.579 | 10 | 1 | 0.126 |
| Treatment*Time | 0.048 | 2.003 | 10 | 1 | 0.504 |

Table 3: Repeated Measures MANOVA table testing the effect of lobster density treatment and sampling time on the abundance of five macroinvertebrate taxa collected from macroalgae within random quadrats situated on patch reefs.

| Source | Wilks' lambda | F | Hypothesis df | Error df | p |
|---|---|---|---|---|---|
| Treatment | 0.761 | 0.376 | 5 | 6 | 0.849 |
| Time | 0.261 | 3.405 | 5 | 6 | 0.084 |
| Treatment*Time | 0.551 | 0.976 | 5 | 6 | 0.500 |

Lobster density treatment and sampling period
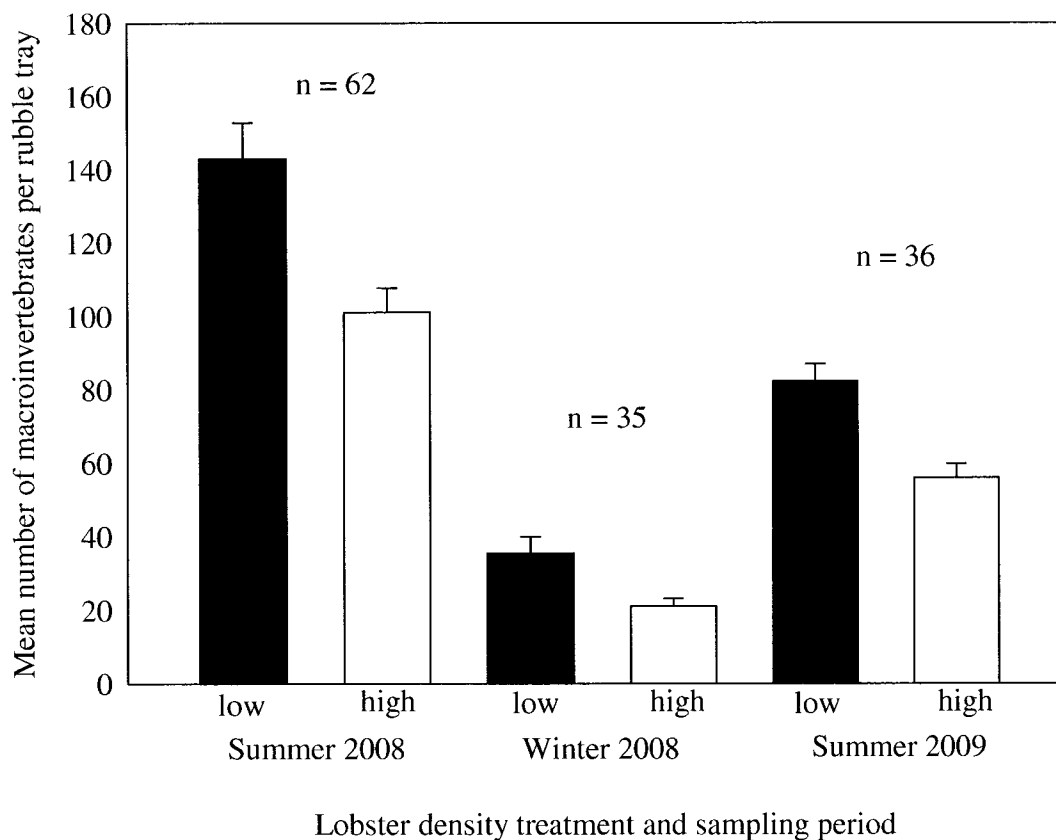
Figure 4: Mean number of macroinvertebrates in rubble trays collected from patch reefs with high and low *P. guttatus* densities during the summer of 2008, winter of 2008, and summer of 2009. Low density treatments are represented by dark bars and high density treatments are represented by light bars. Error bars represent one standard error of the mean.
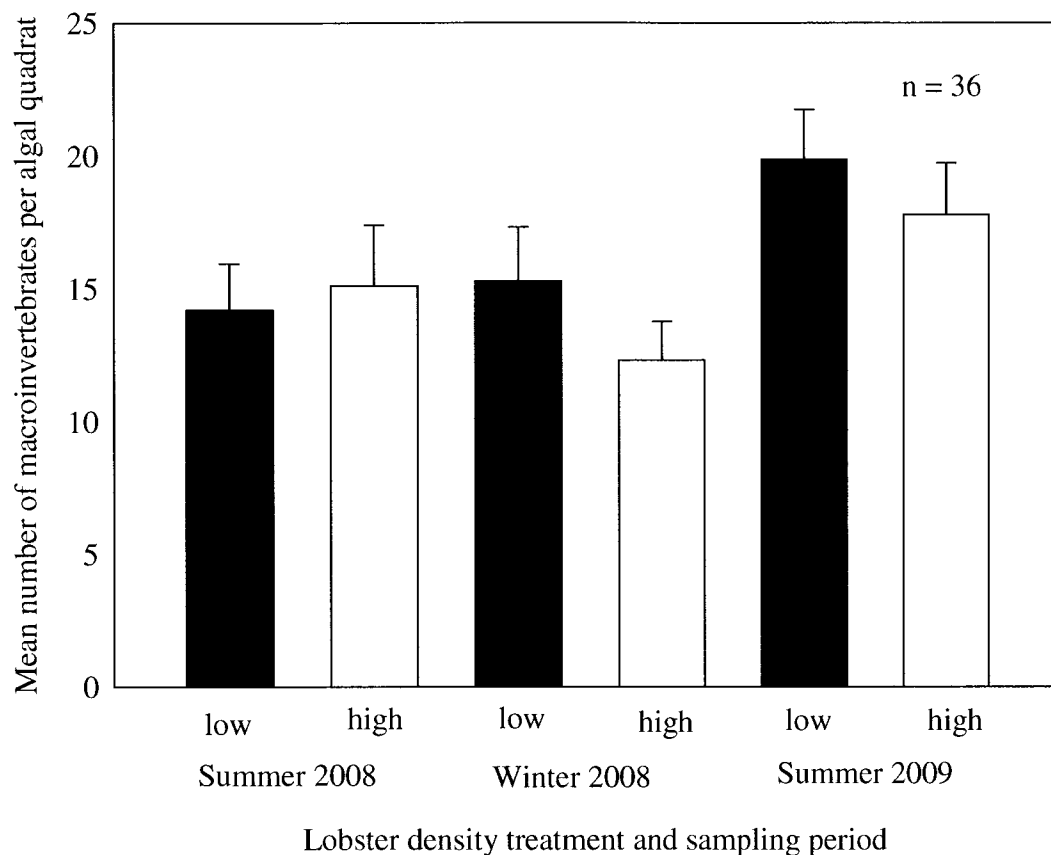
Figure 5: Mean number of macroinvertebrates in algal quadrats collected from patch reefs with high and low *P. guttatus* densities during the summer of 2008, winter of 2008, and summer of 2009. Low density treatments are represented by dark bars and high density treatments are represented by light bars. Error bars represent one standard error of the mean.
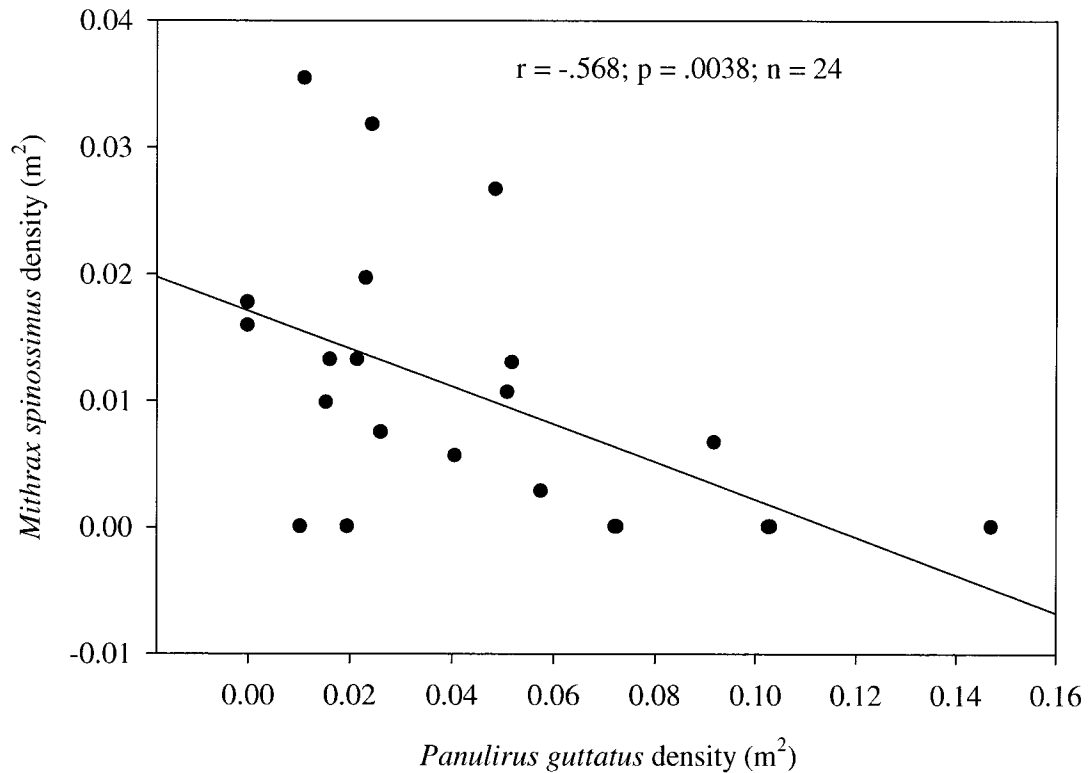
Figure 6: The relationship between *P. guttatus* density (m²)and *M. spinossiumus* density (m²) on experimental patch reefs.

## Lobster Prey Selection

*Panulirus guttatus* readily consumed crabs, gastropods, and sea urchins without preference in laboratory feeding trials (G = 1.537; df = 2; p = 0.466) (Figure 7). These data are consistent with gut content analysis and rubble tray data, which indicate that *P. guttatus* consume a suite of benthic invertebrates.
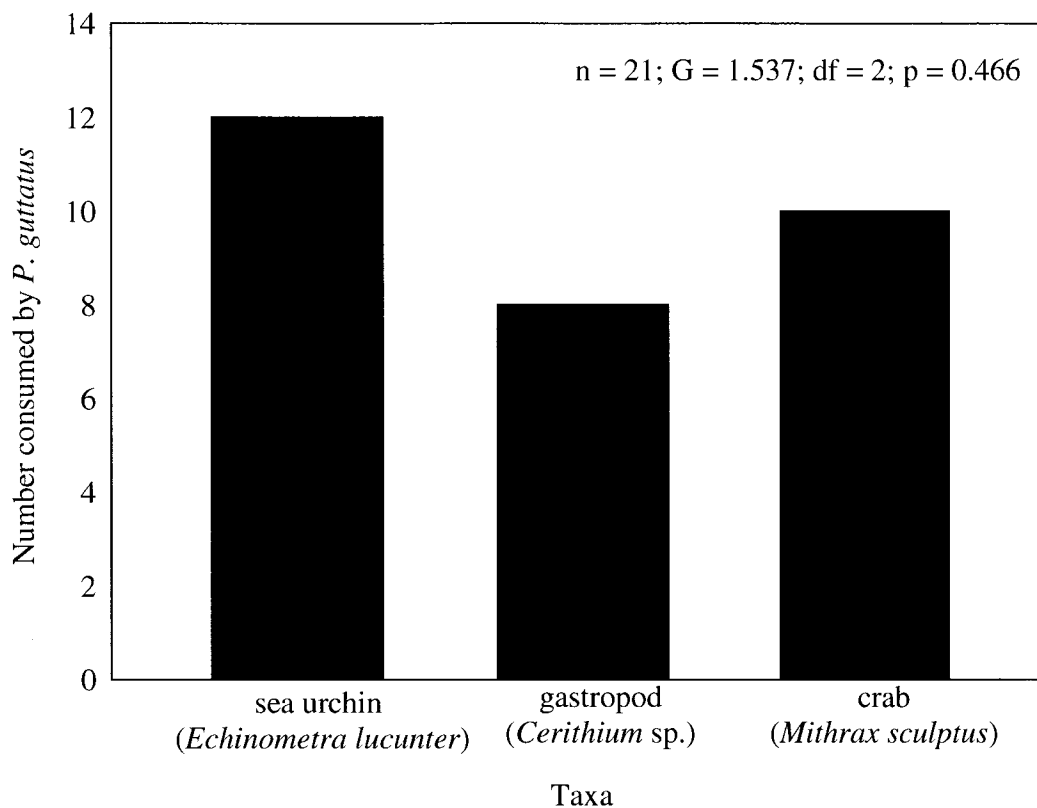
Figure 7: *Panulirus guttatus* consumption of three common patch reef macroinvertebrate taxa in laboratory feeding trials.

