The current state of populations of *Diadema antillarum* on Isla Colón in Bocas del Toro, Panamá, 25 years after mass mortality

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ABSTRACT:

In January 1983, the worst recorded die-off of any marine animal hit the Caribbean beginning near the mouth of the Panama Canal and eventually wiping out nearly 99% of one of the most important herbivores in coral reef communities, *Diadema antillarum*—the long-spined sea urchin or *Diadema*. No populations of *Diadema* in the Western Atlantic are known to have escaped the drastic population declines. The loss of *Diadema* throughout the Western Atlantic has had long-lasting impacts on the structure and composition of many types of communities including coral reefs, mangrove roots, sea grass beds, and sand flats. Though the mortality was widespread, studies of *Diadema* in Panamá have been few because of the limited information on pre-mortality community dynamics. This study investigates the current *Diadema* populations on Sunset Point and a nearby mangrove island on Isla Colón in Bocas del Toro, Panamá using simple census measurements such as test size, population density, and sex ratio as well as qualitative observations of community structure. Without knowing pre-mortality population information, it is difficult to determine how the population has changed over the last 25 years as a result of the mortality. However, this study is an attempt at establishing a baseline of population structure and ecological information of the *Diadema* in one area of Isla Colón in Bocas del Toro, Panamá.

RESUMEN EJECUTIVO:

Empezando en enero de 1983, cerca de la salida del canal de Panamá, habían unos síntomas raros en unos erizos del mar (el nombre común es erizo de espinas largas y el nombre científico es *Diadema antillarum* o solamente *Diadema*). Los erizos empezaron a perder el pigmento en la piel y en las espinas y perder la capacidad de controlar los músculos y la costumbre de esconderse durante los días, eran presas fáciles para los predadores. Los síntomas se trasladaron por todo el mar Caribe siguiendo las corrientes superficiales del agua. En trece meses, la enfermedad flotante cubrió una área de 3.5 millones de kilómetros cuadrados y mató de 85 a 100% de *Diadema* en varios sitios alrededor el Caribe. Los científicos dicen que ésta es la peor mortandad de animales marinos en toda la historia conocida del mar.

Hay muchos estudios sobre *Diadema* en el Caribe y pocas investigaciones en Panamá, las que existen son en gran parte de la costa este del Atlántico cerca de Punta Galeta en Colón y en Kuna Yala, San Blas. Pero, *Diadema*, antes de 1983, era común sobre todo el Atlántico Occidental, y para entender como han recubierto las poblaciones y como están actualmente, es importante estudiar todas las poblaciones alrededor su territorio. Desafortunadamente, no hay mucha información sobre poblaciones antes de la mortandad en muchos lugares. Entonces, la cosa más importante para hacer en el caso de las poblaciones es determinar su estado actual para ver la cantidad de erizos por metro cuadrado, los tamaños, y la proporción entre los sexos. Por eso, esta investigación estudió un área con unas poblaciones desconocidas de *Diadema*, Isla Colón en Bocas del Toro, Panamá. Esta investigación es más o menos un censo de las poblaciones en algunos sitios cerca del Instituto de Investigaciones Tropicales de Smithsonian en Isla Colón, Bocas del Toro, Panamá.

Ésta investigación utilizó tres grupos de cinco transectos en cada uno de los tres ambientes (los arrecifes corales, los pastos del mar, y los manglares) en dos sitios en total. En ésta área, la mayoría de los erizos vivían en los arrecifes, 70.9% el primero sitio, y 100% en el

segundo sitio. También, hay pocos erizos en los pastos del mar y los manglares en Sunset Point, pero en la isla de manglares no hay ningunos erizos en estos dos ambientes. En Sunset Point la cantidad de erizos en los arrecifes es 0.10 por metro cuadrado. Esto es el sitio más poblado.

