The sea urchin *Diadema antillarum* – keystone herbivore or redundant species?

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Abstract

Two main hypotheses have been developed for describing the role and importance of the sea urchin *Diadema antillarum* on reefs of the Caribbean region in both space and time. The first and most crucial is whether *D. antillarum* was the most important "keystone" grazer on Caribbean reefs? The alternate to this hypothesis is that *D. antillarum* was merely a redundant species, playing a secondary role to herbivorious fishes which only came into dominance after herbivorous fishes had been removed by man through exploitive fishing practices. To resolve this debate, we pose the question: "What is the role of *Diadema antillarum* in altering the composition of the benthic community on Caribbean coral reefs in time and space?" The interpretation presented herein implies that *D. antillarum* was and is the most important shallow-water herbivore on Caribbean coral reefs. This is contrary to a prevailing model but in substantial agreement with the historical importance of the species. If correct, the continued and future recovery of this sea urchin may be the key ingredient to facilitating coral reef recovery throughout the region. In addition, on coral reefs where the natural recovery of *Diadema* has been delayed or is absent (e.g. the Florida Reef Tract); measures to actively restore these urchins may be the most efficient and cost-effective tool for conserving and enhancing the ecological function of reefs. This debate also emphasizes the requirement for implementing ecologically-based, not ideologically-based management of natural systems.

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Introduction

The long-spined sea urchin, *Diadema antillarum*, was once one of the most conspicuous organisms found living on coral reefs throughout the Caribbean and western Atlantic region. Its abundance and reputation conjured images of both beauty and danger (Figure 1). Prior to 1983, populations of *D. antillarum* were routinely found in densities of about four individuals per square meter ($4/m^2$) in shallow reef environments and in some areas as many as 40 individuals per square meter ($40/m^2$) were recorded (Randall et al. 1964, Bauer 1980, Sammarco 1980, 1982a, 1982b, Bak et al. 1984, Hughes 1994, Kissling et al. 2014).

Figure 1. Artist's rendition of a typical shallow-water reef scene in the U.S. Virgin Islands prior to 1983, replete with *Diadema*. Photo of oil on canvas by Tiller from private collection of Dr. Sal Genovese by WF Precht.

During 1983 and 1984, *D. antillarum* populations were catastrophically reduced by a regional, waterborne epizootic (Lessios et al., 1984a, 1984b, Hughes et al. 1985, Hunte et al. 1985). Approximately 93-98% of the extant *Diadema* populations from throughout the

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region were killed in this event (Lessios 1988). This mass mortality of *D. antillarum* is considered by many to be the most dramatic natural decline ever recorded in a marine species. To emphasize the importance of this ecological disturbance, Knowlton (2004) put it in a human context by stating *"... consider how the Center for Disease Control (CDC) would handle an organism with lethality greater than Ebola and contagion greater than the chicken pox."*

Diadema antillarum has been heralded by some reef scientists as a keystone species, controlling coral and macroalgal community dynamics on Caribbean coral reefs (Powers et al. 1996). Other researchers argue, however, that it was only in recent times, due to the effects of overexploitation of herbivorous fishes by man, that *D. antillarum* became more important ecologically (Hay 1984a, 1984b, Jackson 1994, 2001).

These two alternate hypotheses lead to an important question: "*What is the role of* Diadema antillarum *in altering the composition of the benthic community on Caribbean coral reefs in time and space?*" To approach this question, a careful review of the primary literature was undertaken to define which key indicators and metrics could be used to address the efficacy of grazing by *D. antillarum* in the presence and/or absence of herbivorous fish and *vice versa*. The analysis of these results should lead to one of two very different recommendations concerning how reefs could be managed, conserved and restored in the future. One where *Diadema* takes a prominent role in the recovery process, while in the other, herbivorous fishes are the main target of conservation efforts.

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Background -- Biology of *Diadema*

Diadema antillarum Philippi (Echinodermata: Echinoidea) is a herbivorous species of sea urchin that is found throughout the Caribbean and sub-tropical/tropical regions of the Atlantic Ocean. This regular sea urchin, commonly known as the long-spined black sea urchin, or black sea egg, is recognized by its long, black spines, which radiate up to 30 cm from its hemispherical test (Figure 2).
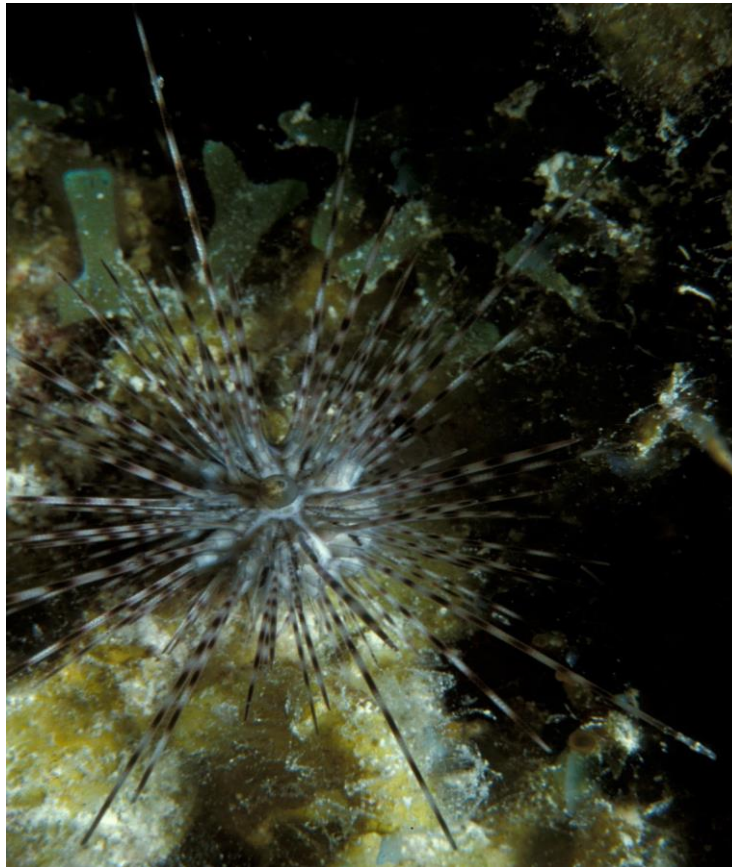
Figure 2. *Diadema antillarum* grazing on abundant macroalgae (*Dictyota* spp.), San Salvador Island, Bahamas in 1980. Photo by WF Precht.