## Rubble disturbance experiment

*Panulirus guttatus* foraged more effectively in the small rubble treatment than in the large rubble treatment, and consumed the shrimp in every trial with the small rubble treatment but only about half of the shrimp in the large rubble treatment (G = 12.19; df = 1; p < 0.0005) (Figure 8). Analysis of photographs of painted rubble taken before and after *P. guttatus* foraging indicated that a significant amount of rubble was overturned during the experiment (F = 17.141; df = 1,37; p < 0.0005), more so in the small rubble

trays compared to the large rubble trays (F = 33.930; df = 1,37; p < 0.0005) (Table 4)

(Figure 9).
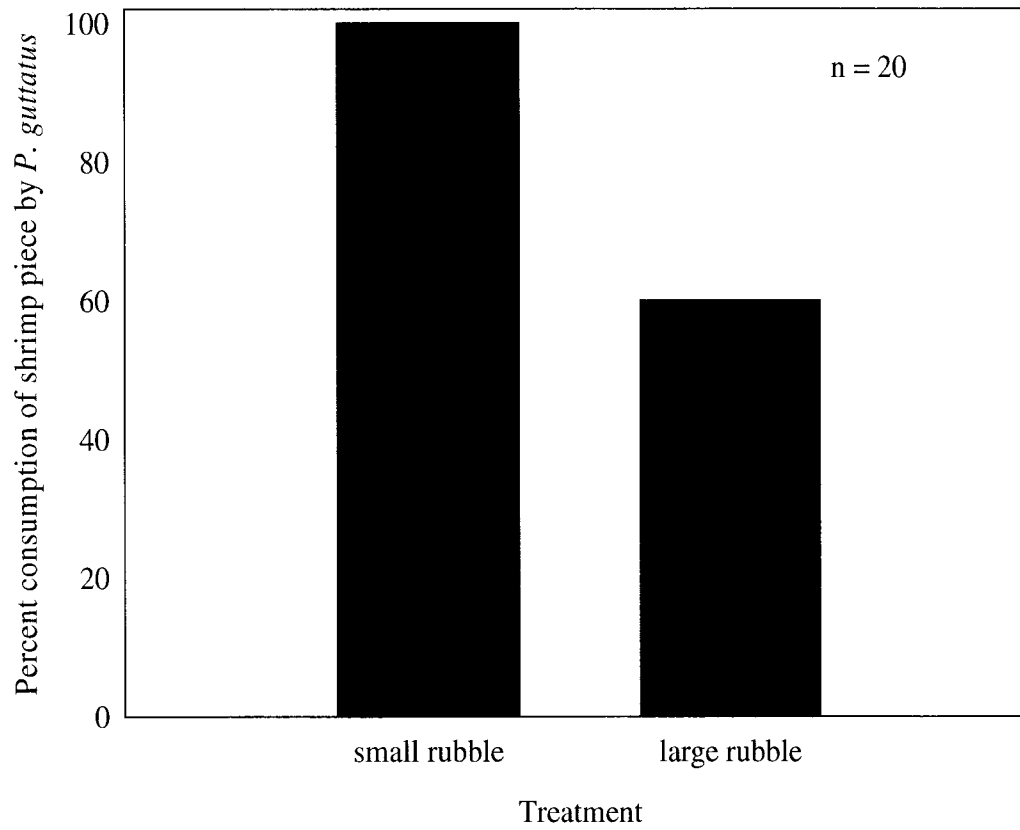


Figure 8: Percentage of shrimp consumed by *Panulirus guttatus* in laboratory trials where shrimp were buried under large and small rubble.

Table 4: Repeated Measures ANOVA table examining the percent of red rock visible in small and large rubble trays (treatment) before and after *P. guttatus* foraging (time).

| Source | Type III Sum of Squares | df | Mean Square | F | p |
|--------|--------|--------|--------|--------|--------|
| Treatment | 4109.086 | 1 | 4109.086 | 33.930 | >0.0005 |
| Time | 2075.885 | 1 | 2075.885 | 17.141 | >0.0005 |
| Error | 4480.863 | 37 | 121.104 | | |
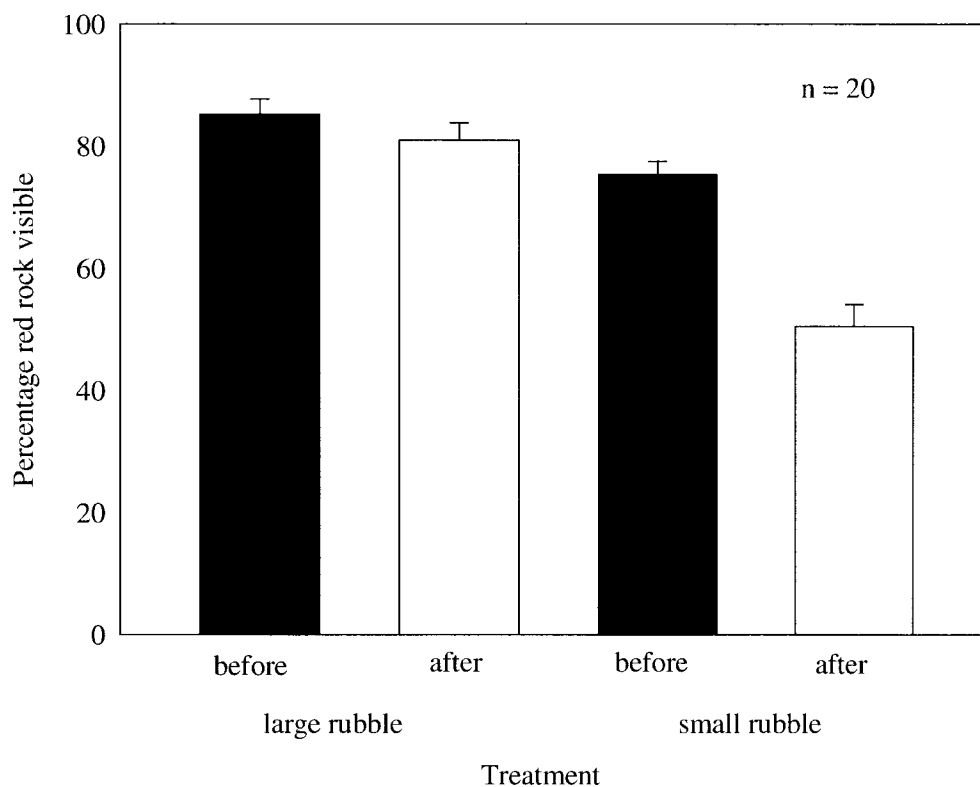
Figure 9: Perecentage red rock visible in both small and large rubble treatments in photographs taken before and after *P. guttatus* foraging in laboratory trials. Before photographs are represented by dark bars while after photographs are represented by light bars. Error bars represent one standard error of the mean.

## Discussion

This study is the first demonstration of top-down community control by a lobster in a tropical system where the effects of predation are generally diffuse and difficult to document. Like most spiny lobsters, *P. guttatus* is a generalist carnivore that preys opportunistically on a suite of small, cryptic macroinvertebrate taxa. Yet, because of its local abundance and philopatric nature on coral reefs, *P. guttatus* exerts a demonstrable effect on prey abundance and community composition that has not been demonstrated for

tropical spiny lobsters, although such effects are common in temperate species. Stomach content analysis indicates that *P. guttatus* has a broad diet dominated by crabs, similar to other spiny lobster species. Consumption of crabs and other crustaceans drove the pattern of decreased invertebrate abundance in rubble on high *P. guttatus* density reefs. There was also a significant negative correlation between *P. guttatus* density and the density of the herbivorous crab *M. spinossiumus* that may be a consequence of *P. guttatus* predation on *M. spinossimus* recruits. Despite the abundance of crabs in *P. guttatus* stomach contents, *P. guttatus* demonstrated no preference for crabs or any other taxa in laboratory feeding trials. Whereas foraging by *P. guttatus* significantly impacted the abundance of macroinvertebrates in reef rubble, it had no impact on invertebrate abundance in algal clumps. Additionally, *P. guttatus* foraging resulted in significant disturbance to rubble substrate, which has potential consequences for reef bioturbation, community structure of rubble-dwelling organisms, and perhaps even the recruitment of corals.

Crabs comprised the largest portion of the diet of *P. guttatus*; however, many other taxa were also consumed by them. For example, bivalves, gastropods, and sea urchins comprise nearly a third of *P. guttatus* stomach contents. These data are likely to be more representative of the natural diet of *P. guttatus* than other published reports of spiny lobster diets (Griffiths et al. 2000) because the lobsters in this study were caught by divers in Florida where *P. guttatus* is not commercially or recreationally fished. Trap based studies are inappropriate for diet assessment as they skew the gut contents of lobsters constrained in traps where they only have access to bait and organisms present in the traps. My data indicate that *P. guttatus* is a generalist carnivore, a foraging strategy

that can significantly impact the size and density of temperate prey populations subject to predation by lobsters (Joll and Philips 1984, Jernakoff 1987, Edgar 1990, Mayfield et al. 2000, Castaneda-Fernadez et al. 2005, Guest et al. 2009). Yet, the diet of *P. guttatus* differed from that of its congener *P. argus*, which is found on the same coral reefs, even within the same den. *Panulirus argus* forages off the reef at night in adjacent sea grass beds and rubble zones and its gut content is dominated by mollusks (ca. 75% of its diet; Cox et al. 1997). In contrast, *P. guttatus* forages on the reef itself and almost half of its diet consists of crabs; mollusks contribute only 22% of its diet. These differences in foraging and diet provide a means of niche differentiation for these sympatric lobsters and lend support to my hypothesis that of the two lobsters *P. guttatus* is more likely to directly influence the abundance and type of small macroinvertebrates found on shallow reef communities.

Indeed, experimental increases in *P. guttatus* density on patch reefs significantly altered the abundance of macroinvertebrates present in coral rubble, although the impact was not uniform across seasons or taxa. High *P. guttatus* densities resulted in significantly fewer crabs, mollusks, and echinoderms on coral patch reefs. Seasonal differences in prey abundance were most pronounced among mollusks, echinoderms, polychaetes and rarer macroinvertebrate taxa that I categorized as "other". Seasonal differences in macroinvertebrate communities are no doubt a consequence of a number of factors that influence prey life histories and community structure, perhaps among them are seasonal changes in predation by *P. guttatus*. Lobsters like nearly all invertebrates and many vertebrates have lower metabolic rates during colder winter conditions (O'Connor et al. 2007) which presumably impacts foraging activities. Indeed, studies of

herbivory on patch reefs in the Florida Keys have demonstrated seasonal differences in foraging by reef fish (Paddack et al. 2006). Nevertheless, despite seasonal differences in the abundance of several prey taxa, *P. guttatus* significantly depressed the density of macroinvertebrates dwelling in rubble zones on patch reefs.

Some of the invertebrates consumed by *P. guttatus* are important herbivores on coral reefs, thus the effects of predation by *P. guttatus* on the small recruits of these species can potentially cascade through the community. Most obvious was the effect of increased *P. guttatus* density on the abundance of a large, herbivorous spider crab, *Mithrax spinosissimus*. Although *M. spinosissimus* may avoid reefs where *P. guttatus* is abundant, it seems more likely that this inverse relationship is maintained by *P. guttatus* consumption of small *M. spinosissimus* as demonstrated in my laboratory prey choice experiments and field experiments using rubble trays. Indeed, small crabs were the only organism consistently more abundant in rubble trays on low lobster density treatment reefs across all sampling events. Despite the dominance of crabs in stomachs of *P. guttatus* caught in the field and the impact of *P. guttatus* on crab abundance in experimental rubble trays, *P. guttatus* did not prefer crabs over other taxa offered to them in laboratory feeding trials, suggesting that *P. guttatus* is an opportunistic rather than a selective predator. Regardless of the mechanism, high *P. guttatus* densities resulted in decreased densities of this potentially important reef herbivore. Additionally, *M. spinosissimus* forages less effectively in predator-rich environments (Mojica 2009), so high densities of *P. guttatus* are also likely to reduce the foraging rates of small *M. spinosissimus* that are most vulnerable to predation by lobsters.

*Panulirus guttatus* density had no detectable impact on the invertebrate communities that reside in macroalgae, even though I often observed *P. guttatus* foraging in macroalgae on the patch reefs during my night dives. *Halimeda*, the dominant alga on my experimental patch reefs, is a calcareous green alga that is both structurally and chemically defended from herbivores (Paul and Fenical 1983). Within its tightly clumped and structurally complex branches, potential prey items also find a spatial refuge from predation. Benthic cover data indicated that there was more algae, specifically *Halimeda* sp., on my experimental patch reefs than coral rubble where the effect of *P. guttatus* predation was clearly observed. I suspect that the expansive coverage of macroalgae on those reefs along with rapid recolonization of macroalgae by prey may explain why the effects of foraging by lobsters was discernable in one habitat and not the other. Studies in temperate systems have demonstrated that propagule supply drives algal community assemblages (Lee and Bruno 2009). On tropical coral reefs, Martin-Smith (1994) observed full community re-colonization in as little as 6 hours after removing invertebrate fauna from the brown algae *Sargassum fissifolium*. Similarly, macroinvertebrates removed from clumps of macroalgae on shallow hardbottom areas in the Florida Keys were completely recolonized overnight (Butler et al. 1997). Thus, the effect of *P. guttatus* foraging on small macroinvertebrates within *Halimeda* is conceivably more diffuse and difficult to detect than in rubble where prey are larger and less motile.

