THE EFFECT OF HERBIVORY BY THE LONG-SPINED SEA URCHIN, DIADEMA SAVIGNYI, ON ALGAE GROWTH IN THE CORAL REEFS OF MOOREA, FRENCH POLYNESIA

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Abstract. Herbivory plays an important role in shaping coral reef community structure. Herbivores consume algae on the reef, helping to prevent coral dominated reefs from "phase shifting" to algae dominated ones. Here I examine how the presence of an herbivorous sea urchin, Diadema savignyi, influences algae growth on Porites sp. coral heads using inclusion and exclusion cages. Corals were either assigned no cage, a cage with D. savignyi or a cage with no D. savignyi. Treatments were applied for 25 days and percent algae cover was estimated weekly while algae length was measured on day 25. After 25 days, variation in algae cover and algae length were not significantly associated with D. savignyi presence. Corals kept in the presence of D. savignyi had the same amount of algae as corals that D. savignyi had been excluded from. These results are identical to a similar experiment that was performed in the laboratory in which corals were either placed with or without D. savignyi. These results suggest that at the current time, D. savignyi does not have a strong impact on reducing algae growth in the coral reefs of Moorea, French Polynesia. This may be due to the health of the reef, the ability of live corals to prevent new algae settlement and growth or the presence of superior fish herbivores.

Keywords: herbivory, algae-coral-herbivore interactions, Diadema savignyi, reef ecosystem, percent algae cover, Moorea, French Polynesia

INTRODUCTION

Coral reefs are one of the world's most diverse and productive ecosystems. provide many goods and services, ranging from fisheries to wave buffering to tourism (Moberg & Folke 1999). Coral reefs are able to provide so many goods and services because of their complex, but dynamic, community structure. Coral reef community structure is determined by many abiotic and biotic Physical factors such as temperature and pH (Hoegh-Guldberg 2007), depth, disturbances (Gilmour 2004), water quality (Bak & Meesters 1999, Meesters et al. 2001) and flow rate (Sebens et al. 1998) can affect coral growth. Biotic factors influencing coral reef structure include life history characteristics of reef organisms (Hughes & Jackson 1985, Meesters et al. 2001) and interactions between herbivores and their environment.

Herbivory plays a large role is shaping species distributions and community structure. The most common herbivores in the reef community are the fishes and the sea urchins. The common herbivorous reef fishes include scarids and acanthrurids (Mapstone et al. 2007). *Diadema*, a common genus of long-

spined sea urchin in coral reefs, is usually viewed as herbivorous. However, it is also known to feed on detritus and is occasionally carnivorous (Bak & Van Eys 1975). Although there is some evidence that reef fishes and sea urchins compete for algae (McClanahan et al. 1984, Hay & Taylor 1985, Carpenter 1990), there is little question that the density and grazing intensity of these herbivores influence the amount of algal growth on the reef (Ogden & Lobel 1978, Hay & Taylor 1985, Carpenter 1990, Vaziri 1995, Wilder 2003). Some previous studies have determined fish to be the superior algal consumers (Wilder 2003) while others have suggested that sea urchins have a more important role in shaping coral reef community structure (Hay & Taylor 1985, Carpenter 1990, Vaziri 1995).

Since an epizootic disease wiped out the entire population of the long-spined sea urchin, Diadema antillarum, in 1983 (Lessios et al. 1984), extensive research in the Caribbean has been done on herbivore-algae Although Bak and Van Eys interactions. (1975) observed *Diadema* consuming live coral, a large amount of research has suggested that D. antillarum has a strong impact on the amount of algae that grows on High Diadema density is coral reefs.

associated with less algal biomass (Sammarco 1982, Hay & Taylor 1985, Carpenter 1990) and increased abundances of scleractinian corals (Edmunds & Carpenter 2001, Carpenter & Edmunds 2006, Myhre & Acevedo-Gutiérrez When Diadema are abundant, they consume algae on the reef and allow corals to thrive. When Diadema populations are sparse, algae becomes overgrown and out competes the corals for space and sunlight. This in turn has consequences for organism abundance and diversity and overall reef health. These studies suggest that changing abundances of D. antillarum can cause coral reefs to "phase shift" from a coral dominated reef to an algae dominated one and vice versa (Edmunds & Carpenter 2001, Gardner et al. 2003, Carpenter & Edmunds 2006).