The long, sharp spines are coated with toxic mucus offering them additional protection from all but the most specialized predators (Randall et al. 1964, Bauer 1976, 1982, Ogden

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and Carpenter 1987). Bruno (2010) cleverly described *D. antillarum* as "basically a pin cushion with black hypodermic needles for spines" (Figure 3).
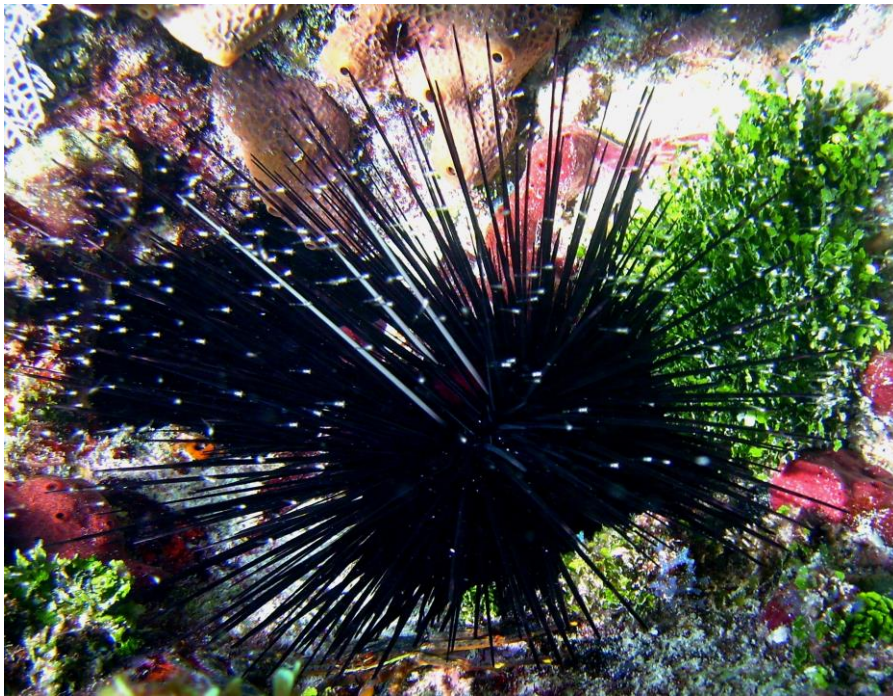
Figure 3. Adult specimen of *Diadema antillarum*. Note the abundance of mysid shrimp swimming amongst the spines. Photo taken on a patch reef off north Key Largo within the Florida Keys National Marine Sanctuary in 2009. Photo by WF Precht.

D. antillarum can be been found in a variety of habitats, but most often occupies shallow hard-bottom, seagrass and mangrove communities associated with coral reef ecosystems (Ogden and Carpenter 1987, McClanahan and Muthiga 2007). During the day, this urchin generally remains in structurally complex areas and under ledges to avoid predation (Lee 2006). At night, however, it is known to migrate out to more exposed areas to forage (Ogden et al. 1973). *D. antillarum's* preferred food includes benthic algal turf and macroalgae (seaweed), but when those are in limited supply, it will feed on essentially anything that is available, including coral (Randall et al. 1964, Bak and van Eys 1975, Muthiga and McClanahan 2007). Also, when found in significant numbers these urchins

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are known to graze on coral spat as well as other benthic invertebrates (Bak and van Eys 1975, Sammarco 1980). This non-selective feeding ability gives *Diadema* a distinct advantage over other herbivores that have selective preferences (Sammarco et al. 1974, Ogden and Lobel 1978, Glynn 1990). For instance, Littler et al (1983) noted that of 21 species of macroalgae examined in Belize most had exceptionally low losses to fish grazing, probably due to chemical defenses. However, they found that *D. antillarum*, was more inclined to feed on most algae including those with known toxic secondary metabolites. In a similar analysis, Solandt and Campbell (2001) found that *D. antillarum* consumed macroalgae previously considered unpalatable to other coral reef herbivores, especially fish.

Carpenter (1981, 1986) demonstrated *D. antillarum's* preference for algae above all other treatments (see also Carpenter 1997). Its voracious appetite combined with high population abundances resulted in the control of turf and macroalgae on coral reefs. *D. antillarum* is also among the most important substratum modifiers in the Caribbean, bioeroding the reef framework (Ogden 1977, Sammarco 1982, Bak 1994). The *D. antillarum's* teeth-like Aristotle's Lantern allows them to be much more efficient than browsing bioeroders (i.e. herbivorous parrotfish) and therefore is responsible for more carbonate bioerosion than any other taxonomic group (Hunter 1977, Ogden 1977, Sammarco 1982, Bak 1994; see Figure 4).

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The Mass Mortality Event

The signs of an extensive mortality event effecting only individuals of the sea urchin *Diadema antillarum* was first observed in mid-January, 1983 off the Caribbean coast of Panama (Lessios et al. 1984a, 1984b). The initial symptoms of the disease included sticky, motionless spines. Next, the affected urchins were unable to rid their test of sediment. This coating of sediment was soon followed by a loss of pigment turning the urchins white. As the disease quickly progressed, the urchins were unable to remain attached to their substrates by their tube feet and were moved about by the wave and currents. The next and final observed malady was a complete loss of remaining spines and the rapid disarticulation of whole skeletons (see Figure 5). In less than one week from the first observation of the disease, most individuals were dead (Lessios et al. 1984a, 1984b).