Porque no hay información sobre las poblaciones anteriormente para comparar, la próxima cosa por hacer, después de determinar las poblaciones actuales, es investigar como están otras poblaciones de *Diadema* alrededor el Caribe, no solamente en Panamá, y ver la comparación entre todos los sitios y como están relacionadas las poblaciones de Bocas del Toro. Entonces, sería posible hacer algunas suposiciones generales sobre la población de Isla Colón. En el futuro es muy importante continuar con este mismo tipo de investigación en más sitios en Bocas del Toro para ver como cambian las poblaciones alrededor las islas. Después, será fácil decidir como se han desarrollado las poblaciones entre 1983 y 2008 y hacer predicciones de la recuperación en el futuro.

INTRODUCTION:

The black, long-spined sea urchin, *Diadema antillarum*, often referred to as *Diadema*, is considered by many scientists one of the keystone herbivores in marine ecosystems throughout the Western Atlantic. They can be found in habitats including rock, coral reefs, mangrove roots, sea grass beds, and sand flats throughout the Caribbean. *Diadema* are important grazers and can drastically affect the amount of algal cover, and therefore the health, of coral reefs throughout their range. However, in January 1983, peculiar symptoms were noted in many long-spined sea urchins off the coast of Colón near the exit of the Panama Canal causing large populations of *Diadema* to disappear. *Diadema* mortality spread throughout the Western Atlantic following water currents and by January 1984, an estimated 85-100% of all *Diadema* in the Caribbean had died. The loss of such a large percentage of *Diadema*, as predicted, has had profound affects on the compositions of benthic communities around the region. There have been several studies of populations around the Caribbean, but in Panamá there have been few such studies on the recovery of *Diadema*, limited mostly to the areas around Galeta Point and Kuna Yala on the eastern Atlantic coast of Panamá where populations had been coincidentally monitored before and during the mass mortality. No studies of note have been conducted on the western Atlantic coast in Bocas del Toro, Panamá.

The original intent of this study was to look at how the population on Isla Colón has recovered since the mortality of 1983 and compare it to other populations of *Diadema* along the Atlantic coast of Panamá. However, resulting from lack of information about populations of *Diadema* in Bocas del Toro prior to the massive die-off in 1983, making assumptions about how the species has recovered becomes very difficult. The purpose of this investigation, as a result, changed more toward a means of establishing a baseline of population information for a few selected locations on the islands of Isla Colón in Bocas del Toro by measuring population density, test size, and sex ratio as well as making qualitative observations of the areas surrounding *Diadema* populations within a small study area. Once this baseline is established, it will be possible to compare current populations in Bocas del Toro with those at Punta Galeta and in Kuna Yala as well as other populations throughout the Caribbean where ongoing monitoring provides information on continuing changes in *Diadema* populations, and perhaps make inferences about the population through comparison with several locations.

LITERATURE REVIEW

Characteristics of Echinoderms

The phylum Echinodermata is made up of the families of sea stars, brittle stars, sea feathers, sand dollars, sea urchins, and sea cucumbers (Hendler et al. 1995). There are approximately 900 species of echinoderms in the world (Hendler et al. 1995) with at least 67 of these species found around the Bocas del Toro archipelago on the western Atlantic shore of Panamá (STRI 2008). Fifteen of these species are in the class Echinoidea, which includes 10 species of sea urchins (STRI 2008). The sea urchins, in the Echinoderm family, are split into two distinct groups, "regular" or round-bodied, radially symmetrical urchins and "irregular" or flat-bodied, bilaterally symmetrical urchins. The body is made of a hollow shell, or test, of flattened plates that interlock around the edges. Growth occurs when new plates are added to the test at the outer edge with the rate of plate growth determining the shape. Echinoderm tests are covered by tube feet that are used for locomotion, sensory perception, and manipulation of nearby objects for food sources or for cryptic covering. In addition, the tests of sea urchins are covered by many large, primary and small, secondary spines each with its own muscular collar allowing spines to move independently (Hendler et al. 1995).