Wilder (2003) studied algae-herbivore interactions in the coral reefs of Moorea, French Polynesia and found herbivory by fish to be the most important factor influencing This finding differs from algal biomass. previous studies that have been done in the Caribbean coral reef ecosystems. In this study, I wish to reexamine Wilder's findings. For my study, I will examine how the presence and absence of the long-spined sea urchin, Diadema savignyi, influences the ratio of coral to algal cover on small Porites sp. coral heads using inclusion and exclusion cage experiments. This study examines the following hypothesis:

• Diadema savignyi plays a large role in shaping coral reef community structure. D. savignyi consumes algae, preventing algae domination in reefs. Corals with D. savignyi nearby will have less algae present than corals that do not have D. savignyi around.

METHODS

Study Organism

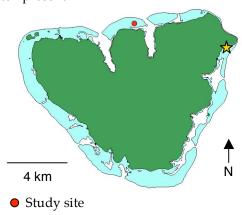
The long-spined sea urchin, Diadema savignyi (Michelin 1845), is found in the entire western Pacific, including the Society Islands. Diadema savignyi is commonly characterized by dark elongate spines, a dark anal sac and bright blue pigmentation on the aboral surface (Gosliner et al. 1996). This species is found shallow commonly in Individuals can be found hiding among coral heads or aggregated together on the sandy bottom during the day. At night, they move <1 meter to forage on algae.



FIGURE 1. Diadema savignyi.

Study site description

To determine whether D. savignyi has a in determining coral reef community structure, cages were built to exclude or include D. savignyi around coral heads. The cage experiments were conducted at 17°28'53.36"S 149°50'3.27"W in the barrier reef between Opunohu and Cook's Bays on the north side of the island of Moorea, French Polynesia (Figure 2). In general, herbivorous fishes and sea urchins are abundant in the lagoons and fringing reefs surrounding Moorea (Mapstone et al. 2007). preliminary daytime surveys, high coral and fish diversity, but moderate abundances of *D*. savignyi characterized this reef. Several D. savignyi were observed hiding in coral rubble and large coral heads, but exact abundance is unknown. There was also little algal cover present in this reef. The reef occurred in no more than two meters of water and received 11-12 hours of sunlight daily. A moderate to strong westwardly flowing current was also often present.



☆ Source population site

FIGURE 2. Study site location and source population site.

Field methods

Twenty-four small coral heads of Porites sp. 65-110 centimeters in circumference and 20-35 centimeters tall were selected and marked so that they could be found later. As a control, eight randomly selected coral heads were not caged off, representing predation by both fish and urchins (No Cage). Cages 30-50 centimeters³ constructed of 0.6 or 2.0 centimeter² mesh and zip ties and weighed down with bricks and lead weights enclosed eight random coral heads. One Diadema with a test size of 4.37-5.84 centimeters collected from Temae Pubic Beach (Figure 2; 17°30'0.67"S 149°45'34.19"W) was placed in each of these eight cages, representing predation by only urchins (Cage-Diadema). The remaining eight coral heads were also caged off but did not contain any Diadema, representing no predation (Cage-No Diadema; Figure 3).

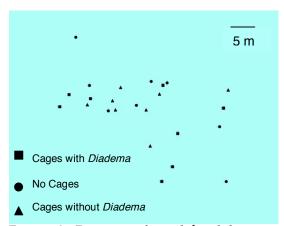


FIGURE 3. Diagram of coral head locations. Treatments were applied randomly and algae growth was monitored for 25 days. Sites are accurate to seven meters.

Coral heads were monitored every 1-3 days for a total of 25 days. If *D. savignyi* were found missing from their respective cages, they were replaced as quickly as possible. Cages were cleaned every week to allow for sufficient sunlight and water flow across the coral heads. Every week, photographs were taken of the aerial surface and the sides of each coral head using a SeaLife DC800 underwater camera and brought back to the lab for image analysis.