Following the loss of *D. antillarum* in Panama (Lessios et al. 1984a), the disease was being reported elsewhere throughout the Caribbean region (Bak et al. 1984, Hughes et al. 1985, Hunte et al. 1985, Levitan 1988a, and many others). Eventually, all known extant populations of *D. antillarum* were affected by this disease. The spread of the disease traveled in a pattern generally consistent with major surface currents (Lessios et al. 1984b, Ogden and Carpenter 1987), and by January 1984, some 3.5 million square kilometers of area had been affected (Lessios 1988).

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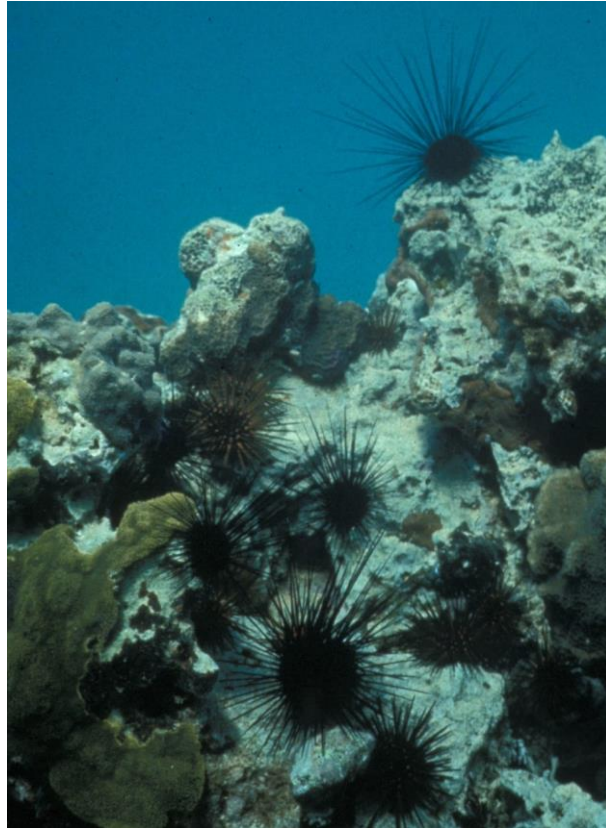
Figure 4. Photo of high concentration of *D. antillarum* on a patch reef at Discovery Bay Jamaica in 1978. Note lack of macroalgae and significant bioerosion. Photo by WF Precht.

While the ultimate pathogen(s) which caused the original mortality event were never formally confirmed using Koch's postulate, it is commonly assumed that the epizootic was a waterborne pathogen of bacterial origin (probably *Clostridium perfringens* and/or *C. sordelli*; see Bauer and Agerter 1987).

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Figure 5. Photo of dead and disarticulated *Diadema* tests and spines from the Florida Keys in July 1983. Photo courtesy of Dr. Billy Causey, Florida Keys National Marine Sanctuary.

Importantly, this mass mortality event gave reef scientists a unique, unprecedented opportunity to study and validate, via a natural *in vitro* regional experiment, the two hypotheses regarding the role of *D. antillarum* in structuring Caribbean reef communities. While some aspects of the debate have been analyzed in a number of recent papers (Bellwood et al. 2004, Mumby et al. 2006, Bruno et al. 2009, Idjadi et al. 2010), a thorough review has not been published. By understanding how the reefs responded to the lack of *D. antillarum* following the 1983 event and then how they will change again when and if *D. antillarum* return, should yield important scientific clues that will assist resource managers in the conservation and restoration of coral reef ecosystems.

After the Fall

The life history characteristics of *D. antillarum* should make it an excellent candidate for rapid recovery from a catastrophic decrease in population (Uthicke et al. 2009, but see Lessios et al. 1984a). This is because the adult females produce large numbers (millions) of eggs throughout the year, and the planktonic larvae are well-suited to dispersal (Levitan 1988b, Muthiga and McClanahan 2007). For a variety of reasons, the recovery of *D. antillarum* to pre-disease "baseline" conditions has failed to occur for more than three decades (Karlson and Levitan 1990, Hughes et al. 2010; Levitan et al. 2014, Rodríguez-Barreras et al. 2015a) at most Caribbean reefs. More recently, however, increasing numbers of *D. antillarum* have been recorded at a number of locations throughout the Caribbean (Woodley 1999, Aronson and Precht 2000, Chiappone et al. 2001, Edmunds and Carpenter 2001, Cho and Woodley 2002, Miller et al. 2003, Macintyre et al. 2005, Weil et al. 2005, Carpenter and Edmunds 2006, Noriega et al. 2006, Debrot and Nagelkerken 2006, Steiner and Williams 2006, Myhre and Acevedo-Gutiérrez 2007, Jordán-Garza et al. 2008, Idjadi et al. 2010, Blanco et al. 2010, 2011; Ruiz-Ramos et al. 2011, Bodmer et al. 2015, Lessios 2016). These reports could mark the start of a regional recovery of the *Diadema* and possibly the return of Caribbean reefs ecosystems to the prior state (Knowlton 2001).

It appears that the locations with the greatest reported recovery of *D. antillarum* to date are generally those reefs with the lowest fish populations, especially invertivores that consume *Diadema* (Rogers 2011; Figure 6). Conversely, Harborne et al. (2009) indicated that in the Exuma Land and Sea Park in the Bahamas that the relationship between the

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biomass of urchin predators and the proportion of transects containing *Diadema* was nonlinear, suggesting that small increases in fish biomass dramatically reduce urchin abundances. In a similar analysis, Rodríguez-Barrerasa et al. (2015b) recently showed experimentally that efforts to recover *D. antillarum* populations would be strengthened if densities of *Thalassoma bifasciatum* and *Halichoeres bivittatus* (two common fish predators of *Diadema*) remained low. Thus, protecting reef fishes through networks of Marine Protected Areas (MPAs) could ultimately slow the recovery of *Diadema.* It should therefore not be too surprising that presently many MPAs show no recovery of *Diadema* long after their designation.