Characteristics of* Diadema antillarum*:

Before 1983, the long-spined black sea urchin, *Diadema antillarum* (most commonly referred to as *Diadema*), was ubiquitous throughout the Caribbean and tropical Western Atlantic. The species range covered much of the Caribbean Sea from Florida to Bermuda, south to Tobago, and east to the African coast (Lessios 1988a). These irregular sea urchins are broadcast spawners and are incredibly fecund, releasing up to 12 million eggs annually (Knowlton 2001). The larvae spend one month in the water column among the plankton before settling (Birkelund 1997). Larvae then metamorphose after about 60 days, though very little is known about this process (Lessios 1988a), and reach sexual maturity when test sizes reach between 30-60mm in diameter (Ogden & Carpenter 1987) or within approximately six months to one year (Birkelund 1997). Animal longevity is approximately 4 years in the field (Birkelund 1997). There are few predators of *Diadema*. A study by Randall and Starck (1964) observed 15 species of fish predators including grunts (Haemulidae), wrasses (Labidae), triggerfish (Balistidae), porgies (Sparidae), porcupinefish (Diodontidae), and toadfish (Batrachoididae). Abundance of *Diadema* within an environment is often related to predator abundance (Ogden & Carpenter 1987).

Diadema are abundant in rocks, coral reefs, mangrove roots, sea grass beds, and sand flats (Randall & Starck 1964) and prefer environments with clean, highly oxygenated, circulating water where wave action is light to moderate (Ogden & Carpenter 1987). Population densities vary throughout the Caribbean, but *Diadema* are common throughout. They have been one of the most abundant marine animals in Caribbean coral reefs throughout history (Jackson 1997). At Galeta Point near Colón, Panamá, populations averaged 1.38 individuals per square meter or approximately 14,000 individuals per hectare prior in 1983. Populations at several sites in San Blas, Panamá averaged approximately 2.3 individuals per square meter (Lessios et al. 1984a). Some areas in San Blas reached population densities as high as 3-73 individuals per square meter (Bauer 1980). Populations of more than 20 individuals per square meter were not uncommon before 1983 (Ogden & Carpenter 1987; Hendler et al. 1995), while other sites around the Caribbean noted population densities as high as 71 individuals per square meter (Knowlton 2001). *Diadema* are often gregarious animals and have been found in shallow areas in congregations of over 100 individuals, often grouped together by similar size class (Steiner 2006). Congregation is an adaptation for protection and to facilitate successful spawning (Randall & Starck 1964).

Some scientists believe the high abundance and densities of *Diadema* are the result of overfishing and the release of competition from herbivorous fish (Lessios 1988a; Jackson 2001). Lessios (2001), using DNA analysis, determined the high abundance of *Diadema* most likely started about 10,000 years before present and it is unlikely to have started more recently. Anthropogenic effects on populations have most likely been minor (Lessios 2001).

Diadema are fast growing urchins, and estimations on the growth rate range from 3.5mm (Randall & Starck 1964) to 8mm (Bauer 1982) per month. They reach the size at which they are first visible to investigators, 10mm, within one to two months after settling as larvae (Ogden & Carpenter 1987). However, growth rate slows as *Diadema* age and larger individuals, 32-42 mm, grow at a rate of only 1.9mm per month (Hendler et al. 1995). Juveniles are considered those individuals with test sizes 4-25mm in diameter while adults have test sizes greater than 25mm (Randall & Starck 1964). Maximum test size can be greater than 100mm (Birkelund 1997; Ogden & Carpenter 1987). Populations with a high frequency of individuals with large test sizes (>40mm) indicates a population in which a high percentage of individuals are over two years old (Ogden & Carpenter 1987). *Diadema* are considered "irregular," flat urchins. Their tests are low and flat with the width often equaling only 50% of the height. The spines, which contain toxins, can be more than three times the length of the test or up to 300-400mm long. From spine tip to spine tip *Diadema* can often measure over 500mm (Hendler et al. 1995). Additionally, the long spines of adults provide protection for the success and survival of *Diadema* larvae (Miller et al. 2007). Spines are often also a source of protection for species of fish including grunts (Haemulidae), drums (Sciaenidae), wrasses (Labidae), and butterflyfish (Chaetodontidae) as well as mysid shrimp (Randall & Starck 1964; Ogden & Carpenter 1987).