In Wilder's study (2003), algae grown on tiles for a set period of time was used to quantify herbivory by sea urchins. This present study attempted to examine the effects of *D. savignyi* on coral reefs in a more natural

setting by measuring algal growth following grazing and no grazing. Therefore, percent cover of algae was estimated for each coral head every week using ImageJ. Algae samples were taken at the end of the experiment if present and length was measured using calipers.

Laboratory methods

A flow through tank was divided in half and coral rubble or a loose piece of small live *Porites* sp. was placed in each half. One *D. savignyi* (test size 4.27-5.74) collected from Temae Public Beach (Figure 2) was placed in one half of the tank for 8-12 days. This half was compared to the other half containing no *D. savignyi*. Percent coverage of algae was estimated following 8-12 days. The experiment was repeated two more times, for a total of three trials.

Statistical methods

For my cage experiments, a repeated multivariate analysis of variance (MANOVA) was used to determine if there was a significant difference in algae cover between coral heads predated on by all herbivores, only D. savignyi or no herbivores over the course of a 25 day period. For algae cover after day 25, a one-way ANOVA was used to see if treatments were significantly different. A Fisher's exact test between Cage-Diadema and Cage-No *Diadema* was used to see if there was a significant difference between algae length following 25 days. For the laboratory experiment, a T-test was employed to see if there was a distinguishable difference in percentage of algal cover between tanks containing D. savignyi and tanks containing no D. savignyi.

RESULTS

Field results

Coral heads were not photographed until treatments had been applied for one week. Algae cover on coral heads after one week of treatment appeared unchanged from algae cover before treatments were applied, but it is impossible to quantify because photographs are unavailable. Over the course of 25 days in the field, variation in percent algae cover on coral heads was not significantly associated with treatment (repeated MANOVA, p = 0.17, Figure 4). On all days that photographs were

taken (10/22, 10/30, 11/5 and 11/10), treatments were undistinguishable from each other (one-way ANOVA; p = 0.12, p = 0.23, p = 0.18, p = 0.21 respectively). In spite of this, the Cage-*Diadema* corals always had the least amount of algae cover. Coral heads caged off from *D. savignyi*, representing no predation, exhibited a positive increasing trend in algae cover. Corals that were not caged off exhibited a trend toward decreasing algae cover.

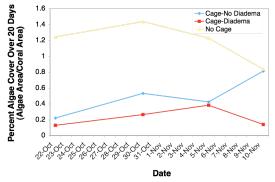


FIGURE 4. Percent algae cover on coral heads over 20 days. Treatments were applied for 25 days, but algae measurements are unavailable for the initial five days.

Following 25 days in the field, variation in algae cover was not found to be significantly correlated with treatment (one-way ANOVA, p = 0.21). However, following the expected trend, the Cage-Diadema corals had the least algae cover while Cage-No Diadema corals and No cage corals had approximately the same amount of algae cover (Figure 5).

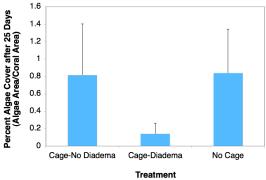


FIGURE 5. Percent algae cover following 25 days in the field. Corals that had been caged off with *D. savignyi* had the least algae cover.

Algae length following 25 days of treatment was not significantly associated with treatment type. Algae length on Cage-

No *Diadema* corals and Cage-*Diadema* corals was undistinguishable (Fisher's exact test, p = 0.47).

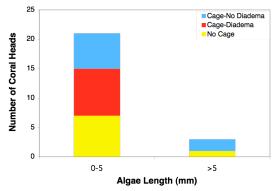


FIGURE 6. Algae length on coral heads following 25 days in the field.