Figure 6. Aggregation of *D. antillarum* at LTS Reef at Discovery Bay, Jamaica, W.I. in 2007. Note the heavily grazed areas are devoid of macroalgae and covered by crustose coralline algae. Photo by WF Precht.

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Ecological Impacts

The epilithic macroalgal community on coral reefs is generally considered to be an important component of the primary productivity in reef ecosystems, and one that is normally kept in check by a consortium of herbivores including a number of fish and urchin species (Glynn 1990, Carpenter 1997, McClanahan and Muthiga 2007, Bruno et al. 2014). Carpenter (1981) noted that *D. antillarum* was the most important herbivore on Caribbean reefs. He predicted that in the absence of these urchins from reef systems, there would be significant growth of benthic algae (see also Sammarco 1982a, 1982b). In fact, throughout the Caribbean, there were numerous examples where the cover of fleshy benthic algae (seaweeds) and filamentous algae increased dramatically immediately following the mass urchin mortality (i.e. Hughes et al. 1987) corroborating both Carpenter and Sammarco's *a priori* predictions.

For example, along the north coast of Jamaica, Liddell and Ohlhorst (1986) documented changes in the composition of the benthic community on shallow reefs following the loss of *Diadema*. Specifically, Liddell and Ohlhorst (1986) noted an increase of macroalgae to nearly 50% absolute cover within two (2) weeks of the event. de Ruyter van Steveninck and Bak (1986) noted an almost identical rapid progression towards macroalgal dominance on the reefs of Bonaire and Curaçao, even though the fishing pressure was light on these reefs of when compared to the Jamaican example cited above. This shift to macroalgal dominance appears to be a long-term effect of great ecological significance and on many reefs is portrayed as a major ecological phase shift from a coral-dominated

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system to a macroalgal-dominated system (Knowlton 1992, Hughes 1994, Bruno et al. 2009, Dudgeon et al. 2010).

**The Role of *Diadema*: a Keystone Species or a Redundant Herbivore**

The reason why the loss of *D. antillarum* was so ecologically important is that along with herbivorous fishes, these sea urchins played an important role as a functional grazer, particularly in shallow reef habitats (<10 m in depth) feeding on a variety of algal species (Lawrence 1975, Glynn 1990, Carpenter 1997, McClanahan and Muthiga 2007). Dart (1972), specifically noted that urchins were more important than herbivorous fishes at controlling algal turfs and opening space for colonization by reef corals. Moreover, herbivore addition and exclusion experiments performed by Sammarco (1982a, 1982b) on patch reefs in Discovery Bay, Jamaica in the 1970s suggested that declining herbivory relative to the space available for colonization promoted algal growth and decreased coral recruitment. Specifically, as *D. antillarum* populations decreased, macroalgal biomass increased. Once the urchins were restored, however, the system returned to its original composition. The response of the benthos to urchin abundance was similar in small-scale plots and whole-reef manipulations (see also Davies et al. 2013).

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For many years it was thought that *Diadema* was the most important herbivore on Caribbean reefs:

> *"Through direct effects on algal communities or indirect effects on other benthic reef organisms, grazing by* Diadema *is a major factor controlling the community structure of coral reefs. ...Perhaps no other single species in the coral reef environment has such profound effects on the other organisms composing the reef community."* (In: Ogden and Carpenter 1987)

Hay (1984a, 1984b) proposed an alternate to this hypothesis arguing that *D. antillarum* was merely a redundant species, playing a secondary role to herbivorious fishes, where grazing fishes represent dominant components of the herbivore guild on relatively undisturbed Caribbean reefs (see also Hay and Taylor 1985, Lewis and Wainwright 1985, Lewis 1986). This second hypothesis contends that it wasn't until these coastal ecosystems were subjected to the loss of herbivorous fishes by intense fishing pressure that *D. antillarum* became more than just a background species.

Jackson (1994, 2001) preferred Hay's explanation noting that the overfishing of the predators of *D. antillarum* as well as the removal of large herbivorous fishes that had competed with *D. antillarum* allowed these urchins to increase in abundance (see Figure 7). Then, when *D. antillarum* were lost to disease there were no other herbivores

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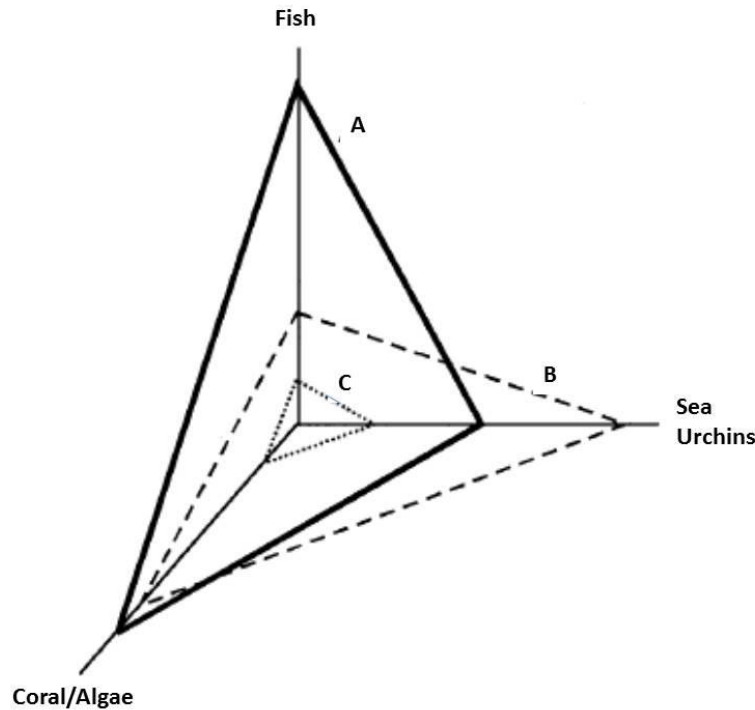
Figure 7. Tripartite model visualizing the purported role of herbivorous fish, *Diadema*, corals and macroalgae following Hay (1984a, 1984b). Triangle A (solid-line), represents the "pristine" condition, with high ratio of corals to macroalgae because of intense grazing of macroalgae by fishes. Triangle B (dashed-line), reveals dramatic increases in *Diadema* grazed macroalgae that were formerly consumed by herbivorous fishes; the ratio of corals to macroalgae, however, still remains high despite intensive fishing. Triangle C (dotted-line), depicts the effect of the mass mortality of *Diadema* which allowed macroalgae to proliferate (modified from original in Jackson 1994).