The most important competitors of *Diadema* include herbivorous fish, especially parrotfish (Scaridae) and damselfish (Pomacentridae) along with other urchins, specifically *Echinometra vidris* (Ogden & Carpenter 1987). Ogden and Carpenter (1987) found populations of parrotfish increased in one study after the experimental removal of *Diadema*. In another study, communities of territorial damselfish have been able to exclude *Diadema* from grazing areas. *Diadema* were also found to attack *Echinometra vidris* invading their crevices and grazing territory (Ogden & Carpenter 1987).

Diadema are important herbivores and can drastically change algal abundance, diversity and productivity through their grazing habits. *Diadema* grazing areas are often characterized by dead coral and rock encrusted with a thin layer of filamentous algae (Levitan 1988). Individuals do not graze the same areas on successive nights but return to an area after 2-3 days. *Diadema* are some of the main herbivores of Caribbean reefs and, through grazing, have an indirect, yet important, effect on coral (Birkelund 1997; Knowlton 2001). Grazing reduces algal biomass and creates algae-free settling areas for coral larvae to grow (Birkelund 1997). A study in Jamaica (Edmunds & Carpenter 2001) found macroalgae were rare in an urchin zone where density was high. In St. Croix, algal cover is significantly higher in areas where *Diadema* abundance is below $0.1/m^2$ (Miller et al. 2003). One experiment (Ogden & Carpenter 1987) showed that the exclusion of algae and herbivorous fish created an environment dominated by the algae *Sargassum* spp., *Turbinaria turbinata*, and *Padina jamaicensis*, while another experiment showed *Diadema* is able to remove on average 97% of algal turf biomass in one year (Birkelund 1997). *Diadema* are also involved in the creation of bare zones around reefs by removing the sea grass, *Thalassia testudinum* (Lessios 1988a).

Though *Diadema* are herbivores, preferring to eat algal turf, they can also prey on live coral, which in turn can have a significant influence on coral recruitment. Moreover, *Diadema* are important bioeroders that scrape calcium carbonate ($CaCO_3$) from coral skeletons during grazing. On three study reefs, >75% of the total bioerosion on a reef could be attributed to urchin feeding behavior. In some cases, urchin bioerosion can be equal to or exceed reef $CaCO_3$ production resulting in structural weakness that could ultimately lead to coral breakage. When compared to other organisms, such as parrotfish, that make considerable contributions to bioerosion, *Diadema* is very competitive (Bak 1994).

Mortality

Beginning in January 1983, the urchins at Punta Galeta near the mouth of the Panama Canal began to exhibit unusual symptoms (Lessios et al 1984b; Lessios 1988a; Birkelund 1997).

Diseased urchins were first recognized by an accumulation of sediment on the spines and sloughing off of the spine epidermis. Next, the skin pigment covering the spine muscles, peristome, and anal cone disappeared, spines became brittle and broke off, and the tubefeet that normally hold the urchin to the sea bed weakened and could no longer retract completely. Finally, patches of skin and spines sloughed off and the test disintegrated completely. Additionally, many urchins abandoned daytime cryptic habitats and were making them easy prey (Lessios et al 1984a; Birkelund 1997). Diseased urchins died within 4 days to 6 weeks (Birkelund 1997). A study in Curaçao (Bak et al. 1984) showed more than 50% of the population dying by the fourth day after the onset of symptoms.

During the 13 months following January 1983, similar symptoms appeared over the whole species range (Lessios 1988a). It took approximately one year for the mortality to travel from Panamá to Tobago, 2000 km away. The disease reached the banks of Texas and Florida and finally moved on to Bermuda by August 1984, 4000 km from the origin. By the time outbreaks stopped, they had covered more than 3.5 million square kilometers, not including Barbados. This has been the most extensive die-off ever reported for marine animals. There are no known populations of *Diadema* in the Western Atlantic that escaped the mortality (Lessios 1988a). Estimates of 85-100% of urchins died at sites throughout the range (Lessios et al. 1984b). In Curaçao, population density was reduced to less than 0.01 individual per $100m^2$ in many study sites following mortality (Bak et al. 1984). Population density in Barbados was effectively reduced to 0 $/m^2$ by 1984 in many study sites (Hunte & Younglao 1988). Mortality in this event was density independent, and areas with more highly dense populations were more likely to retain some part of the population, as was the case in Barbados where pre-mortality populations were extremely high (Lessios 1988a) and populations had recovered to 57.4% of their pre-mortality density by August 1985 (Hunte & Younglao 1988).

