

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 herbivorous 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.

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 (4) individuals per square meter in shallow reef environments and in some areas as many as 40 individuals per square meter 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, courtesy of Dr. Sal Genovese.

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

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?*” 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.

Background -- Biology of *Diadema*

Diadema antillarum Philippi (Echinodermata: Echinoidea) is a herbivorous species of sea urchin that is found throughout the Caribbean and tropical regions of the Western 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).

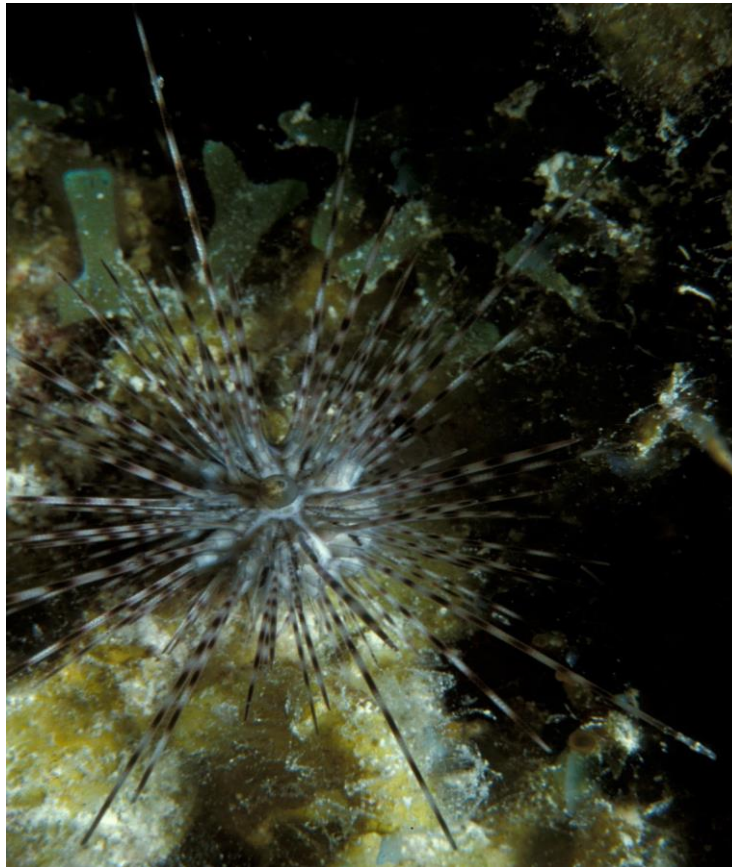


Figure 2. *Diadema antillarum* grazing on abundant macroalgae (*Dictyota* spp.), San Salvador Island, Bahamas in 1980. Photo by WF Precht.

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

and Carpenter 1987). Bruno (2010) cleverly described *D. antillarum* as “basically a pin cushion with black hypodermic needles for spines” (Figure 3).

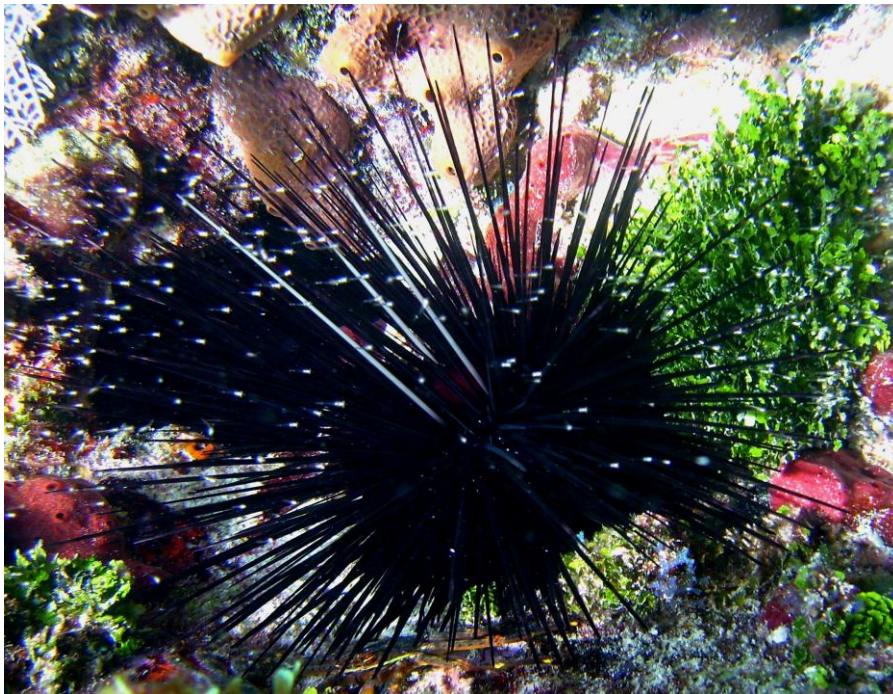


Figure 3. Adult specimen of *Diadema antillarum*. Note the abundance of mysid shrimp swimming amongst the spines. Photo taken on a patch reef off north Key Largo within the Florida Keys National Marine Sanctuary in 2009. Photo by WF Precht.

D. antillarum can be 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 highly 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). 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). Also, when found in significant numbers these urchins are known to graze on coral spat as well as other benthic invertebrates (Bak and van Eys 1975, Sammarco 1980). 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).

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. 1984). 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. 1984), 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).