Physical disturbance can be an important mechanism regulating community structure and composition in many systems (Sousa 1979, Peterson 1991), and the disturbance that high densities of foraging *P. guttatus* impart within reef rubble zones is a

form of bioturbation of potential significance to community structure on coral reefs.

While foraging for prey, *P. guttatus* turn over coral rubble, especially smaller pieces of

rubble. There are several possible ecological consequences that result from this

disturbance, among them are (1) the disruption of invertebrate communities with possibly

higher predation by other opportunistic predators, and (2) changes in algal and sessile

invertebrate community structure associated with frequency of rubble turnover (Sousa

1979). Of particular relevance on coral reefs is the relationship between rubble turnover

and coral recruitment. Corals need stable substrates on which to settle (Fox et al. 2003,

Victor 2008, Perry and Smithers 2009) so the disturbance caused by *P. guttatus* foraging

likely inhibits coral recruitment. Although the percentage of coral species that recruit to

rubble is unknown, corals do recruit to rubble zones (Fox 2004, Nugues and Szmant

2006) and may even be chemically attracted to dead coral skeletons (Norström et al.

2007) that compose coral rubble. In addition to direct disturbance, the rubble movement

caused by *P. guttatus* foraging may indirectly impact coral recruitment by disrupting the

adhesion of coral rubble via sponges and calcium carbonate algae, thus retarding

substrate stabilization. High rates of coral recruitment are necessary for the persistence

and recovery of coral reefs (Mumby and Steneck 2008, Ritson-Williams et al. 2009,

Ritson-Williams et al. 2010), thus the persistent disturbance of small rubble that *P.*

*guttatus* imparts could impact reef recovery on reefs with high *P. guttatus* densities.

Herbivorous fishes (Mumby et al. 2006, Bellwood et al. 2006, Burkepile and Hay

2006, Hughes et al. 2007, Burkepile and Hay 2009, Sotka and Hay 2009), sea urchins

(Morrison 1988, Carpenter 1988, Aronson and Precht 2000, Edmunds and Carpenter

2001, Carpenter and Edmunds 2006, Furman and Heck 2009), and crabs (Stachowicz and

Hay 1996, Stachowicz and Hay 1999, Mojica 2009) are all important consumers of algae that can mediate coral-algal competition and whose loss, especially that of fishes and urchins, contributes to coral reef decline. Thus, through the consumption of small, vulnerable herbivorous crabs and sea urchins, *P. guttatus* may depress algal consumption by these important herbivores resulting in diminished regulation of macroalgae on coral reefs in the Caribbean (Chapter III). If so, high densities of *P. guttatus* may retard reef recovery and reinforce the current algal dominance pervasive on Caribbean reefs by further depressing already low rates of herbivory.

Whereas evidence of strong top-down control on coral reefs exists, such as predation by *Acanthaster planci* (Dulvy et al. 2004), and herbivory by *Diadema antillarum* (Carpenter 1988, Lessios 1988, Edmunds and Carpenter 2001, Idjadi et al. 2010), temperate marine benthic communities offer most of the best evidence for strong top-down community control (Paine 1966, Estes 1998, Pinnegar et al. 2000). This is generally attributed to less diversity in these systems (Strong 1992). Lobsters are known to be important consumers in temperate systems, often controlling community structure via predation (Tegner and Dayton 1981, Robles 1987, Shears and Babcock 2002, Lafferty 2004, Langlois et al. 2005a, Langlois et al. 2005b, Branch 2008). For example, Robles (1987) demonstrated that exclusion of *P. interruptus* lead to increases in the density and size of mussels on a rocky shore, while Langlois et al. (2005b) showed that increased densities of *Jasus edwardsii* associated with marine reserve protection lead to decreased abundance of mollusks both within the reserve and in halos adjacent to the reserve. However, studies have failed to demonstrate an analogous role for lobsters in tropical systems (Nizinski 2007). Localized increases in *P. argus* density associated with

increased shelters had no impact on surrounding molluscan infauna (Nizinski 2007),

despite evidence that mollusks comprise the majority of the *P. argus* diet (Cox et al.

1997). This lack of observed effect on prey abundance was attributed to diffuse

predation in a species rich system. Similarly, *P. guttatus* had no observable effect in

algae where prey are dispersed over a larger area and their rapid recolonization of algae

overwhelms any predatory impact. But in coral rubble, predation by *P. guttatus*

significantly decreased total macroinvertebrate abundance and altered community

composition by decreasing the abundance of crustaceans, echinoderms, and mollusks.

The clustered nature and accessibility of the diverse prey in coral rubble, coupled with

the philopatric nature of *P. guttatus*, results in a concentrated effect of predation, more

analogous to temperate systems. Thus the strong, direct effects of predation by *P.*

*guttatus*, which are focused upon the new recruits of herbivorous crabs and urchins,

potentially influence macroalgal dynamics on coral reef communities.

# CHAPTER III

# INTERACTIONS BETWEEN THE LONG-SPINED SEA URCHIN (*DIADEMA ANTILLARUM*) AND THE SPOTTED SPINY LOBSTER (*PANULIRUS GUTTATUS*)

## Introduction

Coral reefs, one of the most diverse and productive ecosystems in the world (Knowlton 2001), are in a state of decline due to global climate change, eutrophication, coral bleaching, disease, ocean acidification, and loss of herbivores (Lapointe 1997, Hughes et al. 1999, Jackson et al. 2001, Bellwood et al. 2004, Valentine and Heck 2005, Pandolfi et al. 2005, Hoegh-Guldberg et al. 2007, Carpenter et al. 2008). Caribbean coral reefs in particular have seen some of the most drastic declines in coral cover over the past few decades (Gardner et al. 2003, Green et al. 2008, however see Bruno et al. 2009 and Schutte et al. 2010), and a key factor precipitating this decline was the mass mortality of a keystone herbivore: the long-spined sea urchin, *Diadema antillarum* (Carpenter 1988, Lessios 1988, Edmunds and Carpenter 2001, Idjadi et al. 2010).

In the early 1980s, an unknown pathogen spread rapidly throughout the Caribbean sparking a catastrophic die-off of *Diadema* throughout the region, resulting in greater than 99% mortality in some areas (Lessios 1988, Carpenter 1988). Within days of the *Diadema* mass mortality, many reefs experienced rapid phase shifts from coral dominated systems to those dominated by macroalgae (Carpenter 1988). Macroalgae not only competes with coral for space (Box and Mumby 2007), but also decreases the fecundity

of coral (Foster et al. 2008) and inhibits coral recruitment (Birrell et al. 2008, Ritson-Williams et al. 2009, Arnold et al. 2010). Decades after the mass mortality, recovery of *Diadema* populations in the Caribbean has been slow and spatially heterogeneous, but where they have recovered, macroalgal cover has decreased resulting in a corresponding increase in coral recruitment (Carpenter and Edmonds 2006, Edmonds and Carpenter 2001, Myhre and Acevedo-Gutiérrez 2007, Furman and Heck 2009, Idjadi et al. 2010). Thus, the maintenance of a healthy herbivore community and the recovery of important herbivores, such as *Diadem*a, diminished by disease or overfishing is crucial to the reestablishment of coral dominance on reefs.

Coral reefs in the Florida Keys (Florida, USA) represent one of the regions that have seen limited recovery of *Diadema* (Chiappone 2002). Several mechanisms have been postulated to explain the continued absence of *Diadema* in the Florida Keys, including: limited larval supply, lack of appropriate settlement habitat, and high post-settlement mortality (Miller et al 2009, Chiappone 2002, Lee 2006). Recruitment of *Diadema* to the Florida Keys is spatially and temporally variable, and low relative to historic levels in other areas of the Caribbean (Miller et al. 2009). Yet, pulses of *Diadema* recruits are frequent in the Florida Keys (Chiappone 2002), suggesting that post-settlement mortality plays an important role in determining *Diadema* population abundance. *Diadema* recruits often settle in reef rubble where they may be crushed by physical disturbances associated with hurricanes (Miller et al 2009). However, hurricanes are infrequent events whose effect on urchin populations is speculative compared to predation, which has significant direct and indirect impacts on sea urchin

populations worldwide (Tegner and Dayton 1981, Carpenter 1984, McClananhan and

Shafir 1990, Shears and Babcock 2002, Hereu et al. 2005, Freeman 2005).

Direct consumption of prey by predators has demonstrable effects on prey

populations, but even the threat of predation can drastically alter prey behavior and, in

turn, the functional significance of prey in the community (Trussell et al. 2003, Vadas

and Elner 2003, Freeman 2005, Heithaus et al. 2007, Heithaus et al. 2009). For example,

consumption of sea urchins by sea otters (Estes and Palmisano 1974) and spiny lobsters

(Tegner and Dayton 1983) has positive cascading effects on kelp forests by reducing sea

urchin grazing on kelp. Chemical cues alone can inhibit sea urchin grazing, as occurs

when urchins are exposed to lobster odors (Matassa 2010). Other sea urchins flee when

exposed to the odor of potential predators (Vadas and Elner 2003), or in the case of

*Diadema,* when exposed to the odor of an injured conspecific (Snyder and Snyder 1970).

Whether *Diadema* responds directly to predator odors is unknown, but a number of

piscine and invertebrate predators consume *Diadema* (Randall et al 1964), whose

foraging is depressed on reefs where the threat of piscine predation is high (Carpenter

1984). Therefore, predators may slow the recovery of *Diadema* on coral reefs directly

via predation while simultaneously inhibiting the foraging of urchins and thus their

functional significance as reef herbivores.

Spiny lobsters are important predators of echinoderms and mollusks worldwide,

whose predatory activities sometimes result in trophic cascades (Robles 1987, Shears and

Babcock 2002, Langlois et al. 2005a, Langlois et al. 2005b, Branch 2008). The

Caribbean spiny lobster, *Panulirus argus,* is the most numerous species in the region and

although adults shelter on coral reefs by day, at night they feed off the reef in seagrass meadows and rubble zones where *Diadema* rarely occur. In contrast, the spotted spiny lobster, *Panulirus guttatus,* is an obligate inhabitant of coral reefs where it is numerous, 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 (Sutcliffe 1953, Evans and Lockwood 1994, Wynne and Cote 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, Robertson 2001, Chiappone et al. 2002, Miller et al. 2009). Thus, in this chapter I examine whether *P. guttatus* preys on *Diadema*, whether *Diadema* can attain a size specific refuge from *P. guttatus* predation, and whether trait-mediated interactions occur between these species that could have important implications for coral reef communities.

**Methods**

<u>Lobster preference for sea urchin species</u>

To test whether *P. guttatus* prefers to prey on some species of sea urchins over others, I conducted a laboratory experiment to compare lobster consumption of three species of sea urchin that are common on coral reefs in the Florida Keys. A single *P. guttatus* of known size (i.e., carapace length; measured to the nearest mm using Vernier caliper) and sex, was starved for 24 hours and then placed in a 100 L flow-through salt water tank with six sea urchins. The six sea urchins consisted of two animals of similar size (7 - 25 mm test diameter) from each of the following three species: the long spined sea urchin (*D. antillarum*), the rock boring sea urchin (*Echinometra lucunter*), and the

slate pencil sea urchin (*Eucidaris tribuloides*). The lobster was allowed to feed for 24

hours, after which the presence of the urchins was recorded (n = 27).

Lobster size selectivity of *Diadema*

*Panulirus guttatus* is a diminutive species of lobster whose maximum size

(Sutcliffe 1953) is less than half that of its common Caribbean congenor, *P. argus*

(Lozano-Alvarez et al. 2003, Robertson and Butler 2003). Prey consumption by lobsters

is often size-specific (Pollock 1979, Butler et al. 2004) and it is likely that the size of prey

consumed by *P. guttatus* is limited by lobster size. Thus, I determined in laboratory

experiments if this potential anatomical constraint impacts *P. guttatus* consumption of

*Diadema*. The size and sex of a single *P. guttatus*, that had been starved 24 hours

preceding the experiment, was recorded and the lobster was then placed in a 100 L flow-

through saltwater tank. Three *D. antillarum* differing in test size diameter (5.0- >30.1

mm test diameter), measured with calipers to the nearest 0.1 mm, were then added to the

tank and their presence or absence recorded after 24 hours (n = 13). For analysis, the

*Diadema* were grouped into size categories based on test diameter, where every 5 mm

increase in test diameter represented a different size group. Percent consumption of each

size class was determined by dividing the number of *Diadema* consumed in a given size

class by the total number of *Diadema* offered in that size class. Additionally, *Diadema*

were regrouped into two larger size categories: small (<20 mm test diameter) and large (>

20 mm test diameter) and a 2 x 2 (outcome x urchin size) log-linear goodness of fit

analysis was run to determine if consumption of urchins by *P. guttatus* was independent

of urchin size.