Laboratory results

Following 8-12 days exposure to D. savignyi or no D. savignyi, percent algae cover was not significantly associated with the presence of sea urchins (T-test, p=0.41, Figure 7). Algae cover decreased for corals that were exposed to D. savignyi and corals that were not. Following the expected trend, the decrease in algae cover was slightly greater for corals that were exposed to D. savignyi.

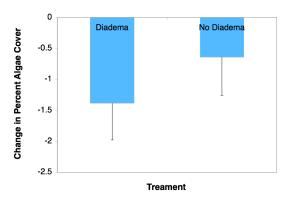


FIGURE 7. Change in percent algae cover following 8-12 days in the presence or absence of *Diadema savignyi*.

DISCUSSION

Over the course of 25 days in the field or 8-12 days in the lab, the presence or absence of *Diadema savignyi* did not have a strong impact on percent algae cover or algae length. Although slight trends suggested that corals in close proximity to *D. savignyi* had less algae than corals that were excluded from *D.*

savignyi, the results of this study are inconclusive. Despite previous studies that have documented increased algae in the absence of sea urchins (Sammarco 1982, Hay & Taylor 1985, Carpenter 1990), a wide array of methodological and ecological factors can explain this seemingly unusual result.

The inconsistency of the underwater proved environment challenging methodology. The cage design worked better than expected, but when the current was extremely strong, cages were found several meters away from their original location. This provided herbivorous fish access to any algae that may have been growing on the coral heads. Cages containing *D. savignyi* were also occasionally found partially collapsed with the D. savignyi missing. It is known that the feeding apparatus of sea urchins, Aristotle's lantern, is very strong, enabling them to chew through thick seaweed thalli (Contreras & Castilla 1987). Therefore, it is possible that *D*. savignyi could use the strong teeth of their Aristotle's lanterns to bend the wire caging material and escape through the bottom of the cage, providing an opening in which fish could access the coral head.

Algae cover may also not have been as high as expected due to additional instances of invasion by small herbivorous fish and shrimp. Small fish were observed hiding at the base of some caged coral heads. These fish may have snuck through the wire mesh or between the base of the cage and the sandy substrate, possibly resulting in reduced algae cover. Small shrimp were also observed on a Cage-No *Diadema* coral that had previously had a large amount of filamentous green algae cover. The appearance of these shrimp coincided with the disappearance of the filamentous green algae, suggesting that the shrimp ate all of the algae on the coral head.

Algae abundance in a coral reef is not only the result of herbivory. A wide range of abiotic factors, including water temperature (Reynolds & Casterlin 1977), sunlight and nutrient load (McCook 1999), influence algae growth. The optimal water temperature for marine algae is between 20-25°C (Fogg 1965). It is known that water temperature around Moorea ranges from 26°C during the cooler drier winter to 29°C during the hotter, more humid summer. The water temperature range around Moorea is slightly warmer than optimal for algae growth, possibly explaining the weak algae response to treatment. A longer study length may have resulted in a stronger algae response.

Algae growth also requires planktonic algae propagules to settle on a hard substrate before growth can ensue. Corals provide abundant hard substrate for algae settlement, but it has been demonstrated that algae propagules are unable to settle on live coral tissue, regardless of coral species (Diaz-Pulido & McCook 2004). This finding is consistent with observations in the field. Algae were never observed growing on live coral. Likewise, algae propagules are able to settle on dead coral substrate (Diaz-Pulido & McCook 2002) and new algae growth was only observed on small dead patches on the coral head. Studies have proposed that live corals are able to prevent algae settlement through mucus secretion or the use of cleaning tentacles (McCook et al. 2001). Widespread algae growth on reefs is often indicative of coral injury or stress (McCook et al. 2001, Diaz-Pulido & McCook 2002, Diaz-Pulido & McCook 2004). The field site of this current study (Figure 2) was characterized by an abundance of healthy, live and diverse coral. The reef's health may have prevented algae from settling, resulting in the weak response to treatment. It is possible that algae settlement at the field site was further reduced due to the prevalence of the strong current. Strong currents are unfavorable for algae settlement because they prevent the propagules from finding a suitable place to attach to.