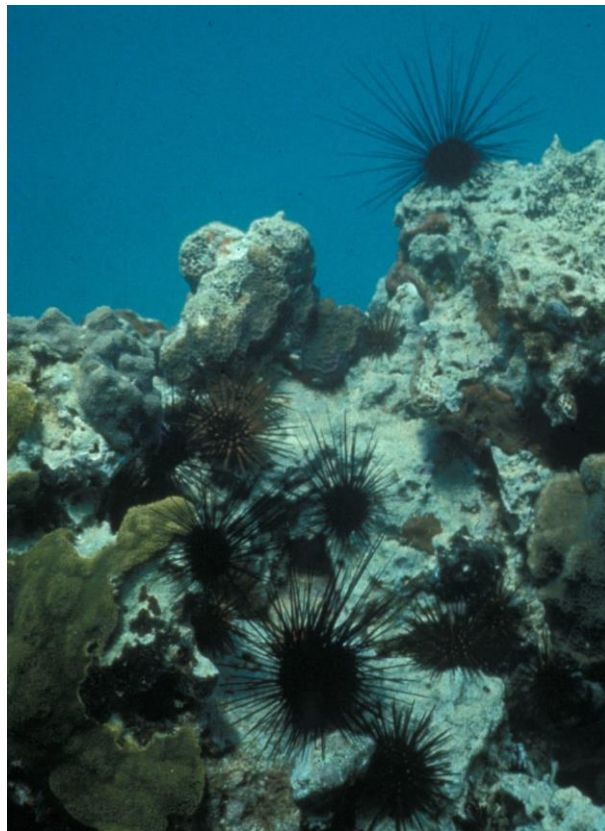


Figure 4. Photo of high concentration of *D. antillarum* on a patch reef at Discovery Bay Jamaica in 1978. Note lack of macroalgae and significant bioerosion. Photo by WF Precht.

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).

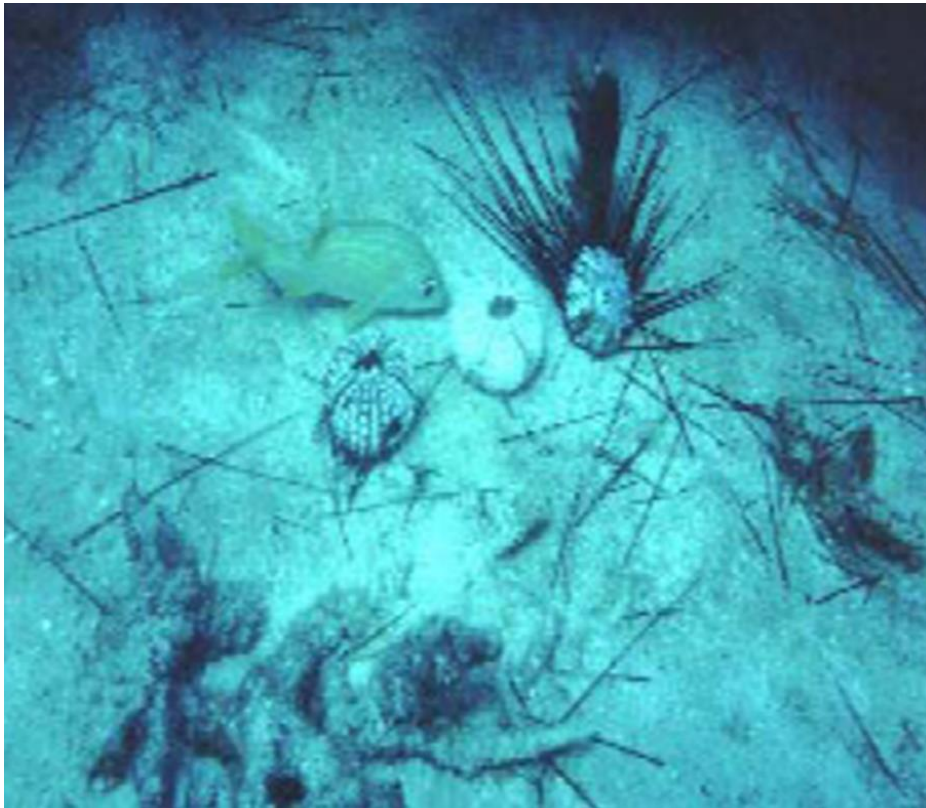


Figure 5. Photo of dead and disarticulated *Diadema* tests and spines from the Florida Keys in July 1983. Photo courtesy of Dr. Billy Causey, Florida Keys National Marine Sanctuary.

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). 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 three decades (Karlson and Levitan 1990, Hughes et al. 2010; Levitan et al. 2014, Rodríguez-Barreras et al. 2015). 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 are those reefs with the lowest fish populations, including invertivores that consume *Diadema* (Harbone et al. 2009, Rogers 2011; Figure 6).



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.

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* prediction.

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 system to a macroalgal-dominated system (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 (Glynn 1990, Carpenter 1997, McClanahan and Muthiga 2007). As previously mentioned, however, considerable debate has arisen since the demise of these once plentiful grazers as to how vital a role they played in the structuring of coral reef communities. The most crucial of these is whether *D. antillarum* was the “keystone” grazer on Caribbean reefs?