<u>*Diadema* response to lobster chemical cues</u>

*Diadema antillarum* flees when exposed to the chemical cue of an injured

conspecific (Snyder and Snyder 1970), but it is not known whether it responds to the

chemical cue of a potential predator. In a laboratory study, I determined whether *D.*

*antillarum* flees in response to the odor of two species of spiny lobster: one a reef

obligate that forages exclusively on the reef (*P. guttatus*) and the other (*P. argus*) a

diurnal inhabitant of coral reefs that primarily forages off the reef. To initiate a trial, I

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 cm x 5 cm grid, and filled with

approximately 45 liters of water. The *D. antillarum* was given 15 minutes to acclimate

before I slowly added approximately 7.5 liters of untreated seawater (control) or the same

amount of treatment water, obtained from an aerated 19 liter aquarium in which a single

45 - 65 mm CL lobster (either *P. guttatus* or *P. argus*) had been held for approximately

24 hours. The movement of the *Diadema* in response to the added water was observed

for five minutes following the introduction of the water and the total distance moved (cm)

during this five min period was recorded. This experiment was performed using 20

*Diadema* with the *P. guttatus* cue and 15 *Diadema* with the *P. argus* cue. Separate

controls equaling the sample size of each lobster treatment were also conducted. Despite

their procedural similarity, the experiments with *P. guttatus* and *P. argus* were not

analyzed using ANOVA because the experiments were entirely separate and conducted at

different time periods with *Diadema* from distinct collection events, (i.e., the same

*Diadema* were not tested against both *P. guttatus* and *P. argus*). Thus for both

experiments, I compared the distance moved by urchins in each lobster predator

treatment and its corresponding control using 2 sample t-tests with unequal variance, as no standard transformation of the data met the homogeneity of variance assumption.

<u>*Diadema* feeding in response to the presence of lobster</u>

To determine if the threat of predation by *P. guttatus* altered the foraging behavior of *D. antillarum*, I measured the consumption of macroalgae by a single urchin in laboratory trials with or without a lobster present. *Diadema* were starved for 24 hours preceding the experiment, then placed in a 100 L flow-through saltwater tank containing two shelters (each shelter consisted of three bricks arranged to create a den) and a known quantity of two types of macroalgae (*Halimeda* sp. and *Dictyota* sp.) collected from nearby patch reefs. Before addition to the experimental tanks, the macroalgae were spun thirty revolutions in a salad spinner, weighed on a top-loading balance (nearest 0.01 g), and inserted into small, square (25 cm$^2$) pieces of rubber bath mat that were attached to the bottom of the tank. The *Diadema* was given 24 hours to graze then the remaining algae was removed, spun, and reweighed. *Diadema* were tested either alone or in the presence of *P. guttatus*, which if present was constrained near one shelter by an 8 cm long monofilament tether attached to its carapace by a monfilament harness. The experiment was replicated 19 times. To determine if there was a difference in consumption of either *Halimeda* sp. or *Dictyota* sp. due to the presence of the *P. guttatus*, a 1-factor model I MANOVA was performed with lobster presence/absence as the factor and consumption of the two algal species as the response variables.

## *Diadema* food preference

To assess if *D. antillarum* has a preference for *Halimeda* sp. or *Dictyota* sp., the two dominant genera of algae on nearshore patch reefs in the Florida Keys (Kintzing personal observation), I measured the consumption of macroalgae by urchins in laboratory trials. Twenty four *D. antillarum*, starved for 24 hours prior to the experiment, were placed in individual flow-through aquaria with known quantities of *Halimeda* sp. and *Dictyota* sp., preweighed and presented to the urchins in small clumps attached to bath mat squares as described in the previous experiment. After 24hrs the amount of each species that had been consumed by *Diadema* was determined by reweighing the algae as described above. A 2-sample t-test assuming unequal variance was used to determine if *Diadema* consumed more of either genus of algae.

## Results

### Lobster preference for sea urchin species

*Panulirus guttatus* consumed all three species of sea urchins offered. Although more *Echinometra lucunter* were consumed than either *D. antillarum* or *Eucidarus tribuloides*, this difference was not significant (G = 3.778; df = 2; p = 0.15) (Figure 10). These results are consistent with other feeding trials and gut content analysis that I conducted (Chapter II), all of which demonstrate a lack of prey selectivity by *P. guttatus*.
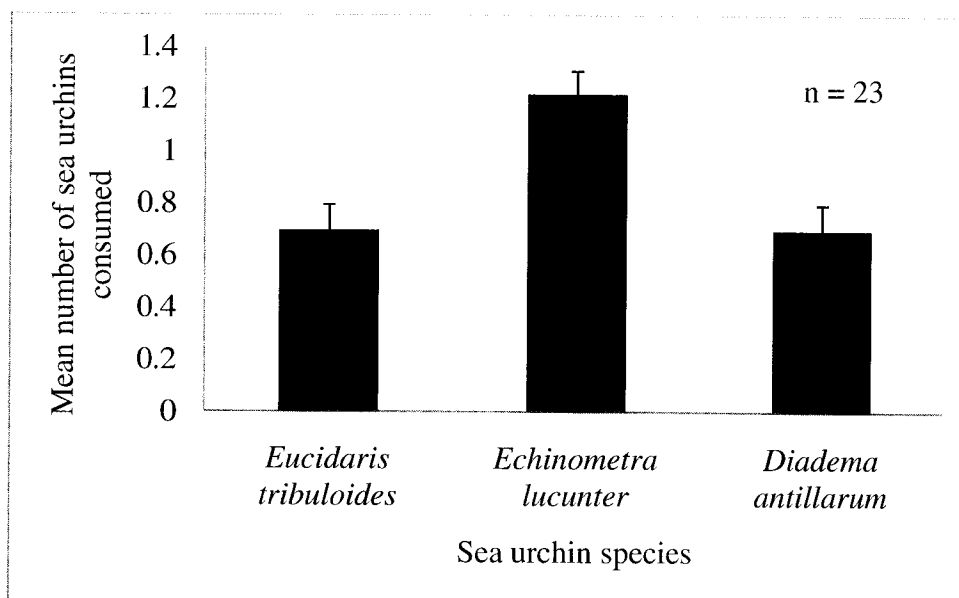
Figure 10: Number of sea urchins of three different species consumed by *Panulirus guttatus*. Error bars represent one standard error.

Lobster size selectivity of *Diadema*:

*Panulirus guttatus* preferred smaller *D. antillarum*: 88% of the *Diadema* in the

smallest size class (5 - 10 mm test diameter) were eaten whereas none of the largest

*Diadema* were preyed upon (Figure 11). The largest *D. antillarum* consumed had a test

diameter of 25.2 mm. Results of a log-linear goodness-of-fit test confirmed that

significantly more small *Diadema* (test diameter of 20 mm or less) were eaten than large

ones (G = 21.5; df = 1; p = 0.0005).
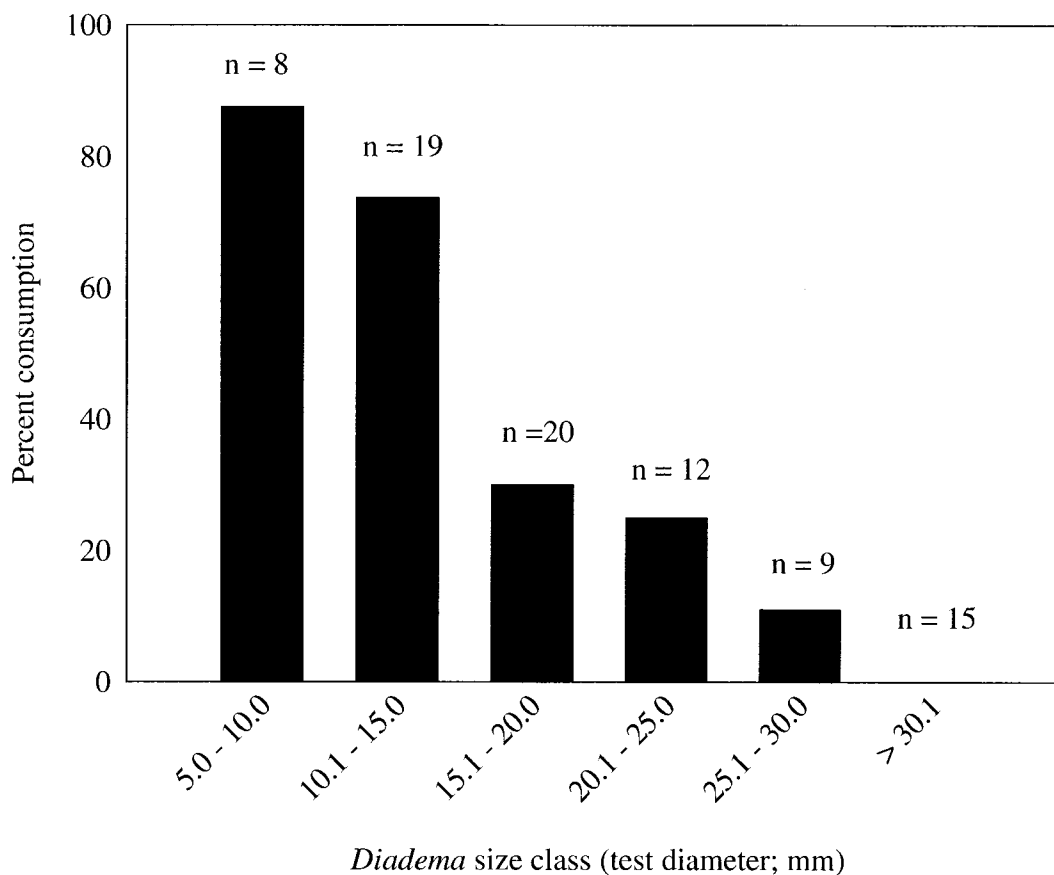
Figure 11: *Panulirus guttatus* consumption of *D. antillarum* (separated by 5 mm test diameter size class) as determined in laboratory feeding trials.

Diadema response to lobster chemical cues:

*Diadema antillarum* moved significantly more in response to the odor of the reef-dwelling lobster *P. guttatus* compared to a seawater control (t = 2.65; df = 8; 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 a significant difference in *Diadema* movement when the results of the two 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) (Figure 12).
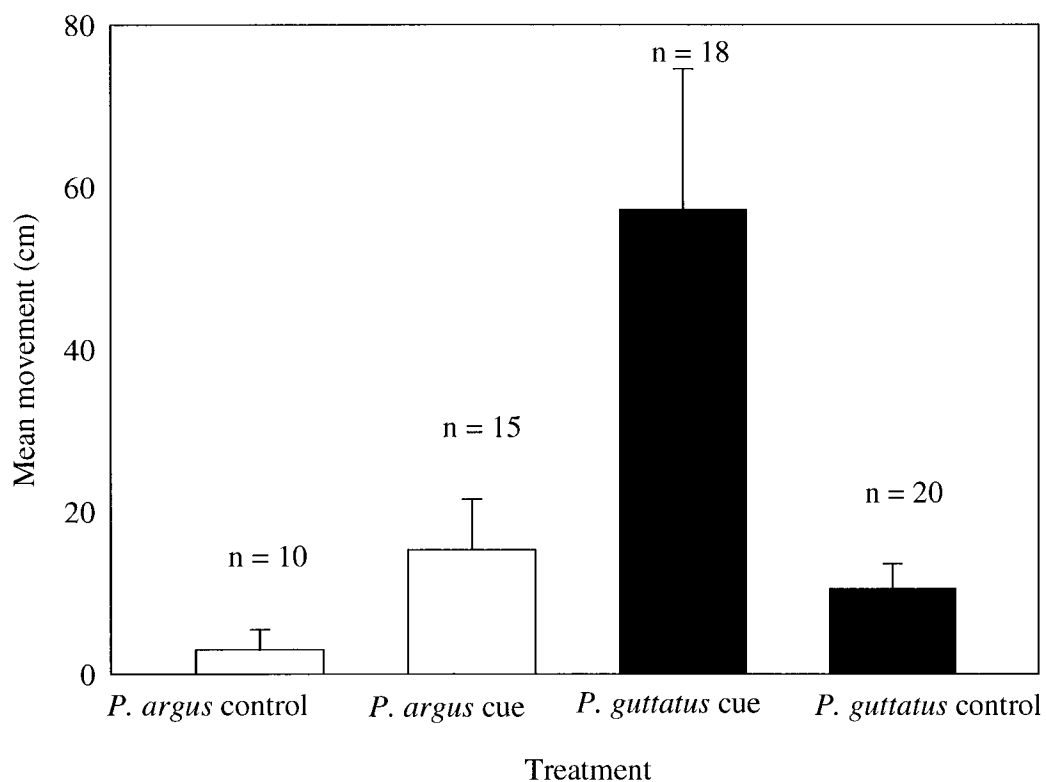


Figure 12: *Diadema* movement (cm) in response to waterborne cues of *P. argus*, *P. guttatus*, and their respective seawater controls. Light bars represent *P. argus* experiment while dark bars represent *P. guttatus* experiment. Error bars represent one standard error.

