UC Berkeley
Student Research Papers, Fall 2008

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

Permalink
https://escholarship.org/uc/item/7xj4g5dm

Author
Hoey, Jennifer

Publication Date
2008-12-01

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

JENNIFER HOEY

Department of Integrative Biology, University of California, Berkeley, California 94720 USA

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 caged with *D. savignyi* or no *D. savignyi*, or not caged at all. 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 placed in a tank either 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, coral reef ecosystem, percent algae cover, Moorea, French Polynesia

INTRODUCTION

Coral reefs are one of the world's most diverse and productive ecosystems. They 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 interactions. 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.

The synergistic effect of all the aforementioned factors determines whether algae or coral dominates in a reef system. Theoretically, it is possible for a coral dominated reef to become algae dominated, or vice versa, if conditions are favorable (Edmunds & Carpenter 2001). This shifting between two different states is termed a "phase shift." "Phase shifts" from coral dominated to algae dominated have been documented in Caribbean reefs (Gardner et al. 2003), but there is little evidence for "phase shifts" in the reverse direction (Edmunds & Carpenter 2001). When a coral reef becomes algae dominated, the entire community structure changes. Species diversity and distributions change, affecting the health of the reef and potentially resulting in lasting ecological changes.

One of the most important factors in preventing a coral dominated reef from "phase shifting" to an algae dominated reef is herbivory. 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). Others have suggested that sea urchins have a more important role in shaping coral reef community structure due to the high densities that they can achieve (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 algae-herbivore interactions. Although Bak and Van Eys (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 coral reefs. High *Diadema* density is 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 2007). 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. Following the mass die-off of *Diadema* in 1983, Caribbean coral reefs "phase shifted" from coral dominated to algae dominated. Although it is widely debated, recent evidence suggests that Caribbean reefs may be "phase shifting" back to coral dominated due to the recovery of *Diadema* (Edmunds & Carpenter 2001, Gardner et al. 2003, Carpenter & Edmunds 2006, Myhre & Acevedo-Gutiérrez 2007). These studies have suggested that the abundance of *Diadema* is causing the "phase shifts," further illustrating the importance of *Diadema* in structuring the reef community.

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 algal biomass. This finding differs from 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. I hypothesize that *Diadema savignyi* plays a large role in shaping coral reef community structure by consuming algae, thereby preventing algae domination in reefs. Therefore, I predict that 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 western Pacific, including the Society Islands. *D. 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 commonly found in shallow reefs. Individuals can be found hiding among coral heads or aggregated together on the sandy bottom during the day. At night, they move less than meter to forage on algae.

FIGURE 1. *Diadema savignyi.*

Study site description

To determine whether *D. savignyi* has a large role in shaping 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). From 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.
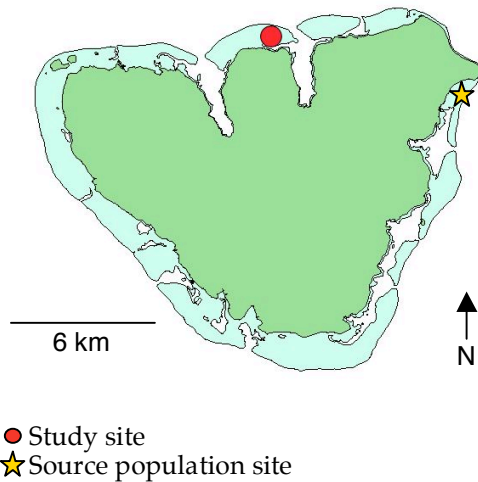

FIGURE 2. Study site location and source population site of *D. savignyi* used in study.

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 centimeters^3 constructed of 0.6 or 2.0 centimeter^2 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).
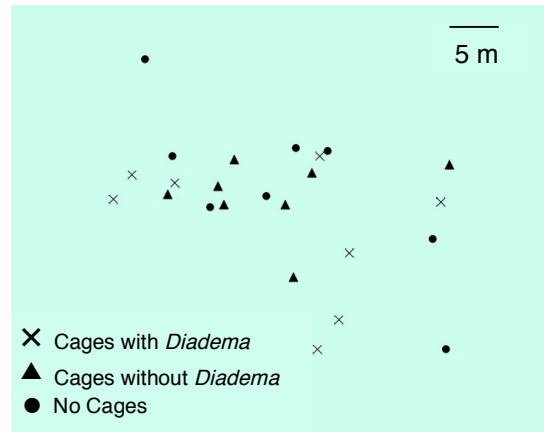

FIGURE 3. Diagram of coral head locations. Treatments were applied randomly and algae growth was monitored for 25 days. Sites are accurate to seven meters.

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 a loose piece of small live *Porites* sp. coral was placed in each half. One *D. savignyi* (test size 4.27-5.74 centimeters) 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.

All statistical tests were performed in JMP. 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 on 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 at the end of the experiment. 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, F = 1.92, df = 2,21, p < 0.17, Figure 4). On all days that photographs were taken (10/22, 10/30, 11/5 and 11/10), treatments were statistically 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.
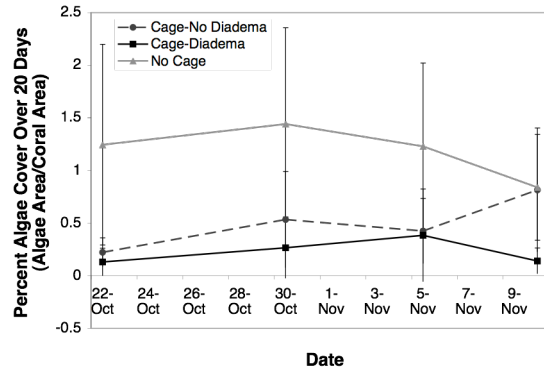

FIGURE 4. Percent algae cover on coral heads over 20 days with standard error bars. Treatments were applied for 25 days, but algae measurements are unavailable for the initial five days.