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 herbivorous 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

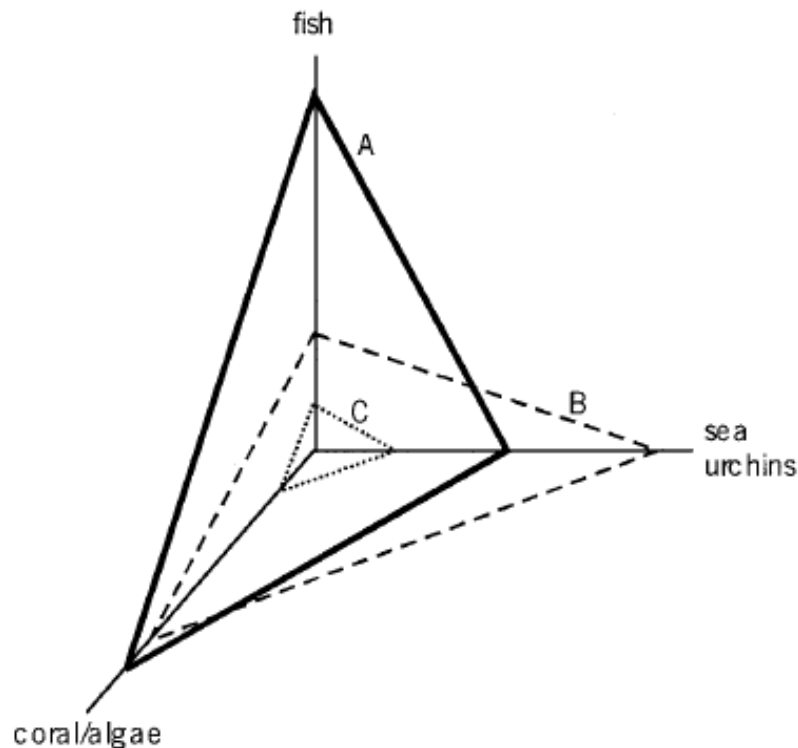


Figure 7. Tripartite model visualizing the role of herbivorous fish, *Diadema*, corals and macroalgae following Hay (1984a, 1984b). Triangle A (solid-line), represents the “pristine” condition, with high ratio of corals to macroalgae because of intense grazing of macroalgae by fishes. Triangle B (dashed-line), 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, 2001).

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. 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 high coral cover and low macroalgal cover).

Bellwood *et al.* (2004) argued that Jamaican reefs as originally described had been overfished 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). Although 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).

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 explaining the superabundance of *Diadema* at locations across the Caribbean. 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 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 may have been 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; 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), and compared these to the abundance of the same constituents found in bulk rock samples taken from the equivalent lithofacies 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.

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.*”

To date, while certain areas of the Caribbean have exhibited increases in *Diadema* population densities, the region as a whole has yet to show signs of recovery approaching historical densities (Hughes et al. 2010; 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 9 & 10). 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.



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.

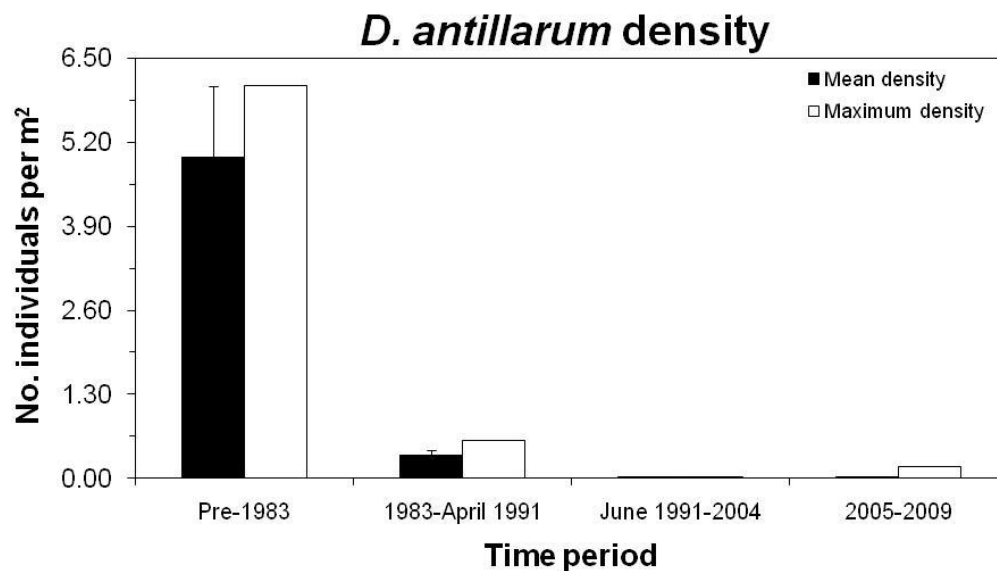


Figure 9. Population densities of *D. antillarum* in the Florida Keys through time. Data compiled from a number of sources including: Randall et al. (1964), Kier and Grant (1965), Bauer (1980), Chiappone et al. (2002a, 2002b, 2010). Modified from original in Kissling et al. (2014).

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 the 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. 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).

Because of the strong relative influence of *Diadema* on limiting macroalgae and enhancing coral recruitment (Sammarco 1980, 1982, Carpenter 1988, Carpenter and Edmunds 2006, Precht and Aronson 2006; Idjadi et al. 2006, 2010, Sandin and McNamara 2011, 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). 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. 2005). 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 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 does not necessarily reduce the cover of macroalgae, increase coral populations, or preserve or increase the topographic complexity that is critical to maintaining and increasing those fish stocks (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 (but see Levitan et al. 2014). 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 10). 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 10. Comparison of recent reef states. 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*. 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 precisely because *D. antillarum* was and is the most important shallow-water herbivore

on Caribbean coral reefs, that the continued and future recovery of this sea urchin may ultimately be the key ingredients to facilitating coral reef recovery throughout the region.