Diadema feeding in response to the presence of a lobster

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

algae in the presence of *P. guttatus* compared to a sea water control (F = 5.449, df = 2,

35, p = 0.009, n = 19). *Diadema* 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* sp. (p = 0.012) and *Halimeda* sp. (p = 0.038)) (Figure 13).
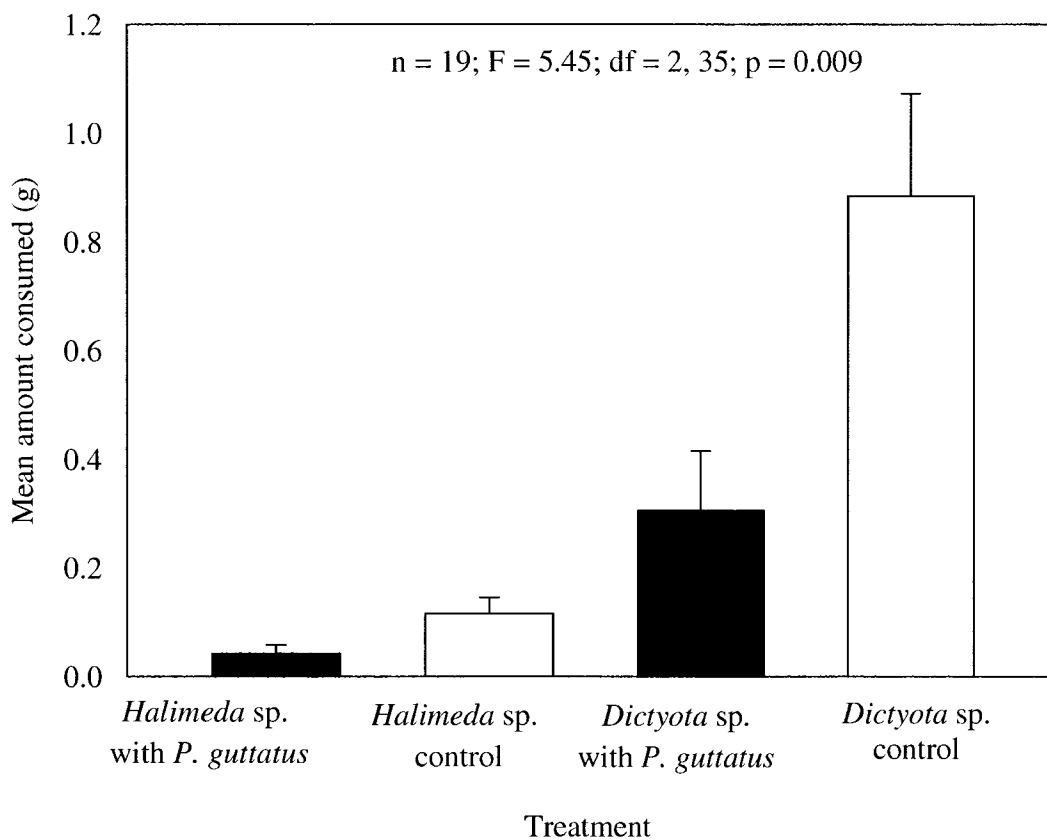


Figure 13: Mean amount (in grams) of *Halimeda* sp. and *Dictyota* sp. consumed by *Diadema* in the presence of a *P. guttatus* versus a control. Light bars represent controls while dark bars represent *P. guttatus* treatments. Error bars represent one standard error.

*Diadema* food preference

Although *Diadema* consumed both species of algae, they preferred *Dictyota* sp.

and consumed almost an order of magnitude more *Dictyota* sp. than *Halimeda* sp. in a 24

hr period, a statistically significant difference in the consumption of the two algae (t =

6.70; df = 28; p = 0.0005) (Figure 14).
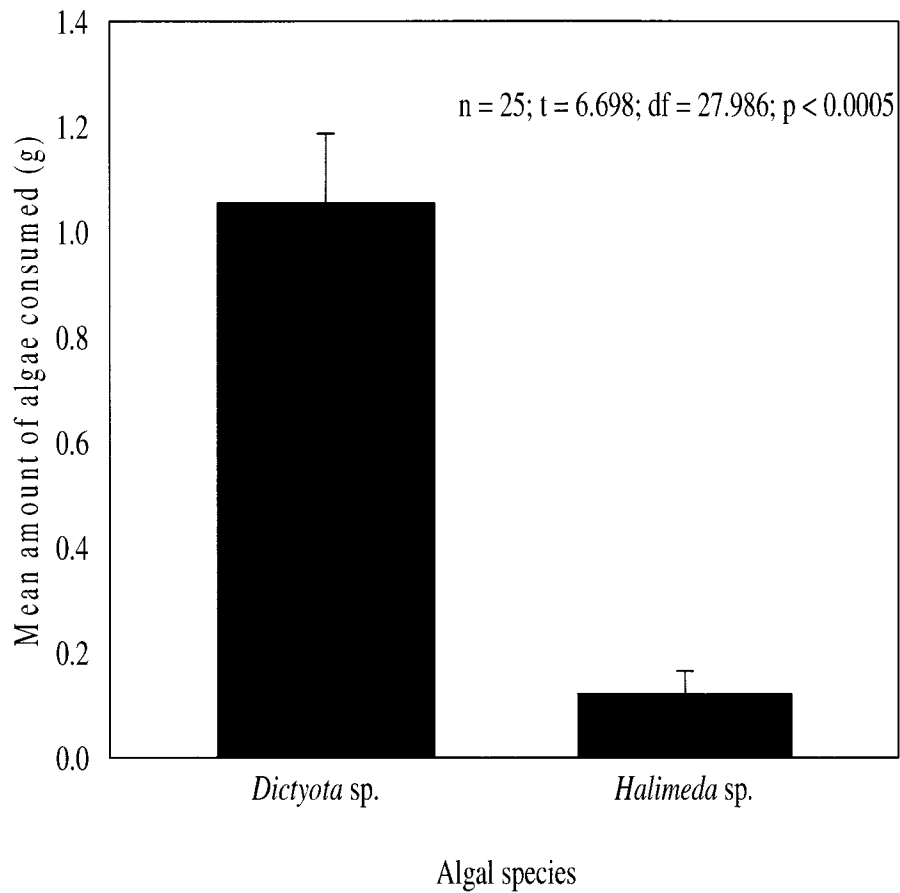


Figure 14: Mean consumption of *Halimeda* sp. and *Dictyota* sp. by *Diadema* during a 24 hr period. Error bars represent one standard error.

## Discussion

Although *Diadema* are potentially important drivers of macroalgal abundance and

thus community structure on Caribbean coral reefs, my results suggest that their

effectiveness as herbivores may be greatly diminished by high juvenile mortality and chemically-mediated reductions in foraging activity when the spotted spiny lobster, *P. guttatus,* is present. *Diadema* consume both *Halimeda* sp. and *Dictyota* sp., the two dominant species of macroalgae on patch reefs in the Florida Keys, but they prefer *Dictyota* sp. However, *Diadema* foraging on both species of algae is significantly reduced in the presence of the predatory spiny lobster *P. guttatus.* This behavior was remarkably specific, as *Diadema* only fled in response to chemical cues produced by *P. guttatus* but not its Caribbean congenor, *P. argus.* Whereas *P. argus* has previously been reported as a predator of *Diadema* (Randall 1964), this is the first demonstration that *P. guttatus* also eats urchins, including *Diadema*, despite the formidable defense posed by *Diadema*'s toxic spines. However, *P. guttatus* is a diminutive species of spiny lobster, and consumes mostly small *Diadema*, offering larger *Diadema* a size specific refuge from predation.

My analysis of algal preference by *Diadema* focused on only two types of macroalgae, *Dictyota* sp. (consisting mostly of *D. pulchella* and *D. menstrualis*) and *Halimeda* sp. (mainly *H. opuntia* but also *H. tuna*), that dominate the biomass of patch reefs in the Florida Keys (Lirman and Biber 2000, Paddack et al. 2006); *Diadema* preferred *Dictyota* sp. and consumed little *Halimeda* sp. Other investigators have examined algal preference in different species of sea urchin in the genus *Diadema* (Coppard and Campbell 2007, Solandt and Campbell 2001, Randall et al. 1964), but their conclusions with respect to algal preference are conflicting. Several studies (Coppard and Campbell 2007, Myhre and Acevedo-Gutiérrez 2007, Maciá et al. 2007) indicate that *Diadema* prefers non-calcareous macroalgae, which is consistent with my findings.

However, Solandt and Campbell (2001) concluded that *Diadema* were non-selective feeders of macroalgae, and consumed even heavily calcified algae. Although *Dictyota* sp. and *Halimeda* sp. are both chemically defended, only *Halimeda* is heavily calcified, which deters grazing by fishes (Paul and Fenical 1983, Hay et al. 1987). Populations of herbivorous fish are by far the most abundant reef herbivores in the Florida Keys (Bohnsack et al. 1994, Paddack et al. 2006), but they alone are unlikely to reverse the algal-dominance on coral reefs if populated largely by chemically defended and calcified algae such as *Halimeda*. Like herbivorous fishes, *Diadema* readily consumes uncalcified algae such as *Dictyota* sp., but its corresponding effect on the *Halimeda* so prolific on some reefs is less certain.

Others have demonstrated that *Diadema* flees in response to predatory cues (Vadas and Elner 2003) or cues from injured conspecifics (Snyder and Snyder 1970), and it has smaller home feeding scars on reefs with high predator densities (Carpenter 1984). However, the evidence I present here is the first direct demonstration of a trait mediated reduction in algal consumption by *Diadema* linked to a specific predator. I found that foraging by *Diadema* on *Dictyota* sp. and *Halimeda* sp. was significantly reduced in the presence of *P. guttatus*, but not *P. argus*. This has important implications for coral reefs in the Caribbean, particularly areas where *P. guttatus* is not fished and thus abundant, such as the Florida Keys. In these areas, the recovery of *Diadema* alone is unlikely to reverse the algal dominance now occurring on many Caribbean coral reefs. One might attempt, for example, to enhance *Diadema* populations via transplantation of large urchins to minimize their risk of predation. However, if *P. gutttatus* is abundant on those reefs the urchins are likely to restrict their foraging close to shelter, thus minimizing their

overall impact on algal communities. Whether *Diadema* respond similarly to others among the suite of predators that dwell on the reef is unknown. Yet, their specificity in response to *P. guttatus* but not *P. argus* is an indication that a large differences in selective pressure exist among seemingly similar predators. Although *P. argus* consumes *Diadema* (Randall 1964), it forages much less on the reef than the philopatric *P. guttatus*, which spends its entire benthic existence there (Sharp et al. 1997). The similar life histories of *Diadema* and *P. guttatus*, coupled with *Diadema's* strong behavioral responses support my hypothesis that *P. guttatus* is a more important predator of *Diadema* than *P. argus*.

*Panulirus guttatus* readily consumed all three species of reef dwelling sea urchins offered them in my laboratory experiments (*Echinometra lucunter*, *Diadema antillarum*, *Eucidaris tribuloides*). Both *Echinometra lucunter* and *Eucidaris tribuloides* were also present in the stomachs of *P. guttatus* that I collected on patch reefs in the Florida Keys (Chapter 2). I never observed *D. antillarum* in the stomachs of *P. guttatus* on those same reefs, but I also never observed *D. antillarum* on those patch reefs either. My laboratory results indicate that *P. guttatus* would likely consume *D. antillarum* in the field if they were encountered, particularly if the urchins were small, new recruits.

Despite a lack of prey selectivity, *P. guttatus* clearly preferred smaller *Diadema*, providing potential prey with a size specific refuge from predation, a finding consistent with studies of urchin predation by other species of lobster (Tegner and Dayton 1981, McClanahan and Muthiga 1989, Robles et al. 1990, Sala 1997, Lopez et al. 1998). Returning *Diadema* populations to historically high densities is viewed by some

(Knowlton 2001, Macía et al. 2007) as the solution for releasing Caribbean reefs from

algal dominance and returning them back to coral dominance, especially reefs with low

rates of piscine herbivory such as the patch reefs of the Florida Keys (Paddack et al.

2006). Indeed, *Diadema* has been associated with reversal of the coral-to-macroalgae

phase shift in areas of the Caribbean where *Diadema* populations have recovered

(Woodley 1999, Edmunds and Carpenter 2001, Carpenter and Edmunds 2006, Myhre and

Acevedo-Gutiérrez 2007, Idjadi et al. 2010). Efforts to jump-start the recovery of

*Diadema* 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

(Nedimyer and Moe 2003, Burdick 2008, Rogers and Lorenzen 2008). Thus far,

transplantation of *Diadema* has generally not been successful (Macía et al. 2007, Burdick

2008, Kintzing personal observation) and the poor recovery of transplanted populations is

likely a result of intense predation, high emigration, or both. My results suggest that

simply outplanting *Diadema*, 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 *Diadema* recovery and their effectiveness as agents of

change on Caribbean coral reefs appears intimately tied to the status of their predators,

including *P. guttatus*. Predation is an important factor that influences the density and

foraging behavior of many species of sea urchins (Carpenter 1984, Sala et al. 1998,

McClanahan 1999, Vadas and Elner 2003, Hereu et al. 2005, Clemente et al. 2009). Not

surprisingly, the areas in the Caribbean where *Diadema* has rebounded tend to be

severely overfished, especially with respect to predatory fish and lobster (Harborne et al.