Following 25 days in the field, variation in algae cover was not found to be significantly different across treatments (one-way ANOVA, F = 1.66, df = 2, p < 0.21). However, following the trend noted above, 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).
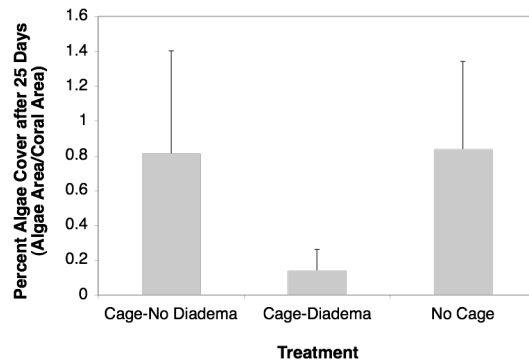

FIGURE 5. Percent algae cover following 25 days in the field with standard error bars. Corals that had been caged off with *D. savignyi* had the least algae cover.

Algae length following 25 days of treatment was not significantly different across treatment types (Figure 6). Algae length on Cage-No *Diadema* corals and Cage-*Diadema* corals was undistinguishable (Fisher's exact test, p = 0.47). It should be noted that the Cage-*Diadema* corals did not have any algae greater than five millimeters, but this was not significant.
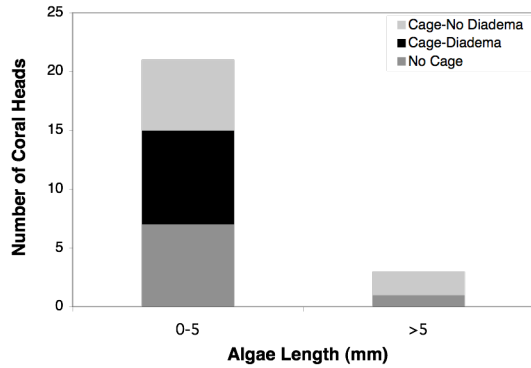
FIGURE 6. Algae length on coral heads following 25 days in the field.

Laboratory results

Following 8-12 days exposure to either *D. savignyi* or no *D. savignyi*, percent algae cover did not differ significantly (T-test, t = 0.75, df = 1, p = 0.41, Figure 7). Algae cover decreased both on corals that were exposed to *D. savignyi* and on corals that were not. Following the expected trend, the decrease in algae cover was slightly greater for corals that were exposed to *D. savignyi*.
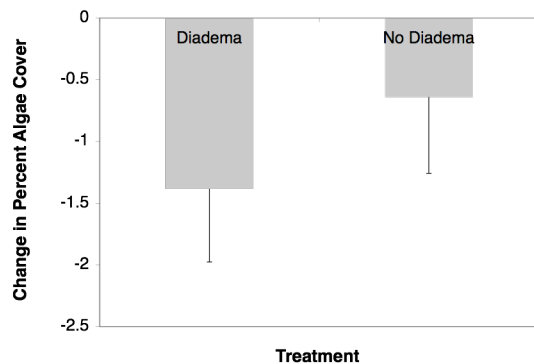

FIGURE 7. Change in percent algae cover following 8-12 days in the presence or absence of *Diadema savignyi*. Error bars represent standard error.

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. In contrast, many studies have examined algae-coral-herbivore interactions

and determined herbivores to have an important role in structuring the coral reef community (Ogden & Lobel 1978, Hay & Taylor 1985, Carpenter 1990, Vaziri 1995, Edmunds & Carpenter 2001, Wilder 2003, Carpenter & Edmunds 2006, Myhre & Acevedo-Gutiérrez 2007). Herbivores help to prevent coral dominated communities from "phase shifting" to algae dominated ones. A reef dominated by algae can affect fish and invertebrate diversity and abundances, and as a result, change community structure and interactions. Previous studies have documented a strong correlation between sea urchin absence and high algae abundance (Hay & Taylor 1985, Carpenter 1990, Vaziri 1995), but many of these studies removed entire *Diadema* populations from Caribbean reefs and examined the consequent response as the *Diadema* populations rebounded over many months. Other studies have watched as the *Diadema* population recovered from the mass die-off of 1983 and have linked high *Diadema* density to increased coral abundance (Edmunds & Carpenter 2001, Carpenter & Edmunds 2006, Myhre & Acevedo-Gutiérrez 2007). These studies in the Caribbean illustrate the importance that one herbivorous species can have in shaping the entire coral reef community. Although the results of this study differ from previous algae-sea urchin studies, a wide array of ecological and methodological factors may explain the seemingly unusual result observed here.

It is 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 (Edmunds & Carpenter 2001, 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 some predate on *D. savignyi* (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 have a large impact on algae growth in the reefs.

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.

The observation that algae were never found on live corals is further supported by the laboratory results of this study. The *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 algal settlement.

It is also possible that methodological challenges and issues influenced the results observed in this study. The cage design worked moderately well, 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.

Although methodological issues may have been a confounding factor, 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. The presence or absence of *D. savignyi* did not influence the amount of algae that was found on the coral heads. 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 a growing human population, 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.

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.