The observation that algae were never found on live corals is further supported by the laboratory results of this study. Porites sp. corals that were either placed with D. savignyi or without D. savignyi consisted of sections of live coral polyps and sections of short algal "turf." Following treatment for 8-12 days, the ratio of algae to coral remained similar to the ratio prior to treatment. The presence of D. savignyi did not significantly influence algae growth. The laboratory corals were placed in a continuously flowing seawater system, but the flow velocity was not significant enough to prevent settlement of algae propagules, as algae was seen growing on the sides of the tank. Therefore, it is reasonable to assume that algae propagules were present in the water, but the live coral polyps were excluding algae settlement.

It is also possible that sea urchins are not the main moderators of algae growth in the reefs surrounding Moorea. As described by Wilder (2003), fish may be superior to sea urchins in limiting algal biomass in Moorean coral reefs. Wilder's findings differ from the

Caribbean studies that have suggested that high sea urchin abundance is associated with low algal biomass (Sammarco 1982, Hay & Taylor 1985, Carpenter 1990). However, it is important to keep in mind that Caribbean reefs have historically been overfished (Gardner et al. 2003), allowing sea urchins, such as D. antillarum, to have a stronger impact on algae growth than would normally be the case. Fishing reduces the number of fish that predate upon sea urchins while also reducing the abundance of herbivorous fish that feed on algae. Reduced predation in addition to reduced competition for algae results in increased sea urchin abundances and a greater impact on algal biomass. In contrast to the Caribbean, French Polynesia has not yet been overfished. Many fish species are present in the waters surrounding Moorea and it is known that D. savignyi is being predated upon (K. Roesch-Goodman personal communication). These observations suggest that D. savignyi populations may be being kept at bay by fish predators while the abundance of herbivorous fish may be having a large impact on algae growth in the reefs.

The results of this study suggest that *D*. savignyi does not have a strong impact on algae growth in the reefs surrounding Moorea, at least under current conditions. presence or absence of D. savignyi did not influence the amount of algae that was found on the coral head. The most probable reason for this finding is that algae do not grow fast enough in Moorean coral reefs due to the health of the reef. The reef is characterized by an abundance of diverse, live coral and many fish, resulting in high algal consumption by the fish and prevention of new algae settlement by the live coral. However, with the increasing prevalence of coral bleaching and global climate change (Brown 1997, Penin et al. 2007), D. savignyi may have a more important role in preventing coral reefs from becoming dominated by algae in the future. It is therefore important to take steps toward reef conservation and education while working to prevent overfishing so that an ecologically, economically and aesthetically important resource is not lost.

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REFERENCES

- Bak, R.P.M. and G. Van Eys. 1975. Predation of the sea urchin *Diadema antillarum* Philippi on living coral. Oecologia **20**: 111-115.
- Bak, R.P.M. and E.H. Meesters. 1999. Population structure as a response of coral communities to global change. American Zoologist 39: 56-65.
- Brown, B.E. 1997. Coral bleaching: causes and consequences. Coral Reefs **16**: S129-S138.
- Carpenter, R.C. 1990. Mass mortality of *Diadema antillarum*: Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. Marine Biology **104**: 79-86.
- Carpenter, R.C. and P.J. Edmunds. 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. Ecology Letters 9: 271-280.
- Contreras, S. and J.C. Castilla. 1987. Feeding behavior and morphological adaptations in two sympatric sea urchin species in central Chile. Marine Ecology Progress Series 38: 217-224.
- Diaz-Pulido, G. and L.J. McCook. 2002. The fate of bleached corals: patterns and dynamics of algal recruitment. Marine Ecology Progress Series 232: 115-128.
- Diaz-Pulido, G. and L.J. McCook. 2004. Effects of live coral, epilithic algal communities and substrate type on algal recruitment. Coral Reefs 23: 225-233.