2009). Several factors (e.g., reproductive success, recruitment, connectivity) have

presumably influenced the heterogeneous recovery of *Diadema* in the Caribbean. My

results suggest that predation on *Diadema* by *P. guttatus* is undoubtedly another.

# CHAPTER IV

# THE INFLUENCE OF SHELTER, CONSPECIFICS, AND PREDATION ON THE BEHAVIOR OF *DIADEMA ANTILLARUM*

## Introduction

Predators can shape the taxonomic structure of animal communities and sometimes control the abundance of prey (Harriston et al. 1960, Paine 1966). In turn, prey have evolved physical (Hoverman et al. 2005), chemical (Bolser and Hay 1996) and behavioral adaptations that limit their vulnerability to predation (Werner et al. 1983, Trussell et al. 2003, Vadas and Elner 2003, Freeman 2005, Smee and Weissburg 2008) and, in some cases, combine these strategies to reduce predation risk. For example, the sharp spines characteristic of sea urchins can contain toxins, providing both physical and chemical deterrence to predation, and they have also evolved a number of defensive behaviors to avoid predators. 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 and Snyder 1970, Vadas and Elner 2003, Freeman 2005). Anti-predatory adaptations like these provide obvious evolutionary advantages to prey, but often come at a cost, such as reduced foraging or restriction to suboptimal habitats where they are concentrated and their growth or fecundity compromised by density-dependence (Katz and 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 and Lucas 1970), an outgrowth of optimal foraging theory first developed to explore how tradeoffs in competitive ability and predation risk impact resource utilization (MacArthur and 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 (Sih 1987, Rosenzweig 1991, Grand and Dill 1999a, Grand and Dill 1999b, Heithaus et al. 2007, Heithaus et al. 2009). Many of these studies confirm Connell's idea (1975) that the threat of predation usually trumps the disadvantages of increased interspecific competition in mediating habitat selection and resource utilization (Heithaus et al. 2007, Heithaus et al. 2009). This ecological tradeoff is common in tropical marine ecosystems.

Predation is intense in low latitude, high diversity ecosystems such as coral reefs (Jeanne 1979, Bertness et al. 1981, Menge and Lubchenco 1981, Fawcett 1984, Heck and Wilson 1987, Bolser and Hay 1996, Smee and Weissburg 2008) where competition for limited space and food is also severe (Jackson and Buss 1975, Williams 1981, Connell et al. 2004, Box and Mumby 2007). The sea urchin *Diadema antillarum*, which inhabits the coral reefs of the tropical Caribbean, offers a case in point. It utilizes crevice shelters and often, but not always, 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, similar to Fretwell's Ideal Free Distribution theory (Fretwell and Lucas 1970). In this chapter, I use *Diadema* as a model organism to explore how the interplay of intra-specific competition and predation threat affect habitat selection. In particular, I examine in a

series of laboratory experiments how the availability of shelter and conspecifics affect

*Diadema* behavior in the presence and absence of a common predator, the spotted spiny

lobster, *Panulirus guttatus*.

**Methods**

All of the experiments described below were conducted in a wet laboratory at the

Goshen College Marine Laboratory on Long Key, Florida (USA) from July 2008 through

October 2009 under natural photoperiod and ambient seawater temperatures (27-31 $^{\circ}$C)

and salinity (32-36 ppt). Unless otherwise noted, experiments were conducted in 200 L

flow through seawater tanks and ran for approximately 24 hrs. Experimental set-ups 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 three

stacked masonry bricks previously soaked in seawater. Table 5 summarizes the

laboratory experiments.

Table 5: Summary of laboratory experiments examining the role of conspecifics and *P. guttatus* cues on *Diadema antillarum* behavior.

| Experiment | Number of *Diadema* | Number of shelters | *P. guttatus* cue | *Diadema* cue | Response variable |
|---|---|---|---|---|---|
| *Diadema* Response to a Predator Odor With and Without a Shelter Present | 1 | 1 | Yes | No | Amount of *Diadema* movement |
| Effect of Conspecific on *Diadema* Shelter Choice | 2 | 2 | No | No | Whether *Diadema* sheltered together or not |
| Effect of Conspecific Odor on *Diadema* Shelter Choice | 1 | 2 | No | Yes | Shelter *Diadema* selected |
| Effect of Conspecific Odor on *Diadema* Shelter Choice When Shelter is Limited | 1 | 1 | No | Yes | Shelter *Diadema* selected |
| *Diadema* shelter choice in the presence of predator odor | 1 | 1 | Yes | No | Shelter *Diadema* selected |
| Effect of Predator and Conspecific Odors on *Diadema* Shelter Choice | 1 | 2 | Yes | Yes | Shelter *Diadema* selected |

<u>*Diadema* Response to a Predator Odor With and Without a Shelter Present</u>

In chapter III, my laboratory experiments demonstrated that *D. antillarum* fled when exposed to a chemical cue (i.e., odor) produced by *P. guttatus*. This is inconsistent

with field observations noting *Diadema* has a smaller home feeding scar, indicating less movement, when predators are abundant (Carpenter 1984). To determine if the protection offered by a shelter mitigates the flight response of *D. antillarum*, I set up a tank marked every 5cm, both length and widthwise, and filled with approximately 45 L of natural seawater. An experimental shelter was constructed at one end of the tank. A *D. antillarum* of known test diameter was introduced into the tank and given 15 min to acclimate, at which point 7.5 L of untreated seawater (control) or treatment water (water containing a *P. guttatus* for approximately 24 hrs) was added to the tank. The movement of the *Diadema* in response to the added water was observed and recorded for the five min (n = 20). A 2-sample t-test assuming unequal variance was used to assess differences between the treatments in the distance moved by *Diadema*.

Effect of Conspecific on *Diadema* Shelter Choice

To determine if the presence of a conspecific affects shelter selection by *Diadema*, two *D. antillarum* were added to an experimental tank containing two shelters. The choice of the *D. antillarum* to shelter together or apart was recorded (n = 26) and tested using Fisher's exact test.

Effect of Conspecific Odor on *Diadema* Shelter Choice

To determine if *D. antillarum* preference to shelter with conspecifics was controlled by the chemical cue of a conspecific, a single *Diadema* was placed in an experimental tank with two shelters. Seawater from a head tank, one empty head tank (i.e., the seawater control) and one containing a single 30-50 mm (test diameter) *D.*

*antillarum,* flowed to separate shelters. At the conclusion of the experiment, the shelter selected by the *Diadema* was recorded (n = 21). Fisher's exact test was used to determine if *Diadema* was attracted to one shelter over the other.

## Effect of Conspecific Odor on *Diadema* Shelter Choice When Shelter is Limited

To see if shelter limitation influences whether *Diadema* 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 30-50 mm (test diameter) *Diadema* flowed to the shelter. I recorded whether the *D. antillarum* utilized the shelter or not (n = 21) and tested this preference with Fisher's exact test.

### *Diadema* shelter choice in the presence of predator odor

*Diadema* sometimes shelter with a known predator the spiny lobster *Panulirus argus* (Randall et al. 1964) on coral reefs (Kintzing personal observation) so I examined the importance of shelter in the presence of a predatory odor. Thus, a single *Diadema* was added to an experimental tank with one shelter. Water from a head tank containing a single *P. guttatus* flowed to the shelter. At the conclusion of the experiment, I recorded whether the *Diadema* utilized the shelter (n = 18) and I tested my data with Fisher's exact test.

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

Finally, I tested shelter choice by *D. antillarum* when given the preference between two shelters from which emitted either a conspecific or predator chemical cue. Each of the two shelters received seawater from one of two head tanks, one containing a

single *P. guttatus* (45-55 mm CL) and the other containing a single 30-50 mm (test

diameter) *D. antillarum*. A single *Diadema* was then added to the experimental tank. At

the conclusion of the experiment, I recorded which shelter the urchin selected (n = 19)

and used Fisher's exact test to examine my results.

**Results**

<u>*Diadema* Response to a Predator Odor With and Without a Shelter Present</u>

A 2-sample t-test revealed no significant difference in movement by *D. antillarum*

in response to waterborne cues produced by *P. guttatus* versus a seawater control when a

shelter was present (t = 1.512; df = 24; p = 0.143) (Figure 15). However, most *Diadema*

in both treatments moved to the shelter during the acclimation period and remained there

throughout the duration of the experiment. There was more movement in the *P. guttatus*

treatment, which generally resulted from *Diadema* moving to the shelter, at which point

movement ceased.
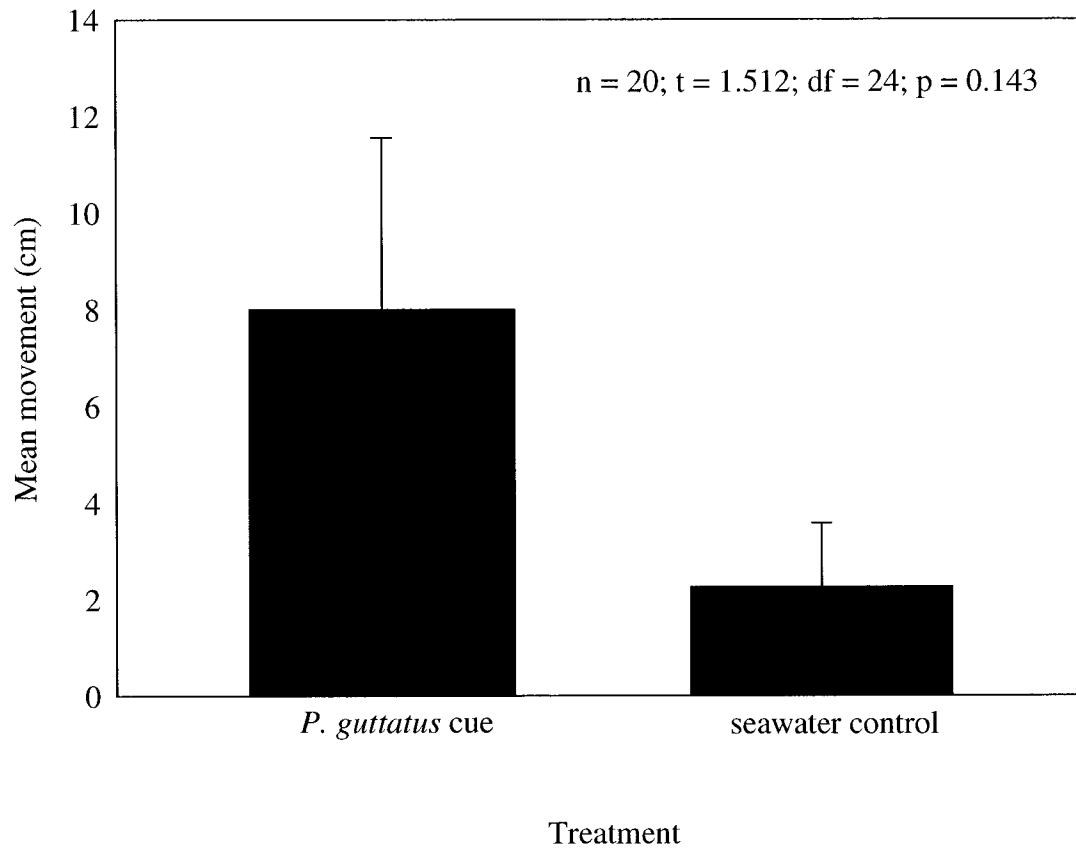
Figure 15: *Diadema* movement in response to *P. guttatus* cue versus a seawater control with a shelter present.

## *Diadema* shelter *choice with conspecific present*

When two *Diadema* were given the choice to shelter together or separately with no threat of predation present and when shelter was not limiting, they preferred to occupy separate shelters (n = 26; p = 0.002) (Figure 16).
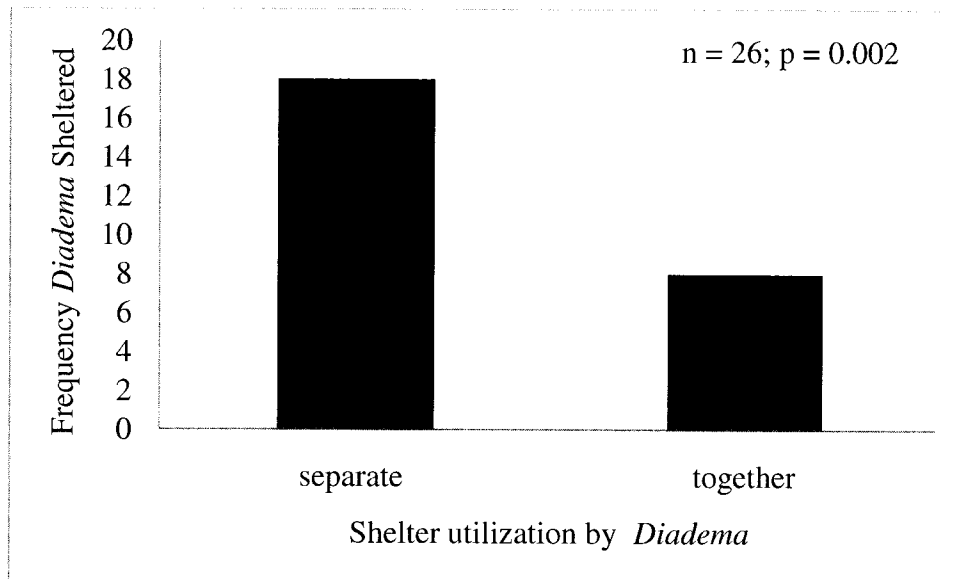
Figure 16: Shelter utilization by two *Diadema* when offered two shelters.