References Cited

- Adam, TC, Burkepile DE, Ruttenberg BI, Paddock MJ. 2015. Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Marine Ecology Progress Series* 520 (2015): 1-20.
- Aldred J. 2014. Caribbean coral reefs ‘will be lost within 20 years’ without protection. The Guardian <http://www.theguardian.com/environment/2014/jul/02/caribbean-coral-reef-lost-fishing-pollution-report>
- Alevizon WS, Porter JW. 2014. Coral loss and fish guild stability on a Caribbean coral reef: 1974–2000. *Environmental Biology Fisheries* 1-11. DOI 10.1007/s10641-014-0337-5.
- Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings Royal Society London B* 276:3019–3025.
- Alvarez-Filip L, Gill JA, Dulvy NK, Perry AL, Watkinson AR, Côté IM. 2011. Drivers of region-wide declines in architectural complexity on Caribbean reefs. *Coral Reefs* 30:1051–1060.
- Aronson RB. 1990. Onshore–offshore patterns of human fishing activity. *Palaios* 5:88–93.
- Aronson RB, Precht WF. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnology Oceanography* 45:251-255.

- Aronson RB, Precht WF. 2001. Evolutionary paleoecology of Caribbean coral reefs. In: Allmon WD, Bottjer DJ (eds) Evolutionary paleoecology: the ecological context of macroevolutionary change. Columbia University Press, New York, pp 171–233.
- Aronson RB, Precht WF. 2006. Conservation, precaution, and Caribbean reefs. *Coral Reefs* 25:441–450.
- Bauer JC. 1976. Growth, aggregation, and maturation in the echinoid, *Diadema antillarum*. *Bulletin Marine Science* 26: 273-277.
- Bauer JC. 1980. Observations on geographic variations in population density of the echinoid *Diadema antillarum* within the western north Atlantic. *Bulletin Marine Science* 30: 509-515.
- Bauer JC. 1982. On the growth of a laboratory-reared sea urchin, *Diadema antillarum* (Echinodermata: Echinoidea). *Bulletin Marine Science* 32: 643-645.
- Bauer JC, Agerter CJ. 1987. Isolation of bacteria pathogenic for the sea urchin *Diadema antillarum* (Echinodermata: Echinoidea). *Bulletin Marine Science* 40:161-165.
- Bak RPM. 1994. Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables. *Coral Reefs* 13:99-103.
- Bak RPM, van Eys G. 1975. Predation by the urchin *Diadema antillarum* Philippi on living coral. *Oecologia* 20:111–115.
- Bak RPM, Carpay MJE, de Ruyter van Steveninck ED. 1984. Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao. *Marine Ecology Progress Series* 17:105-108.

- Bechtel JD, Gayle P, Kaufman K. 2006. The return of *Diadema antillarum* to Discovery Bay: patterns of distribution and abundance. *Proceedings 10th International Coral Reef Symposium, Okinawa* 1:367–375.
- Beck G, Miller R, Ebersole J. 2014. Mass mortality and slow recovery of *Diadema antillarum*: Could compromised immunity be a factor? *Marine Biology* 161:1001-1013.
- Bellwood DR, Hughes TP, Folke C, Nyström M. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Blanco FM, Clero Alonso L, González Sansón G, Pina Amargós F. 2011. Influence of *Diadema antillarum* populations (Echinodermata: Diadematidae) on algal community structure in Jardines de la Reina, Cuba. *Revista de Biología Tropical* 59:1149-1163.
- Blanco FM, González Sansón G, Pina Amargós F, Clero Alonso L. 2010. Abundance, distribution and size structure of *Diadema antillarum* (Echinodermata: Diadematidae) in South Eastern Cuban coral reefs. *Revista de Biología Tropical* 58:663-676.
- Bodmer MD, Rogers AD, Speight MR, Lubbock N, Exton DA. 2015. Using an isolated population boom to explore barriers to recovery in the keystone Caribbean coral reef herbivore *Diadema antillarum*. *Coral Reefs* 34:1011-1021.
- Bonaldo RM, Hoey AS, Bellwood DR. 2014. The ecosystem roles of parrotfishes on tropical reefs. *Annual Review Oceanography Marine Biology* 52:81-132.
- Bruno JF, 2010. What would eat a spiny urchin? <http://www.climateshifts.org/?p=4188>
- Bruno JF, Precht WF, Vroom PS, Aronson RB. 2014. Coral reef baselines: how much macroalgae is natural? *Marine Pollution Bulletin* 80:24-29.

- Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484.
- Burdick DR. 2008. The effectiveness of macroalgal reduction and *Diadema antillarum* addition in limiting macroalgal growth and facilitating coral recovery. *Proceedings of 11th International Coral Reef Symposium*, Ft Lauderdale, Florida
- Carpenter RC. 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *Journal Marine Research* 39:749–765.
- Carpenter RC. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* 56:345–363.
- Carpenter RC. 1988. Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. *Proceedings National Academy Science USA* 85:511–514.
- Carpenter RC. 1990a. Mass mortality of *Diadema antillarum*. 1. Long term effects on sea urchin population-dynamics and coral reef algal communities. *Marine Biology* 104:67–77.
- Carpenter RC. 1990b. Mass mortality of *Diadema antillarum*. II. Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. *Marine Biology* 104:79–86.
- Carpenter RC. 1997. Invertebrate predators and grazers. In *Life and Death of Coral Reefs*, Birkeland C (ed) pp. 198–229. New York: Chapman and Hall.
- Carpenter RC, Edmunds PJ. 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. *Ecology Letters* 9:271–280.

- Chiappone M, Swanson D, Miller S. 2003. One-year response of Florida Keys patch reef communities to translocation of long-spined sea urchins (*Diadema antillarum*). Report to Florida Keys National Marine Sanctuary. NOAA Office of National Marine Sanctuaries, Marine Sanctuaries Conservation Series NMSP-06-12, pp 301-326.
- Chiappone M, Miller SL, Swanson DW, Ault JS, Smith SG. 2001. Comparatively high densities of the long-spined sea urchin in the Dry Tortugas, Florida. *Coral Reefs* 20:137–138.
- Chiappone M, Rutten LM, Swanson DW, Miller SL. 2010. Population status of the urchin *Diadema antillarum* in the Florida Keys 25 years after the Caribbean mass mortality. *Proceedings of the 11th International Coral Reef Symposium*, Ft. Lauderdale, Florida pp 706-710.
- Chiappone M, Swanson DW, Miller SL. 2002a. Density, spatial distribution and size structure of urchins in Florida Keys coral reef and hard-bottom habitats. *Marine Ecology Progress Series* 235:117–126.
- Chiappone M, Swanson DW, Miller SL, Smith SG. 2002b. Large-scale surveys on the Florida reef tract indicates poor recovery of the long-spined sea urchin *Diadema antillarum*. *Coral Reefs* 21:155–159.
- Cho LL, Woodley JD. 2002. Recovery of reefs at Discovery Bay, Jamaica and the role of *Diadema antillarum*. *Proceedings 9th International Coral Reef Symposium*, Bali 1:331–338.
- Côté IM, Precht WF, Aronson RB, Gardner TA. 2013. Is Jamaica a good model for understanding Caribbean coral reef dynamics? *Marine Pollution Bulletin* 76:28-31

- Crabbe MJC. 2009. Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica. *Marine Environmental Research* 67:189–198.
- Debrot AO, Nagelkerken I. 2006. Recovery of the long-spined sea urchin *Diadema antillarum* in Curaçao (Netherlands Antilles) linked to lagoonal and wave sheltered shallow rocky habitats. *Bulletin Marine Science* 79:415–424.
- de Ruyter van Steveninck, ED, Bak RPM. 1986. Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. *Marine Ecology Progress Series* 34:87–94.
- Donovan SK. 2005. The fossil record of *Diadema* in the Caribbean. *Coral Reefs* 24:603–605.
- Donovan, SK, Gordon CM. 1993. Echinoid taphonomy and the fossil record: supporting evidence from the Plio-Pleistocene of the Caribbean. *Palaios* 8:304–306.
- Dudgeon SR, Aronson RB, Bruno JF, Precht WF. 2010. Phase shifts and stable states on coral reefs. *Marine Ecology Progress Series* 413:201–216.
- Edmunds PJ, Carpenter RC. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings National Academy Science USA* 98:5067–5071.
- Elizabeth A. 2014. To Save Coral Reefs, Start With Parrotfish.
<http://voices.nationalgeographic.com/2014/07/02/to-save-coral-reefs-start-with-parrotfish/>
- Forcucci D. 1994. Population, density and recruitment and 1991 mortality event of *Diadema antillarum* in the Florida Keys. *Bulletin Marine Science* 54:917–928.

- Furman B, Heck KL. 2009. Differential impacts of echinoid grazers on coral recruitment. *Bulletin Marine Science* 85:121-132.
- Glynn P. 1990. Feeding ecology of selected coral-reef macroconsumers: patterns and effects on coral community structure. In *Ecosystems of the World*, vol. 25, *Coral Reefs*, Dubinsky Z (ed) pp. 365–400. Amsterdam: Elsevier.
- Gordon CM, Donovan SK. 1992. Disarticulated echinoid ossicles in paleoecology and taphonomy: the last interglacial Falmouth Formation of Jamaica. *Palaios* 7:157–166.
- Halpern BS, Silliman BR, Olden JD, Bruno JP, Bertness MD. 2007. Incorporating positive interactions in aquatic restoration and conservation. *Frontiers Ecology Environment* 5:153–160.
- Harborne AR, Renaud PG, Tyler EHM, Mumby PJ. 2009. Reduced density of the herbivorous urchin *Diadema antillarum* inside a Caribbean marine reserve linked to increased predation pressure by fishes. *Coral Reefs* 28:783-791.
- Hay ME. 1984a. Patterns of fish and urchin grazing on Caribbean coral reefs: Are previous results typical? *Ecology* 65:446-454.
- Hay ME. 1984b. Coral reef ecology: have we been putting all of our herbivores in one basket? *BioScience* 34(5):323-324.
- Hay ME, Taylor PR. 1985. Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia* 65:591-598.
- Hughes TP. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.