Galeta Point in Colón province, Panamá was one of the first, and one of the best studied, sites, hit by the mortality. A census conducted in June 1982 found 14,000 individuals per hectare. The same study conducted in May 1983 found 0.5 individuals per hectare. In February 1984, the same population had recovered to 38 individuals per hectare. In San Blas, the population declined 94.2% from its pre-mortality density. A census conducted in December 1983, seven months following mortality, showed a density of 1.2 individuals per square meter. Additionally, the mean test diameter in these locations reduced from 48.6mm to 25.0mm (Lessios et al. 1984a).

It is unlikely that the cause of the mass mortality will ever be known for certain. Most researchers suspect the die-off was caused by a host-specific water-borne pathogen (Lessios 1988a; Birkelund 1997). Unfortunately, few samples were taken during the die-off for histological or microbiological investigations. Two samples studied showed the presence of gram-positive, anaerobic, spore-forming rods of the bacterial genus *Clostridium* whose spores are transmitted through water (Birkelund 1997). *Clostridium* proved lethal when injected into healthy *Diadema*, yet there is not enough evidence to prove these bacteria were the cause of the die-off (Lessios 1988a).

Community Effects

Diadema is a keystone herbivore, and, as predicted, its loss has had profound effects on the community structure and composition of benthic communities across the Caribbean (Lessios et al. 1984b, Randall & Starck 1964; de Rutyr van Steveninck & Bak 1986). Since some of the earliest coral reef studies in the Caribbean in the 1950s, there had been no noticeable changes in coral communities until the die-off of 1983 (Jackson 2001), and studies done beginning during this time noted *Diadema* was one of the most important factors in the prevention of overwhelming macroalgal blooms (Bellwood 2004). Since the die-off, there has been a distinct change in algae composition from filamentous algae to macroalgae (Birkelund 1997). Some species of algae that were rare or absent in coral reefs before the 1983 were *Padina* spp., *Turbinaria turbinata*, and *Jania adherens* (Ogden & Carpenter 1987). Following the die-off, these species of algae drastically increased in addition to other species, *Lobophora variegata* and *Dictyota* spp. (de Rutyr van Steveninck & Bak 1986). In San Blas, algae cover in shallow reefs in 1983 was 11-24% and increased to 32-70% by 1988. In deeper reefs, algae cover increased from 5% to 58% by 1988 (Shulman et al. 1996). Though there has been only a slight increase in the algae abundance in Panamá, other areas saw an increase in algae biomass by 27% over the first five days following mortality (Birkelund 1997) and up to 100-250% after one year (Phinney et al. 2001).

Furthermore, the *Diadema* mortality has indirectly accelerated the demise of coral reefs (Lessios 2001). The principle cause of coral mortality has been by macroalgae overgrowth as a result of *Diadema* mortality (Jackson 2001). Experimental removal of *Diadema* showed an increase in algal cover and subsequent decrease in coral cover (Colin 1988). Coral cover in another study decreased by approximately 10% in shallow reefs and 15% in deeper reefs (Shulman et al. 1996). In Jamaica (Knowlton 2001), coral cover dropped from 52% to 3% between 1977 and 1993 while seaweed abundance increased from 4% to 92% in the same time frame. However, corals with certain morphologies were more prone to algal growth. *Agaricia agaricites* (de Rutyr van Steveninck & Bak 1986) suffered the highest mortality, but gorgonian soft coral, *Briarium ashestinum*, and zooanthids, *Zooanthus sociatus* and *Zooanthus solanderi* also suffered significant mortality (Lessios 1988a).