## *Diadema* shelter choice with conspecific odor

*Diadema* were averse to utilizing shelter producing a conspecific odor when shelter was not limited (n = 21; p = 0.034) (Figure 17). *Diadema* size did not impact these results because the five individuals that chose the shelter with a conspecific spanned the size range of the *Diadema* tested. This result confirms the outcome of the previous experiment where *Diadema* avoided shelters with a conspecific.
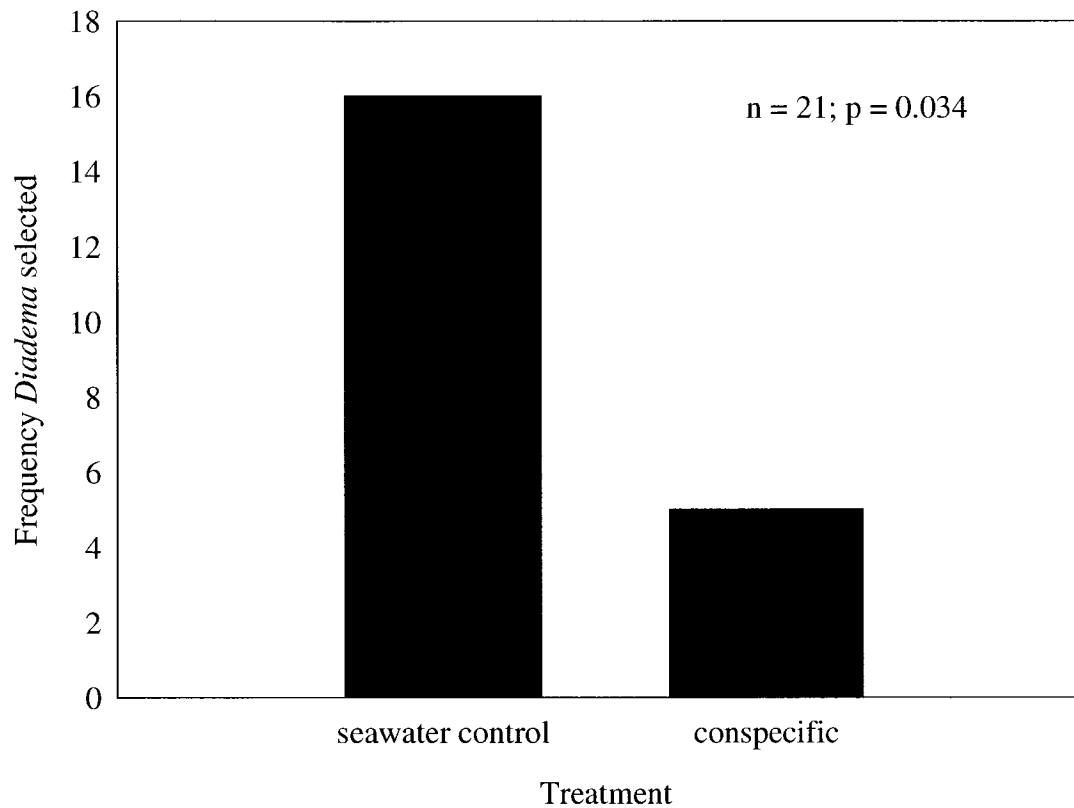
Figure 17: *Diadema* shelter choice between shelters containing a seawater control cue or a conspecific waterborne chemical cue.

## *Diadema* shelter choice with conspecific odor when shelter is limited

When only a single shelter was available, *Diadema* sometimes sheltered in dens from producing a chemical cue of a conspecific, however, they were just as often found alone outside the shelter (n = 21; p = 1.00) (Figure 18).
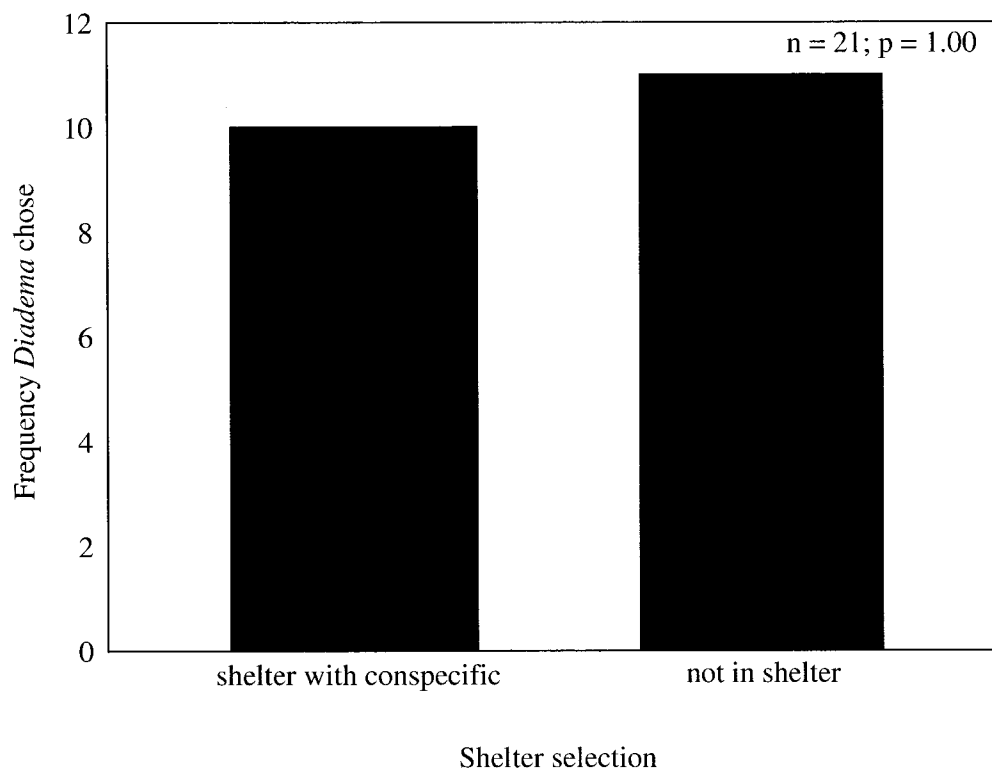
Figure 18: Shelter use by *Diadema* when a conspecific odor is present and shelter is limited.

## *Diadema* shelter choice in the presence of predator odor

When shelter was limited and the only available shelter contained a waterborne predator cue, *Diadema* just as often remained in the open outside a shelter as entered a shelter producing the scent of a predator (*P. guttatus*) (n = 18; p = 1.00) (Figure 19).
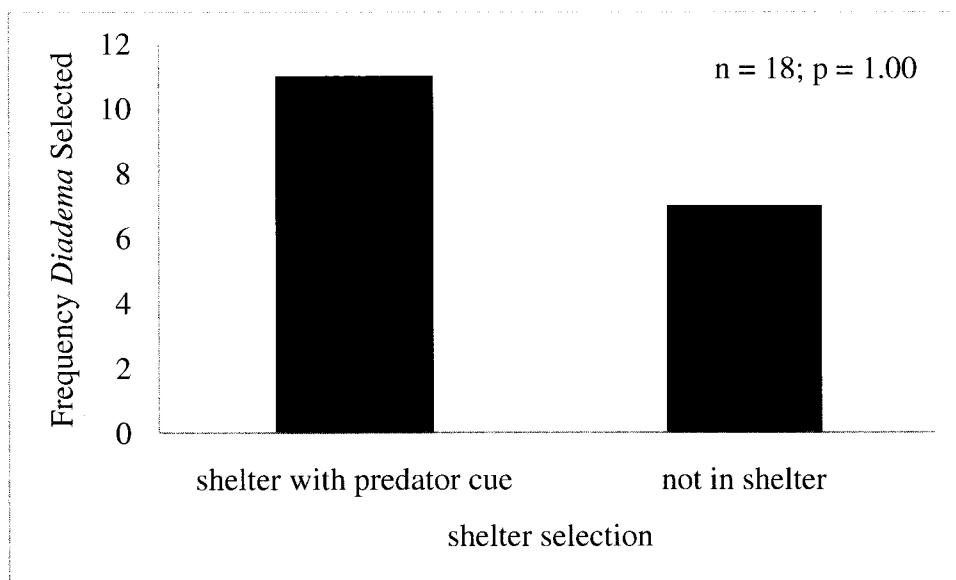
Figure 19: Shelter usage by *Diadema* when a predator odor is present and shelter is limited.

## *Diadema* shelter choice with both predator and conspecific odors

When given the choice between utilizing a shelter with either a conspecific odor

or that of a potential predator, *Diadema* more often selected the shelter with the

conspecific odor than the predatory cue (n = 19; p = 0.011) (Figure 20).
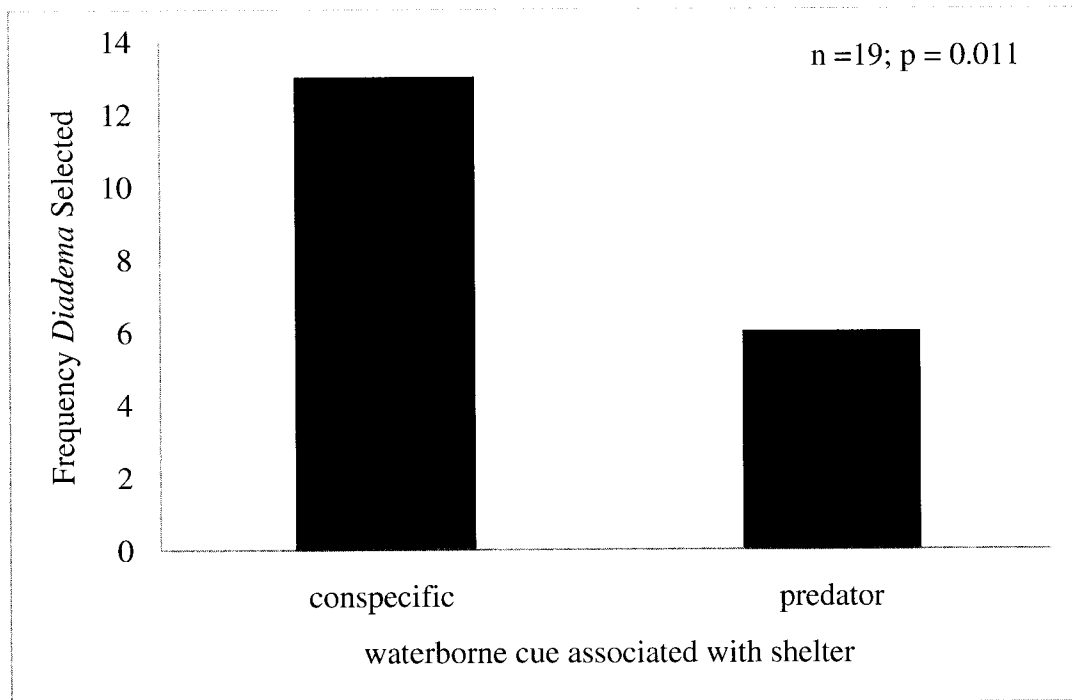
Figure 20: *Diadema* shelter choice when conspecific and predator odors are present.

## Discussion

Several studies have examined the independent effects of shelter and reef complexity, predators, and conspecifics on *Diadema* behavior (Lee 2006, Clemente and Hernandez 2008, Carpenter 1984, Miller et al. 2007), but this is the first study to examine all three concurrently. My laboratory results indicate that *Diadema* are first and foremost attracted to shelter, although the chemically-mediated threat of predation also strongly influences *Diadema* behavior. The presence of conspecifics deters aggregation among *Diadema* in most circumstances, but when the threat of predation arises, *Diadema* aggregates, indicating a clear trade-off between reduced predation risk and increased competition.