remaining and a shift to macroalgal dominated reef communities ensued. Thus, the loss

of *D. antillarum*, combined with decades of intense fishing pressure, resulted in a

dramatic increase in macroalgal cover on many Caribbean reefs (Aronson, 1990;

Knowlton 1992, Hughes 1994). Jackson (2001; Jackson et al. 2001) argued that the

ecological redundancy of the *D. antillarum* obscured the effects of the loss of herbivorous

fishes for well over a century until they too were lost.

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Bellwood *et al*. (2004) argued that Jamaican reefs as originally described had been over-fished for numerous decades (possibly centuries), with no apparent negative effects on the coral assemblages. However, once the herbivorous fishes were exploited by local fishers, the herbivorous echinoid *D. antillarum* was able to become superabundant.   This was the scenario until 1983-1984 when *D. antillarum* was abruptly removed by a disease epizootic.   Soon thereafter, the reef was converted to a 'vast carpet' of macroalgae (Jackson 2001, Jackson et al. 2001). This scenario, based on the reefs at Discovery Bay, is the most often cited model for the recent dynamics of all Caribbean reefs (see Google Scholar citation results for Hughes 1994, Jackson et al. 2001, and Bellwood et al. 2004); but is this model correct? (see Côté et al. 2013 for an alternate view).

Subsequent to his published account of the model that *D. antillarum* was a redundant herbivore (Jackson 1994); Jackson (1997) made a strong case for reconsidering the relationship between *D. antillarum*, overfishing, coral mortality, and macroalgae on coral reefs (*contra* Hay 1984a, 1984b).   Using historical writings from naturalists, Jackson questioned the assumption that overfishing allowed a superabundance of *D. antillarum* to proliferate, with *D. antillarum* taking over the role previously carried out by the fish. Jackson (1997) noted "*These sources make it clear that* Diadema *was indeed very abundant in the seventeenth century when human populations were very small, and therefore long before overfishing could have caused their increase*."

Interestingly enough, Jackson (2001) once again reversed his position citing overfishing as the critical overriding structuring force on Caribbean reef communities as well as for

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explaining the superabundance of *Diadema* at locations across the Caribbean. In addition, Jackson et al. (2001; see also Bellwood et al. 2004), asserted that 'overcrowded conditions' of *Diadema* populations due to overfishing was directly responsible for their collapse by increasing their susceptibility to disease as a result of increased rates of density-dependent transmission.

Being able to discern which of these two hypotheses is "ecologically correct" is crucially important for understanding what management steps could be employed in the future to return Caribbean reefs to their former state (e.g. reefs with higher coral cover and lower macroalgal cover). The only way to extricate the "scientific truth" from these disparate models requires attention to the question posed in the introduction. By addressing this question through a number of testable hypotheses, it should be possible to unravel this debate. Clearly, as ecologists we seek to evaluate the relative importance of the many possible causes underlying the observed pattern (Quinn and Dunham 1983).

Tests of the Hypotheses

The first significant test of the original Hay (1984a, 1984b) model was performed by Levitan (1992). Using ratios of Aristotle's Lantern-to-test size in museum specimens of *D. antillarum* collected over the century before 1983, Levitan (1992) uncovered a small but positive relationship between population density of *D. antillarum* and increasing levels of fishing pressure through time. Specifically, Levitan (1992) noted that when populations of *D. antillarum* increase, there is an increase in jaw size and a reduction in

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test diameter (see also Levitan 1991a, 1991b). Levitan (1992) noted, however, there were confounding influences in geographic distribution (island reef samples versus continental reef samples) that might preclude the direct correlation between human impacts and *D. antillarum* test diameter. In fact, the human impact was small relative to natural geographic variation; regardless of this confounding factor, his measurements supported Hay's (1984a, 1984b) contention that *D. antillarum* density was positively related to fishing pressure. An important issue with regard to the over-fishing scenario, however, is whether or not all reefs of the Caribbean have had the same history of resource exploitation. With the exception of some overpopulated islands with high extractive fishing pressure like Jamaica, Haiti, and St. Croix there is little evidence that herbivorous fishes have been removed *en masse* throughout the entire region, leaving *D. antillarum* as the only herbivore having any ecological consequence (Aronson and Precht 2001). Thus, as Jackson (1997) noted, the superabundance of *Diadema* at a few heavily fished locations "*is at best a secondary consequence of the degradation of Caribbean reefs.*"

In fact, on most Caribbean reefs over-fishing has led to preferential removal of larger-bodied predatory fishes and invertivores, and not primary consumers. The resulting compensatory trophic response therefore should have been an increase and not a decrease in the sizes and numbers of herbivorous prey species (Precht and Aronson 2006, Bruno et al. 2009, Dudgeon et al. 2010, Bruno et al. 2014). Short-term increases in grazing and long-term increases in population sizes of herbivorous fishes were reported subsequent to the regional demise of the sea urchins (Carpenter 1986, 1988, 1990a; Morrison 1988;

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Robertson 1991). However, a key feature of this trophic response was that the increase in grazing pressure by herbivorous fishes was not sufficient to compensate for the loss of *D. antillarum* at either the scale of individual reefs or the region, no matter what the degree of fishing pressure (Paddock et al. 2006).