- Edmunds, P.J. and R.C. Carpenter. 2001. Recovery of Diadema antillarum reduces macroalgal cover and increased the abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Sciences 98: 5067-5071.
- Fogg, G.E. 1965. Algal cultures and phytoplankton ecology. University of Wisconsin Press, Madison, 126 pp.
- Gardner, T.A., I.M. Côté, J.A. Gill, A. Grant and A.R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. Science **301**: 958-960.
- Gilmour, J.P. 2004. Size-structures of populations of the mushroom coral *Fungia fungites*: the role of disturbance. Coral Reefs **23**: 493-504.
- Gosliner, T.M., D.W. Behrens and G.C. Williams. 1996. Coral Reef Animals of the Indo-Pacific. Sea Challengers, Monterey, California. 74 pp.
- Hay, M.E. and P.R. Taylor. 1985. Competition between herbivorous fishes and urchins on Caribbean reefs. Oecologia 65: 591-598.
- Hoegh-Guldberg, O., P.J. Mumby, A.J. Hooten, R.S. Steneck, P. Greenfield, E. Gomez, C.D. Harvell, P.F. Sale, A.J. Edwards, K. Caldeira, N. Knowlton, C.M. Eakin, R. Iglesias-Prieto, N. Muthiga, R.H. Bradbury, A. Dubi and M.E. Hatziolos. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318: 1737-1742.
- Hughes, T.P. and J.B. Jackson. 1985. Population dynamics and life histories of foliaceous corals. Ecological Monographs 55 (2): 141-166.
- Lewis, S.M. 1985. Herbivory on coral reefs: Algal susceptibility to herbivorous fishes. Oecologia (Berlin) **65**: 370-375.
- Lessios, H.A., D.R. Robertson and J.D. Cubit. 1984. Spread of *Diadema* mass mortality through the Caribbean. Science **226**: 335-337.
- Mapstone, B. D., N. L. Andrew, Y. Chancerelle and B. Salvat, 2007. Mediating effects of sea urchins on interactions among corals, algae and herbivorous fish in the Moorea lagoon, French Polynesia. *Marine Ecology Progress Series* **332**: 143-153.
- McClanahan, T.R., M. Nugues and S. Mwachireya. 1984. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: The role of reef management. Journal of Experimental Biology and Ecology 184: 237-254.
- McCook, L.J. 1999. Macroalgae, nutrients and

- phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18: 357-367.
- McCook, L.J., J. Jompa and G. Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19: 400-417.
- Meesters, E.H., M. Hilterman, E. Kardinaal, M. Keetman, M. deVries and R.P.M.Bak. 2001. Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. Marine Ecology Progress Series 209: 43-54.
- Moberg, F. and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics 29: 215-233.
- Myhre, S. and A. Acevedo-Gutiérrez. 2007. Recovery of sea urchin *Diadema antillarum* populations is correlated to increased coral and reduced macroalgal cover. Marine Ecology Progress Series **329**: 205-210
- Ogden, J.C. and P.S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. Environmental Biology of Fishes 3: 49-63.
- Penin, L., M. Adjeroud, M. Schrimm and H.S. Lenihan. 2007. High spatial variability in coral bleaching around Moorea (French Polynesia): patterns across locations and water depths. Comptes Rendus Biologies 330: 171-181.
- Reynolds, W.W. and M.E. Casterlin. 1977. Effect of temperature on the growth rate of *Griffithsia tenuis* C. Agardh (Rhodophyta: Ceramiales). Hydrobiologia **56**(3): 225-227.
- Sammarco, P.W. 1982. Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. Journal of Experimental Marine Biology and Ecology **65**: 83-105.
- Sebens, K.P., S.P. Grace, B. Helmuth, E.J. Maney Jr. and J.S. Miles. 1998. Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa* and *Porites porites*, in a field enclosure. Marine Biology **131**: 347-360.
- Vaziri, N. 1995. Habitat partitioning and susceptibility of *Sargassum sociale* to herbivory by sea urchins. UC Berkeley: Moorea Student Research Papers 4: 16-24.
- Wilder, R.M. 2003. Algae-Herbivore Interactions on the Coral Reefs of Moorea,

French Polynesia, Ph.D. Dissertation publ. by Holbrook, Sally J. University of California, Santa Barbara.