The presence of suitable shelter, which mitigates predation risk, clearly affects the behavior of *D. antillarum* (Lee 2006) including the response to predatory cues. In Chapter III, *Diadema* fled when exposed to *P. guttatus* waterborne cues in the absence of shelter. In this chapter I describe a similar experiment but with shelter present. Under these circumstances, *Diadema* typically began the trial in the shelter and remained there, but in the few instances when movement was observed it usually involved *Diadema* entering the shelter after the introduction of the cue. Thus, the presence of shelter mitigated the flight response by *Diadema* in response to a predator cue. These laboratory results are consistent with field observations of decreased movement and foraging by *Diadema* in predator rich environments (Carpenter 1984) and support the theory that reduced predation risk comes at the cost of lost foraging opportunities. *Diadema* appears to prioritize the protection afforded by shelter, moving little once a suitable shelter has been located, which limits resource acquisition outside of shelter. This also explains why *Diadema* would utilize a shelter producing the odor of a predator as seeking shelter appears to be an evolved response to mitigate predation threat. Few studies have examined the impact of predation pressure on *Diadema* (Carpenter 1984), but several have demonstrated that decreased food availability negatively impacts their growth, fecundity, and survivorship (Levitan 1988, Levitan 1989). Thus, if predation pressure results in decreased foraging opportunities, then just the threat of predation is sufficient to decrease the fitness of *Diadema*.

*Diadema* aggregate in the field (Randall et al. 1964, Miller et al. 2007, Kintzing personal observation) and these aggregations have positive density-dependent effects on the survival of juveniles (Randall et al. 1964, Miller et al. 2007). However, few studies

have examined the potential negative effects of aggregation and restricted movement

(e.g., decreased growth or fecundity) on *Diadema* (Levitan 1988, Levitan 1989). My

laboratory studies suggest that such forces may indeed be important. Without the threat

of predation, *Diadema* avoided shelters containing a conspecific or even its odor.

Introducing the threat of predation changed the behavioral response of *Diadema* to

conspecifics. When given the choice between shelters containing either a waterborne cue

from a lobster predator or a conspecific, *Diadema* preferred to shelter with a conspecific.

These results are consistent with the hypothesis that sheltering with conspecifics

decreases *Diadema* fitness due to sharing of food resources in close proximity to the

shelter, so conspecifics are avoided unless under threat of predation because predators

present a greater threat to fitness. These results are consistent with the Ideal Free

Distribution theory (Fretwell and Lucas 1970, Grand and Dill 1999b) and the growing

body of research that the immediate threat of predation more strongly impacts habitat

selection than the delayed impacts associated with increased competition (Rosenzweig

1991, Heithaus et al. 2007, Heithaus et al. 2009). They also support Connell's classic

notion (1975) that competition is a preeminent force directing animal interactions when

the threat of predation is limited. Under natural circumstances, large fish and invertebrate

predators of urchins are abundant on coral reefs and thus drive urchins to shelter with

conspecifics. However, over-fishing on Caribbean reefs is rampant (Dulvy et al. 2004,

Aronson and Precht 2006) and it may be no coincidence that *Diadema* populations have

recovered from the massive die-off of the 1980s more quickly in areas where over-fishing

is particularly severe (Harborne et al. 2009) and on nearshore reefs where sea urchins

often recruit and large fish predators are either naturally less abundant or more easily accessed by fishermen.

Caribbean coral reefs are also becoming less structurally complex due to bleaching, disease, algal over-growth, and ultimately the loss of scleractinian corals, which compose the reef framework (Alvarez-Filip et al. 2009). 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* populations in light of my results demonstrating the importance of shelter to *Diadema* and similar results by others (Hereu et al. 2005, Lee 2006, Clemente and Hernandez 2008). *Diadema* abundance increases on structurally complex environments (Lee 2006, Clemente and Hernandez 2008), a pattern shared with various reef fishes (Gratwicke and Speight 2005, Ledlie et al. 2007, Alvarez-Filip et al. 2009). *Diadema* populations are already subject to intense predation pressure and further loss of habitat structural complexity will likely exacerbate losses to predation (Chiappone et al. 2002, Miller et al. 2009, Harborne et al. 2009). Recovery of *Diadema* populations in areas subject to reef breakdown and the associated recovery of algal-dominated reefs as a result of *Diadema* grazing (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006, Idjadi et al. 2010) may require not only *Diadema* stock enhancement (Macia et al. 2007) but also supplementation of crevice shelters suitable for *Diadema* of various sizes (Lee 2006, Gratwicke and Speight 2005). However, increased habitat complexity also often increases the abundance and diversity of predators (Mattila et al. 2008). If so, then my results demonstrate that predation threat is likely to constrain foraging by *Diadema* and limit their importance in reef recovery. Therefore, it will be necessary to determine the right balance between structural habitat

enhancement and urchin stock enhancement to achieve the hoped for gains in coral reef

recovery.

# CHAPTER V

# CONCLUSIONS

The decline of Caribbean coral reefs can be attributed to a number of factors, but a key factor precipitating the coral-to-algal phase shift is the loss of herbivores that normally keep in check the growth of competitively dominant macroalgae. Determining what factors have contributed to the decline of key herbivores, such as the long-spined sea urchin, *Diadema antillarum*, and their inability to recover to historical densities is believed to be key in reversing this phase shift.

This is the first study to examine in detail the impact of the spotted spiny lobster, *Panulirus guttatus*, on patch reef communities and, in particular, its potential impact on *Diadema* behavior, shelter use, and mortality. *Panulirus guttatus* negatively impacts the abundance of several invertebrate herbivores including *Diadema*. Foraging by *P. guttatus*, and thus its impacts on the invertebrate community, is minimized in the cooler winter months, but is especially important in the summer and for macroinvertebrate taxa that dwell within coral rubble - again, this includes *Diadema*. *Panulirus guttatus* likely has a negative impact on coral recruitment, as coral need stable substrate to settle, and *P. guttatus* overturns reef rubble while foraging. This disturbance is more intense for smaller rubble. Thus, *P. guttatus* is negatively impacting herbivory and coral recruitment, the two key components for reef recovery,

In addition to density-mediated effects on *Diadema*, *P. guttatus* also strongly influences *Diadema* behavior. *Diadema* fled when exposed to the chemical scent of *P.*

*guttatus*, but not its co-occurring congenor *P. argus*, and consumed significantly less

algae in the presence of *P. guttatus*. This decrease in the functional significance of

*Diadema* given the threat of predation has important implications for reef communities.

Restoration of *Diadema* populations is a key priority for reef managers, even though I

and others have been unsuccessful in maintaining sizeable *Diadema* populations by

transplantation. It is unlikely that *P. guttatus* is the only predator impacting *Diadema*

density and behavior, however, *Diadema* only exhibited a flight response to a *P. guttatus*

cue and not to that of another known predator *P. argus*, supporting my hypothesis that *P.*

*guttatus* is the more important of the two lobster species to reef communities.

　　　*Diadema* behavior and distribution conform to the Ideal Free Distribution theory.

Predation seems to be the most important factor influencing *Diadema* behavior and the

mere scent of *P. guttatus* cues mitigated the importance of intra-specific competition for

shelter by *Diadema*. When the threat of predation was removed, competition became

important in determining shelter use by *Diadema*. Thus, avoidance of the more

immediate threat of predation outweighed the delayed costs associated with intra-specific

competition. The shelter that rugose, structurally complex coral reefs provide is a crucial

spatial refuge from predation for *Diadema*, thus declining reef complexity threatens to

further complicate the recovery of this key herbivore. Artificial habitat can increase the

abundance of *Diadema*, but it also increases aggregations of potential predators. The *in*

*situ* interplay of shelter and predation threat merits further investigation to determine

whether supplementing natural shelters will be beneficial to Caribbean reefs.

　　　*Panulirus guttatus* has the potential to be a keystone species on the degraded

shallow reefs of the Caribbean. Through its negative impact on the abundance and

behavior of herbivores, especially the keystone herbivore *Diadema*, as well as substrate stability, high densities of *P. guttatus* potentially contribute to coral-to-algae phase-shifts on coral reefs of the Caribbean.

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# APPENDIX A

## GPS LOCATION AND SUMMARY OF EXPERIMENTAL PATCH REEF CHARACTERISTICS

| Site | Latitude | Longitude | Lobster Density Treatment | Area (m$^2$) | Rugosity |
|---|---|---|---|---|---|
| FG 6 | 24 50.189 | 80 43.754 | High | 295.24 | 1.32 |
| FG 8 | 24 50.243 | 80 43.739 | Low | 153.07 | 1.43 |
| FG 10 | 24 50.287 | 80 43.768 | High | 235.46 | 1.71 |
| FG 13 | 24 50.322 | 80 43.708 | Low | 81.81 | 1.31 |
| FG 21A | 24 50.186 | 80 43.609 | High | 67.95 | 1.84 |
| FG 31 | 24 50.269 | 80 43.619 | High | 185.12 | 1.75 |
| FG 32 | 24 50.283 | 80 43.630 | Low | 185.42 | 1.71 |
| FG 33 | 24 50.275 | 80 43.679 | Low | 83.95 | 1.81 |
| FG 33A | 24 50.284 | 80 43.672 | Low | 96.32 | 1.53 |
| FG 34 | 24 50.317 | 80 43.738 | Low | 129.15 | 1.78 |
| FG 35 | 24 50.311 | 80 43.790 | High | 165.5 | 1.78 |
| FG 36 | 24 50.262 | 80 43.655 | High | 136.09 | 1.63 |

**APPENDIX B**
UNIVARIATE ANOVA TABLE FOR DIFFERENT TAXA FROM EXPERIMENTAL
RUBBLE TRAYS

| Taxa | Source | Type III Sum of Squares | df | Mean Square | F | p |
|---|---|---|---|---|---|---|
| Crustaceans | Treatment | 1495.885 | 1 | 1495.885 | 19.310 | 0.001 |
| | Time | 0.874 | 1 | 0.874 | 0.016 | 0.901 |
| | Time*Treatment | 2.245 | 1 | 2.245 | 0.041 | 0.843 |
| Molluscs | Treatment | 416.228 | 1 | 416.228 | 7.377 | 0.022 |
| | Time | 2254.669 | 1 | 2254.669 | 52.539 | >0.0005 |
| | Time*Treatment | 5.283 | 1 | 5.283 | 0.123 | 0.733 |
| Polychaetes | Treatment | 81.933 | 1 | 81.933 | 0.982 | 0.345 |
| | Time | 4327.693 | 1 | 4327.693 | 33.979 | >0.0005 |
| | Time*Treatment | 6.314 | 1 | 6.314 | 0.049 | 0.829 |
| Echinoderms | Treatment | 151.618 | 1 | 151.618 | 5.574 | 0.040 |
| | Time | 93.102 | 1 | 93.102 | 5.267 | 0.045 |
| | Time*Treatment | 128.668 | 1 | 128.668 | 7.279 | 0.022 |
| Other | Treatment | 0.015 | 1 | 0.015 | 0.005 | 0.944 |
| | Time | 44.717 | 1 | 44.717 | 15.456 | 0.003 |
| | Time*Treatment | 0.184 | 1 | 0.184 | 0.064 | 0.806 |

# APPENDIX C

## UNIVARIATE ANOVA TABLE FOR DIFFERENT TAXA FROM ALGAL QUADRATS

| Taxa | Source | Type III Sum of Squares | df | Mean Square | F | p |
|---|---|---|---|---|---|---|
| Crustaceans | Treatment | 22.357 | 1 | 22.357 | 2.196 | 0.169 |
| | Time | 13.530 | 1 | 13.530 | 1.075 | 0.324 |
| | Time*Treatment | 17.819 | 1 | 17.819 | 1.416 | 0.262 |
| Molluscs | Treatment | 1.054 | 1 | 1.054 | 0.216 | 0.652 |
| | Time | 0.505 | 1 | 0.505 | 0.265 | 0.618 |
| | Time*Treatment | 0.031 | 1 | 0.031 | 0.016 | 0.901 |
| Polychaetes | Treatment | 1.111E-5 | 1 | 1.111E-5 | <.0005 | .999 |
| | Time | 6.521 | 1 | 6.521 | 2.431 | 0.150 |
| | Time*Treatment | 0.840 | 1 | 0.840 | 0.313 | 0.588 |
| Echinoderms | Treatment | 2.502 | 1 | 2.502 | 0.524 | 0.486 |
| | Time | 0.265 | 1 | 0.265 | 0.164 | 0.694 |
| | Time*Treatment | 0.010 | 1 | 0.010 | 0.006 | 0.938 |
| Other | Treatment | 0.001 | 1 | 0.001 | 0.001 | 0.971 |
| | Time | 0.263 | 1 | 0.263 | 1.644 | 0.229 |
| | Time*Treatment | 0.338 | 1 | 0.338 | 2.119 | 0.176 |

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**37th Benthic Ecology Meeting**, Providence, RI, April 2008. Investigating the role of the spotted spiny lobster (*Panulirus guttatus*) on the coral reef communities of the Florida Keys.

**11th International Coral Reef Conference**, Fort Lauderdale, FL, July 2008. Assessing the ecological significance of interactions between the spotted spiny lobster (*Panulirus guttatus*) and the long spined sea urchin (*Diadema antillarum*) in shaping coral reef communities in the Florida Keys.

**38th Benthic Ecology Meeting**, Corpus Christi, TX, March 2009. Impacts of the spotted spiny lobster and the long-spined sea urchin on the patch reef communities of the Florida Keys.

**39th Benthic Ecology Meeting**, Wilmington, NC, March 2010. The tale of the spotted spiny lobster: innocuous crustacean by day, bane of coral reef recovery by night.