But what is the response of reefs now dominated by macroalgae when and if, *D. antillarum* populations return? This ongoing natural experiment is presently being witnessed along much of the north coast of Jamaica (i.e. Idjadi et al. 2006, 2010). There, shallow reef areas have recovered steadily since the late 1990s following the return of *Diadema*, resulting in top–down alterations to the benthic community (Woodley 1999, Aronson and Precht 2000, Edmunds and Carpenter 2001, Cho and Woodley 2002, Bechtel et al. 2006, Crabbe 2009, Precht and Aronson 2006, Idjadi et al. 2010). Specifically, there has been a phase shift reversal back to coral from macroalgae (Idjadi et al. 2006, 2010). Carpenter and Edmunds (2006) reported similar observations from reefs elsewhere in the Caribbean (see also Chiappone et al. 2001, Miller et al. 2003, Macintyre et al. 2005, Weil et al. 2005, Debrot and Nagelkerken 2006, Steiner and Williams 2006, Noriega et al. 2006, Myhre and Acevedo-Gutiérrez 2007, Jordán-Garza et al. 2008, Blanco et al. 2010, Ruiz-Ramos et al. 2011, Bodmer et al. 2015).

To evaluate Jackson's (1997) assertion that *D. antillarum* were historically abundant on at least some Caribbean reefs, Precht and Aronson (2006) took a paleobiological approach and used diadematid test and spine fragments found in sediment core samples that had been collected from the shallow fore-reef at Discovery Bay (taken prior to 1983),

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and compared these to the abundance of the same constituents found in bulk rock samples taken from the equivalent biofacies in the Pleistocene age fossil reef outcrop of the Falmouth Formation at Rio Bueno, Jamaica. These samples, separated by ~125,000 years, revealed a remarkable fidelity in the abundance of urchin fragments (see also Gordon and Donovan 1992, Donovan and Gordon 1993, Gordon 2005). Precht and Aronson (2006) stated "*If we take these comparative data at face value, it appears that* Diadema *was always an important herbivore on Jamaican reefs*."

Possibly the most convincing scientific evidence that *D. antillarum* were the most important reef herbivore for millennia comes from mitochondrial DNA samples. Lessios et al. (2001) performed genetic analysis of *D. antillarum* populations from throughout the region to determine population size through time. Based upon a variety of mutation and coalescence algorithms they determined that *D. antillarum* attained a population density similar to the pre-1983 population sometime during the Pleistocene epoch, long before humans could have influenced ecological processes. Interestingly, the Precht and Aronson (2006) data from Jamaica appear to confirm the Lessios et al (2001) algorithms.

To test whether the spread of the 1983-1984 *Diadema* disease epizootic was due to their overcrowded conditions as a result of overfishing (*sensu* Jackson et al. 2001), we looked at the characteristics of the population structure of *Diadema* at the time of the mortality event. Firstly, the disease was initially observed in Punta Galeta, Panama in January 1983 where pre-mortality *Diadema* populations were measured at 1.38/m^2 (Lessios et al. 1984a). This population density for *Diadema* is low when compared to the pre-mortality baseline averages for the Caribbean (~ 4/m^2) and far below the "crowded" conditions

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described by some authors (40/m^2). Secondly, the vast ocean distances between reef areas throughout the Caribbean containing *Diadema* argues against density-dependent transmission. Lastly, the mass mortality of remote, isolated, and relatively sparse populations such as those at the Flower Garden Banks in the Gulf of Mexico are more parsimoniously explained by density-independent processes (Precht and Aronson 2006). Thus, overcrowding *per se* is an unlikely explanation for the cause and/or spread of this pandemic.

Finally, prior to its demise in 1983-1984, *D. antillarum* competed strongly with other herbivores and where abundant, *Diadema* negatively affected population densities of herbivorous fishes, although there was no evidence of a converse effect (Hay and Taylor 1985; Carpenter 1988, 1990b; Morrison 1988; Robertson 1991). Thus, the preponderance of ecological and paleoecological evidence strongly implies that herbivorous fish are ecologically redundant to the keystone herbivore, *D. antillarum* (see Carpenter 1986), and not the other way around (argument proffered by Hay 1984a, 1984b, and affirmed in Hughes 1994, Jackson 2001, and Bellwood et al. 2004) on shallow Caribbean reefs. As Sandin and McNamara (2011) recently noted "*spatially constrained herbivory (as by sea urchins) is more effective than spatially unconstrained herbivory (as by many fish) at opening space for the time needed for corals to settle and to recruit to the adult population.*" Similarly, Furman and Heck (2009) stated "Diadema *grazing is integral to the maintenance of low-biomass high-turnover algal turfs and prostrate coralline algal crusts that characterize healthy reef systems.*"

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Recovery?