- Hughes TP, GrahamNAJ, Jackson JBC, Mumby PJ, Steneck RS. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends Ecology Environment* 25:633-642.
- Hughes TP, Keller BD, Jackson JBC, Boyle MJ. 1985. Mass mortality of the echinoid *Diadema antillarum* Philippi in Jamaica. *Bulletin Marine Science* 36:377-384.
- Hughes TP, Reed DC, Boyle MJ. 1987. Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *Journal Experimental Marine Biology Ecology* 113:39-59.
- Hunte W, Cote I, Tomascik T. 1986. On the dynamics of the mass mortality of *Diadema antillarum* in Barbados. *Coral Reefs* 4:135-139.
- Hunte W, Younglao D. 1988. Recruitment and population recovery of *Diadema antillarum* (Echinodermata; Echinoidea) in Barbados. *Marine Ecology Progress Series* 45:109-119.
- Hunter IG. 1977. Sediment production by *Diadema antillarum* on a Barbados fringing reef. *Proceedings 3rd International Coral Reef Symposium, Miami* 2:105-109.
- Huntington BE, Karnauskas M, Lirman D. 2011. Corals fail to recover at a Caribbean marine reserve despite ten years of reserve designation. *Coral Reefs* 30:1077-1085.
- Idjadi JA, Haring RN, Precht WF. 2010. Recovery of the sea urchin *Diadema antillarum* promotes scleractinian coral growth and survivorship on shallow Jamaican reefs. *Marine Ecology Progress Series* 403:91-100.
- Idjadi JA, Lee SC, Bruno JF, Precht WF, Allen-Requa L, Edmunds PJ. 2006. Rapid phase-shift reversal on a Jamaican coral reef. *Coral Reefs* 25:209-211.

- International Union Conservation Nature, IUCN. 2014. From despair to repair: Dramatic decline of Caribbean corals can be reversed. <http://www.iucn.org/?16050/1/From-despair-to-repair-Dramatic-decline-of-Caribbean-corals-can-be-reversed>
- Jackson JBC. 1994. Community unity? *Science* 264:1412–13.
- Jackson JBC. 1997. Reefs since Columbus. *Coral Reefs* 16:S23–S32.
- Jackson JBC. 2001. What was natural in the coastal oceans? *Proceedings National Academy Sciences USA* 98:5411–5418.
- Jackson JBC. 2014. Executive Summary. In: Jackson JBC, Donovan MK, Cramer KL, Lam VV (eds) Status and Trends of Caribbean Coral Reefs:1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.
- Jackson JBCJ, Elizabeth Johnson A. 2014. We Can Save the Caribbean’s Coral Reefs. NY Times – The Opinion Pages Sept.18, 2014. http://www.nytimes.com/2014/09/18/opinion/we-can-save-coral-reefs.html?_r=0
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629-638.
- Jordán-Garza AG, Rodríguez-Martínez RE, Maldonado, Baker DM. 2008. High abundance of *Diadema antillarum* on a Mexican reef. *Coral Reefs* 27:295.
- Karlson RH, Levitan DR. 1990. Recruitment-limitation in open populations of *Diadema antillarum*: an evaluation. *Oecologia* 82:40–44.
- Kier PM, Grant RE. 1965. Echinoid distribution and habits, Key Largo Coral Reef Preserve, Florida. *Smithsonian Miscellaneous Collections* 149:1-68.

- Kintzing MD, Butler MJ. 2014. Effects of predation upon the long-spined sea urchin *Diadema antillarum* by the spotted spiny lobster *Panulirus guttatus*. *Marine Ecology Progress Series* 495:185-191.
- Kissling DL, Precht WF, Miller SL, Chiappone M. 2014. Historical reconstruction of population density of the echinoid *Diadema antillarum* on Florida Keys shallow bank-barrier reefs. *Bulletin Marine Science* 90:665-679.
- Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32:674–682.
- Knowlton N. 2001. Sea urchin recovery from mass mortality: new hope for Caribbean coral reefs? *Proceedings National Academy Science USA* 98:4822–4824.
- Knowlton N. 2004. Multiple ‘stable’ states and the conservation of marine ecosystems. *Progress Oceanography* 60:387–396.
- Lazar KE, Vaughan D, Grober-Dunsmore R, Bonito V. 2005. Relatively low densities of *Diadema antillarum* on the Florida reef tract do not indicate population recovery. *Proceedings Gulf Caribbean Fish Institute* 56:837-838.
- Lee SC. 2006. Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. *Oikos* 112:442-447.
- Lessios HA. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annual Review Ecology Systematics* 19:371–93.
- Lessios HA. 2016. The great *Diadema antillarum* die-off: 30 years later. *Annual Review Marine Science* 8:1.1–1.17.

Lessios HA, Cubit JD, Robertson DR, Shulman MJ, Parker MR, Garrity SD, Levings SC.

1984a. Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama.

Coral Reefs 3:173–182.

Lessios HA, Garrido MJ, Kessing BD. 2001. Demographic history of *Diadema*

antillarum, a keystone herbivore on Caribbean reefs. *Proceedings Royal Society*

London B 268:2347–2353.

Lessios HA, Robertson DR, Cubit JD. 1984b. Spread of *Diadema* mass mortality through

the Caribbean. *Science* 226:335–337.

Levitan DR. 1988a. Algal–urchin biomass responses following mass mortality of

Diadema antillarum Philippi at Saint John, US Virgin Islands. *Journal Experimental*

Marine Biology Ecology 119:167–178.