Other effects of *Diadema* mortality on the larger community were the competitive release of other echinoids, particularly *Echinometra vidris*, whose population increased, though only minimally (Lessios 1988b; Birkelund 1997). Populations of herbivorous fish were also found to increase, particularly surgeonfish and parrotfish, with the removal of competition from *Diadema* but fish grazing did not increase sufficiently to compensate for the loss of *Diadema* herbivory (Birkelund 1997). In addition, rates of bioerosion slowed, and places where the calcium budget was previously negative became positive (Shulman et al. 1996). Main predators of *Diadema* were able to shift their diets and were therefore not significantly affected by the *Diadema* population crash (Lessios 1988a).

Recovery

To determine the effects of mortality on *Diadema* as a whole, it is necessary to see how the urchin has recovered (Lessios 1988a). Unfortunately, it is hard to study the populations of *Diadema* in Panamá because there are few pre-mortality study to which to compare current census data (Lessios 2005). Juvenile recruitment continued immediately, within the first five months, after the die-off but did not last long in Panamá. There was no recruitment at the study sites in San Blas or at Galeta Point between January 1984 and December 1987 (Lessios 1988a), and populations there eventually declined to levels lower than those immediately following the mortality (Lessios 1988b).

Though scientists have generally acknowledged that species with a wide geographic range and planktonic larvae, such as *Diadema*, are quite resistant to extinction (Lessios 1988a), one thing that was not anticipated by scientists was the very slow recovery of *Diadema* populations even though they are highly fecund animals (Knowlton 2001). Recovery of populations will be slow because of the drastic decline in *Diadema* of reproductive maturity. *Diadema* males and females must be within 20cm of each other for there to be successful fertilization. Therefore, successful reproduction is dependent on the size and proximity of populations with a high percentage of sexually mature individuals (Birkelund 1997). Without high population densities, likelihood of reproduction drops dramatically. Additionally, there are lower rates of juvenile recruitment as a result of fewer larvae in the water column (Lessios 1988b) and fewer adults actively recruiting (Lessios 1988b; Lessios 1995; Miller et al. 2007). One study (Miller et al. 2007) determined that larvae settle in larger numbers among more highly dense populations of adults that will be able to protect them, and the percentage loss of juveniles is higher in reefs with low densities of adult *Diadema*. The number of adults ≥49mm diameter and juveniles ≤20mm diameter is positively correlated, and 97% of the studied transects with juvenile abundances ≥1 also had an adult abundance >5 per square meter. A similar study (Hunte & Younglao 1988) found that 59% of recruits on a reef front in Barbados aggregated with adults as opposed to other recruits (34%), or were solitary (7%).

Four and a half years after the die-off, populations had not yet recovered in Punta San Blas or Cayo Limones, Panamá. There had been effectively no recovery of *Diadema* throughout San Blas and larvae ≤1.5cm that had been recruited after the mortality had either died or emigrated. A recent study (Lessios 2005) maintains that *Diadema* recovery has been minimal over the last 20 years at 11 reefs throughout the San Blas archipelago. The current populations there are only 6.5% of the original, pre-mortality density. Even locations with extremely high pre-mortality densities that retained part of the population, specifically Barbados, have recovered very little. Future recovery is predicted to remain slow on account of the scarcity of *Diadema* communities unaffected by the mortality acting as sources of larvae (Lessios et al. 1984b)

Benefits of Recovery

Throughout history *Diadema* has played an important role as a keystone herbivore and its loss has caused a community phase shift from reefs dominated by coral to those dominated by algae (Lessios et al. 1984a, b; Birkelund 1997; Bellwood 2004). One of the most notable benefits of the recovery of *Diadema* is the subsequent revitalization of coral reefs throughout the Caribbean (Bellwood 2004). Reefs throughout the tropics have been under stress by natural and anthropogenic factors including overfishing, sedimentation, pollution, and bleaching that resulted from a severe El Niño event from 1982-1983 (Birkelund 1997). Adding to the myriad stressors is the intense competition with macroalgae. Increasing *Diadema* populations would help reverse the phase shift and return communities back to coral and algal turf dominated communities (Bellwood 2004). *Diadema* populations will help maintain the health and longevity of coral reefs by reducing competition with algae for both sunlight and living space (Birkelund 1997). Recent observations in Jamaica (Knowlton 2001) have seen recruitment rates rising among coral, especially *Acropora* spp. and *Montastraea* spp., two genera of major reef builders thus indicating that reef recovery, as a result of the return of dense *Diadema* populations, may be close at hand at a few locations around the Caribbean.