When we look at the fact that 93-98% of *D. antillarum* Caribbean-wide were lost in the 1983-1984 epizootic, we need to ask; how long should the recovery from the mass mortality event take?   Lessios et al. (1984b) predicted that because there were no unaffected populations in the region, the recolonization of depleted areas would be significantly delayed.   Thus, it should not be surprising that while certain areas of the Caribbean have exhibited local increases in *Diadema* population densities, the region as a whole has yet to show signs of recovery approaching historical densities (Alvarado et al. 2004, Hughes et al. 2010, Beck et al. 2014, Levetan et al. 2014, Rodríguez-Barreras et al. 2015, Lessios 2016). This is especially true in the Florida Keys where populations remain depressed (Forcucci 1994, Chiappone et al. 2002a, 2002b, 2010, Lazar et al. 2005, Miller et al. 2009, Kintzing and Butler 2014, Kissling et al. 2014; Figures 8 & 9).
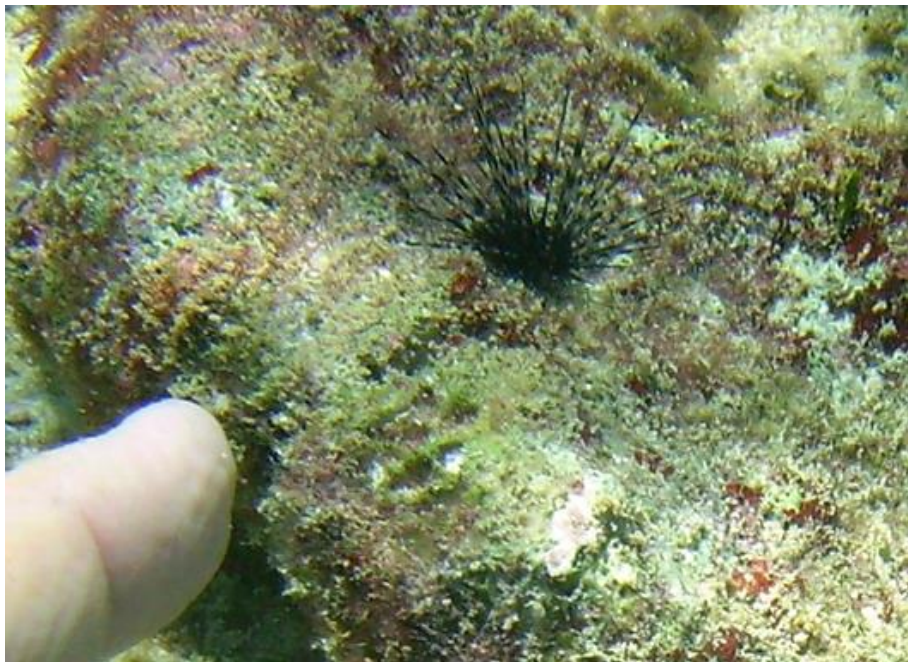
Figure 8. *Diadema* recruit found in back-reef rubble zone at Key Largo Dry Rocks in 2010. High levels of recruits in this zone have not translated to increases in *Diadema* populations on the adjacent reefs. It is unknown whether these recruits are lost to predation, physical disturbance or both.

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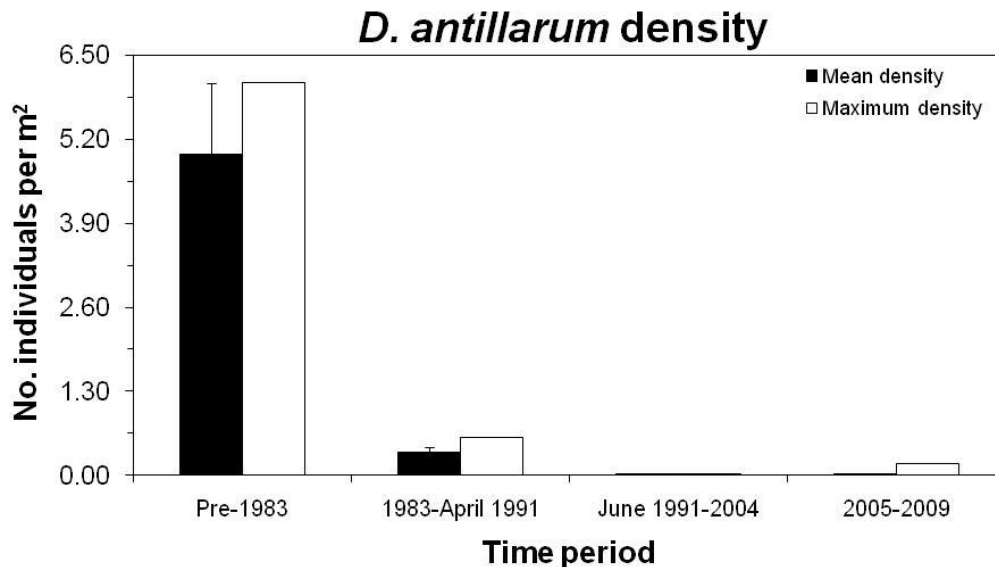
Figure 9. Population densities of *D. antillarum* in the Florida Keys through time. Data compiled from a number of sources including: Randall et al. (1964), Kier and Grant (1965), Bauer (1980), Chiappone et al. (2002a, 2002b, 2010). Modified from original in Kissling et al. (2014).

While a density-dependent relationship was not responsible for the demise of this once plentiful urchin, recovering populations may require positive density-dependent feedbacks that contribute to population increases (Miller et al. 2007, Rogers and Lorenzen 2008, but see Levitan et al. 2014). Further monitoring is required to determine whether the urchin recovery will continue to expand in places where it has already begun, and whether urchin densities will increase regionally, throughout the Caribbean.

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Summary and the Future

Two hypotheses have been developed for describing the role and importance of the sea urchin *Diadema antillarum* on reefs of the Caribbean region. The most important is whether *D. antillarum* was <u>the</u> most important "keystone" grazer on Caribbean reefs? The alternate to this hypothesis is that *D. antillarum* was merely a redundant species. To resolve this debate, the question: "*What is the role of* Diadema antillarum *in altering the composition of the benthic community on Caribbean coral reefs in time and space?*" was evaluated through a review and analyses of the published literature.