Levitan DR. 1988b. Asynchronous spawning and aggregative behavior in the sea urchin

Diadema antillarum (Philippi), p.181–186. In: Burke et al. (eds) *Echinoderm Biology*,

Balkema, Rotterdam.

Levitan, DR. 1991a. Influence of body size and population density on fertilization

success and reproductive output in a free-spawning invertebrate. *Biological Bulletin*

181:261–268.

Levitan DR. 1991b. Skeletal changes in the test and jaws of the sea urchin *Diadema*

antillarum in response to food limitation. *Marine Biology* 111:431–435.

Levitan DR. 1992. Community structure in times past: influence of human fishing

pressure on algal–urchin interactions. *Ecology* 73:597–605.

- Levitan DR, Edmunds PJ, Levitan KE. 2014. What makes a species common? No evidence of density-dependent recruitment or mortality of the sea urchin *Diadema antillarum* after the 1983–1984 mass mortality. *Oecologia* 175:117-128.
- Lewis JB. 1964. Feeding and digestion in the tropical sea urchin *Diadema antillarum* Philippi. *Canadian Journal Zoology* 42:549-557.
- Lewis JB. 1966. Growth and breeding in the tropical echinoid *Diadema antillarum* Philippi. *Bulletin Marine Science* 16:151-158.
- Lewis SM. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* 56:183–200.
- Lewis SM, Wainwright PC. 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. *Journal Experimental Marine Biology Ecology* 87:215–228.
- Liddell WD, Ohlhorst SL. 1986. Changes in benthic community composition following the mass mortality of *Diadema antillarum*. *Journal Experimental Marine Biology Ecology* 95:271–278.
- Macia S, Robinson MP, Nalevanko A. 2007. Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a coral reef. *Marine Ecology Progress Series* 348:173–182.
- Macintyre IG, Glynn PW, Hinds F. 2005. Evidence of the role of *Diadema antillarum* in the promotion of coral settlement and survivorship. *Coral Reefs* 24:273.
- McClanahan TR, Muthiga NA. 2007. Ecology of *Echinometra*, In: Chapter 15 *Developments in Aquaculture and Fisheries Science*, 37:297-317.
- Miller MW, Kramer KL, Williams SM, Johnston L, Szmant AM. 2009. Assessment of current rates of *Diadema antillarum* larval settlement. *Coral Reefs* 28:511-515.

- Miller MW, Szmant AM. 2006. Lessons learned from experimental key-species restoration. In: Precht WF (ed) Coral Reef Restoration Handbook. The Rehabilitation of an Ecosystem Under Siege. CRC Press, Boca Raton, FL.
- Miller RJ, Adams AJ, Ogden NB, Ogden JC, Ebersole JP. 2003. *Diadema antillarum* 17 years after mass mortality: Is recovery beginning on St. Croix? *Coral Reefs* 22:181–187.
- Moe Jr M. 2003. Coral reef restoration: returning the caretakers to the reef. *SeaScope* 20:1-4.
- Morrison D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* 69:1367–1382.
- Mumby PJ, Hedley JD, Zychaluk K, Harborne AR, Blackwell PG. 2006. Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: fresh insights on resilience from a simulation model. *Ecological Modeling* 196:131–148.
- Muthiga NA, McClanahan TR. 2007. Ecology of *Diadema* . In: Chapter 11 *Developments in Aquaculture and Fisheries Science*, 37:205-225.
- Myhre S, Acevedo-Gutiérrez A. 2007. Recovery of sea urchin *Diadema antillarum* populations is correlated to increased coral and reduced macroalgal cover. *Marine Ecology Progress Series* 329:205–210.
- Nedimyer K, Moe Jr MA. 2003. Technique development for the reestablishment of the long-spined sea urchin, *Diadema antillarum*, on two small patch reefs in the upper Florida Keys. Report to Florida Keys National Marine Sanctuary. NOAA Office of National Marine Sanctuaries, Marine Sanctuaries Conservation Series NMSP-06-12 pp 268-300.

- Noriega N, Pauls SM, del Mónaco C. 2006. Abundancia de *Diadema antillarum* (Echinodermata: Echinoidea) en las costas de Venezuela. *Revista de Biología Tropical* 54:793-802.
- Ogden JC. 1977. Carbonate-sediment production by parrotfish and sea urchins on Caribbean reefs. In: Frost SH, Weiss MP, Saunders JB (eds) Reefs and related carbonates— ecology and sedimentology. Stud Geol 4, AAPG, Tulsa, OK, p 281–288.
- Ogden JC, Brown RA, Salesky N. 1973. Grazing by the echinoid *Diadema antiIlarum* Philippi: formation of halos around West Indian patch reefs. *Science* 182:715-717.
- Ogden JC, Carpenter RC. 1987. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida) -- Long-Spined Black Sea Urchin. U.S. Fish Wild. Serv. Biol. Rep. 82(11.77). U. S. Army Corps of Engineers, TR EL-82-4. 17 pp.
- Ogden, JC, Lobel PS. 1978. The role of herbivorous fishes and sea urchins in coral reef communities. *Environmental Biology Fishes* 3:49-63.
- Paddack MJ, Cowen RK, Sponaugle S. 2006. Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* 25:461-472.
- Precht L. 2008. Effects of herbivorous sea urchins on reef algae: algal biomass responses to caging experiments. *Abstracts - Reefs for the Future*. 11th International Coral Reef Symposium, Ft. Lauderdale, FL. p.533.
- http://www.nova.edu/ncri/11icrs/11icrs_abstractbook_final.pdf