While it was impossible to fully predict the catastrophic-scale disturbance caused by the regional ecological extirpation of *D. antillarum,* manipulative experiments performed prior to 1983 allowed reef scientists to predict *a priori* the response of the benthos to relative changes in herbivory that followed, especially the loss and/or addition of *D. antillarum* in space and time (Sammarco 1982a, 1982b). Given that this regional disturbance did occur, the increase in macroalgae that followed the loss of *D. antillarum* and the subsequent reduction of macroalgae following the local recovery of *D. antillarum,* clearly highlights the predictive value of ecological experimentation in solving important conservation problems (Dudgeon et al.2010; see Figure 10).

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Figure 10. Photo in upper panel shows extensive growth of the chemically defended macroalga, *Bathophora oerstedii* on a submerged sheet-metal bulkhead, Turks and Caicos Islands. Herbivorous fish, especially juvenile parrotfish species were abundant at this location. Upper limit of algae growth is lower-limit of spring-low tide. Photo in lower panel shows the near complete removal of *Bathophora* in an area grazed by a single *D. antillarum* specimen within 48 hours of its introduction to the base of the bulkhead. Introduced *Diadema* was collected from nearby seagrass bed. Photos by WF Precht (November 2014).

Because of the strong relative influence of *Diadema* on limiting macroalgae and

enhancing coral recruitment (Sammarco 1980, 1982a, 1982b, Carpenter 1988, Carpenter

and Edmunds 2006, Precht and Aronson 2006; Idjadi et al. 2006, 2010, Rogers 2011,

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Sandin and McNamara 2011, Davies et al. 2013, Lessios 2016), restoration of this keystone herbivore could serve as an important tool for local reef conservation and management, especially on reefs that are overfished (Moe 2003, Aronson and Precht 2006, Halpern et al. 2007, Rogers and Lorenzen 2008, see also Simberloff 2008). This conservation tool is still in its infancy, and early demonstration projects have met with mixed results (Chiappone et al. 2003, Nedimyer and Moe 2003, Miller and Szmant 2006, Macia et al. 2007, Burdick 2008). However, this tool could be among our best options for implementing a rapid and effective increase in herbivory that facilitates coral recruitment, survival, and growth, especially when employed with other conservation measures (Aronson and Precht 2006, Serefy et al. 2013).

The ecological role of herbivores on Caribbean reefs is complex (Sandin and McNamara 2011, Adam et al. 2015). However, contrary to recent press-releases, opinion pieces and editorials (Aldred 2014, Elizabeth 2014, IUCN 2014, Jackson and Elizabeth-Johnson 2014), it appears that enhancing (and restoring) *Diadema* populations may be far more important to conserving Caribbean coral reefs for future generations than parrotfish. Evidence is rapidly mounting, that overfishing is not the major threat to benthic assemblages on coral reefs, nor is the recovery of parrotfish the solution (Russ et al. 2015). If that were the case, reefs in the Florida Keys should have experienced considerably less coral loss, and faster recovery than that reported for the rest of the Caribbean region because reefs of the Florida Keys have maintained relatively high populations of herbivorous fishes (Bohnsack et al. 1994, Alevizon and Porter 2014). Coral loss in Florida, however, was significantly greater than the Caribbean average

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throughout this period (Schutte et al. 2010), while coral recruit survival and reef recovery have been limited (Toth et al. 2014, van Woesik et al. 2014). At the other end of the spectrum, the high coral cover reefs of Bonaire and Curaçao, coral cover was not correlated with the biomass of any fish groups, failing to provide a clear link between fish activities (e.g., herbivory) and the health and persistence of corals (Sandin et al. 2007). Thus, protecting fish stocks through networks of Marine Protected Areas does not necessarily reduce the cover of macroalgae, increase coral populations, reverse coral/macroalgal phase shifts, or preserve or increase the topographic complexity that is critical to maintaining and increasing coral reef resilience (Idjadi et al. 2006, Kramer and Heck 2007, Sandin et al. 2007, Alvarez-Filip et al. 2009, Selig and Bruno 2010, Alvarez-Filip et al. 2011, Huntington et al. 2011, Reyes-Bonilla et al. 2014, Toth et al. 2014).

We anticipate that as *Diadema* populations continue to increase slowly across the region, so will the number of phase-shift reversals. Early evaluations suggest, however, that reversing phase shifts will also depend on successfully reducing the causative stressors causing coral mortality (Aronson and Precht 2006, Dudgeon et al. 2010) and having sufficient rates of activity by functional groups that play key roles in reversing the changes (Figure 11). Devising restoration and management programs that enhance or restore critical components of the ecosystem that reduce macroalgae and promote the success of corals should foster resilience and accelerate recovery, at least locally (Precht and Aronson 2006, Furman and Heck 2009, Idjadi et al. 2010, Edwards et al. 2011, Sandin and McNamara 2012).

Figure 11. Comparison of recent reef states. Photo in upper panel shows generally low coral cover, high cover of turf algae, and suppressed coral recruitment at Carysfort Reef in the northernmost portions of the Florida Keys National Marine Sanctuary. This reef has high parrotfish densities and extremely low populations of *Diadema antillarum*. Photo in lower panel shows similar habitat on Dancing Lady Reef at Discovery Bay, Jamaica. Note abundant coral recruitment and lack of algal turfs. Here parrotfish populations are extremely low while *Diadema* populations are high (see Idjadi et al. 2010). Photo panel courtesy of Dr. Phil Dustan.

Contrary to the view of Jackson et al. (2001; Jackson 2014, Bonaldo et al. 2014),

overfishing of parrotfish is not the major threat to benthic assemblages on coral reefs. It is

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precisely because *D. antillarum* was and is the most important shallow-water herbivore on Caribbean coral reefs (Figure 11), that the continued and future recovery of this sea urchin may ultimately be the key ingredient to facilitating coral reef recovery throughout the region.

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