- Precht WF, Aronson RB. 2006. Death and resurrection of Caribbean coral reefs: a paleoecological perspective. In: Côté I, Reynolds J (eds) Coral reef conservation. Cambridge University Press, Cambridge, p 40–77.
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystones. *BioScience* 46:609–620.
- Quinn JF, Dunham AE. 1983. On hypothesis testing in ecology and evolution. *American Naturalist* 122:602–617.
- Randall JE, Schroeder RE, Starck WA. 1964. Notes on the biology of the echinoid *Diadema antillarum*. *Caribbean Journal Science* 4:421-433.
- Reyes-Bonilla H, Millet-Encalada M, Álvarez-Filip L. 2014. Community structure of scleractinian corals outside protected areas in Cozumel Island, Mexico. *Atoll Research Bulletin* 601:1-13.
- Reinthal PN, Kensley B, Lewis SM. 1984. Dietary shifts in the queen triggerfish, *Balistes vetula*, in the absence of its primary food item, *Diadema antillarum*. *Marine Ecology* 5:191-195.
- Robertson DR. 1991. Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. *Marine Biology* 111:437–44.
- Rodríguez-Barreras R, Pérez ME, Mercado-Molina AE, Sabat AM. 2015. Arrested recovery of *Diadema antillarum* population: Survival or recruitment limitation? *Estuarine Coastal Shelf Science* 163:167-174.

- Rogers, A. 2011. Recovery dynamics of the Caribbean long-spined sea urchin, *Diadema antillarum*. Doctoral dissertation, Imperial College London
- Rogers A, Lorenzen K. 2009. Recovery of *Diadema antillarum* and the potential of for active rebuilding measures: Modeling population dynamics. *Proceedings 11th International Coral Reef Symposium*, Ft. Lauderdale, 20:956-960.
- Ruiz-Ramos DV, Hernández-Delgado EA, Schizas NV. 2011. Population status of the long-spined urchin *Diadema antillarum* in Puerto Rico 20 years after a mass mortality event. *Bulletin Marine Science* 87:113-127.
- Russ GR, Questel SLA, Rizzari JR, Alcala AC. 2015. The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. *Marine Biology* 162:2029-2045.
- Sammarco PW. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *Journal Experimental Marine Biology Ecology* 45:245–272.
- Sammarco PW. 1982a. Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. *Journal Experimental Marine Biology Ecology* 65:83–105.
- Sammarco PW. 1982b. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. *Journal Experimental Marine Biology Ecology* 61:31–55.
- Sammarco PW, Levinton JS, Ogden JC. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): A preliminary study. *Journal Marine Research* 32:47-53.
- Sandin S, McNamara D. 2012. Spatial dynamics of benthic competition on coral reefs. *Oecologia*. 168:1079–1090.

- Sandin SA, Sampayo EM, Vermeij MJ. 2007. Coral reef fish and benthic community structure of Bonaire and Curaçao, Netherlands Antilles. *Caribbean Journal Science* 44:137-144.
- Selig ER, Bruno JF. 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. *PLoS ONE* 5:e9278. doi:10.1371/journal.pone.0009278
- Sellers AJ, Casey LO, Burge EJ, Koepfler ET. 2009. Population Growth and Distribution of *Diadema antillarum* at Discovery Bay, Jamaica. *Open Marine Biology Journal* 3:105-111.
- Simberloff D. 1998. Flagships, umbrellas, and keystones: is single species management passe' in the landscape era? *Biological Conservation* 83:247–257.
- Solandt JL, Campbell AC. 2001. Macroalgal feeding characteristics of the sea urchin *Diadema antillarum* Philippi at Discovery Bay, Jamaica. *Caribbean Journal Science* 37:227-238.
- Sommer B, Harrison PL, Brooks L, Scheffers SR. 2011. Coral community decline at Bonaire, southern Caribbean. *Bulletin Marine Science* 87:541-565.
- Steiner SCC, Williams SM. 2006. A recent increase in the abundance of the echinoid *Diadema antillarum* in Dominica (Lesser Antilles) 2001–2005. *Revista de Biología Tropical* 54:97–103.
- Uthicke S, Schaeffelke B, Byrne M. 2009. A boom-bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecological Monographs* 79:3-24.

- Vermeij MJ, Debrot AO, van der Hal N, Bakker J, Bak RP. 2010. Increased recruitment rates indicate recovering populations of the sea urchin *Diadema antillarum* on Curacao. *Bulletin Marine Science* 86:719-725.
- Weil E, Torres JL, Ashton M. 2005. Population characteristics of the sea urchin *Diadema antillarum* in La Parguera, Puerto Rico, 17 years after the mass mortality event. *Revista de Biología Tropical* 53:219–231
- Williams SM, Yoshioka PM, Sais JG. 2010. Recruitment pattern of *Diadema antillarum* in La Parguera, Puerto Rico. *Coral Reefs* 29:809-812.
- Woodley JD. 1999. Sea urchins exert top-down control on Jamaican coral reefs (1). *Coral Reefs* 18:192.
- Woodley JD, Gayle PMH, Judd N. 1999. Sea-urchins exert top-down control of macroalgae on Jamaican coral reefs (2). *Coral Reefs* 18:193-193.