RESEARCH QUESTION

- What are the characteristics of the current populations of *Diadema antillarum* on Isla Colón in Bocas del Toro, Panamá 25 years after mass mortality in the Caribbean, and how do the populations compare to other current populations around the Caribbean?

RESEARCH OBJECTIVES:

- Investigate the population of the sea urchin, *Diadema antillarum* near Smithsonian Tropical Research Institute at Sunset Point and a nearby island of mangroves.
- Compare the population data in Bocas del Toro with the populations at Galeta Point and Kuna Yala, Panamá as well as several other locations in the Caribbean to determine the population and community structure similarities and differences between populations.

METHODS AND MATERIALS

Site Description

The two study sites on Isla Colón were chosen for their close proximity to the Smithsonian research facilities and ease of access during a limited time period for study (Figure 1). Investigations were made May 10, 2008 through May 15, 2008 during the afternoons of each of those days. Wave action was mild at each of the sites. Temperature averaged 28-33 C. Water temperature was 30 C.

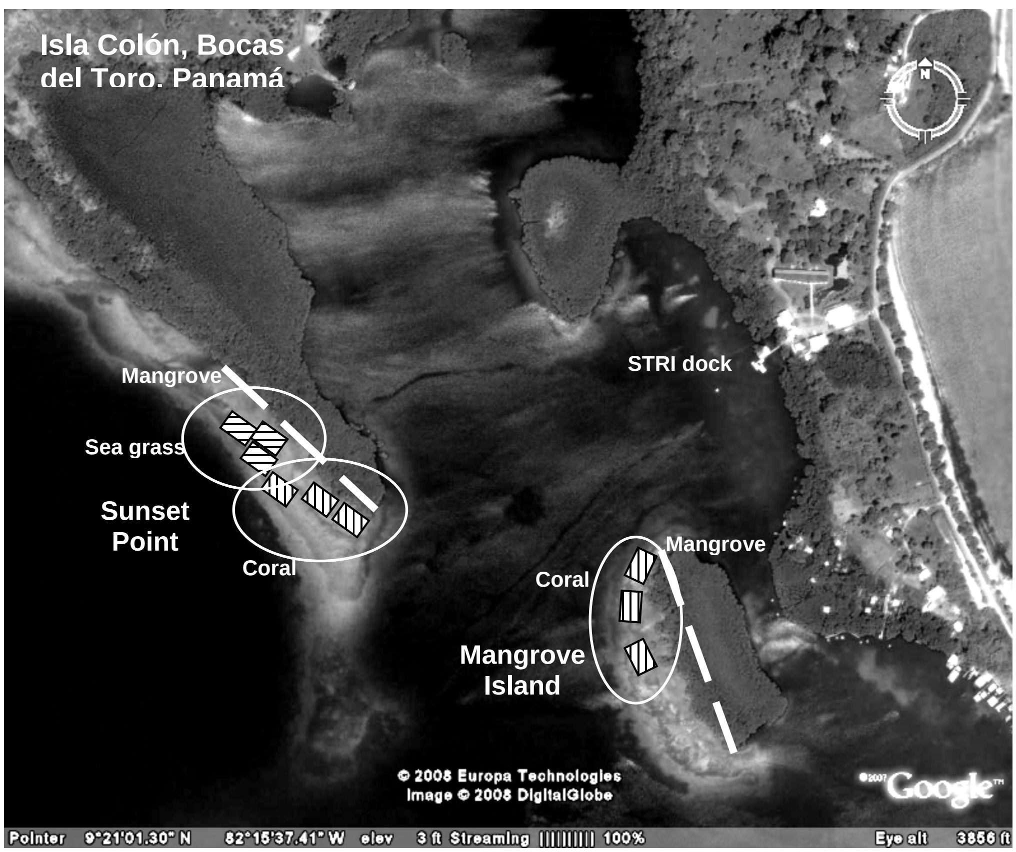

Figure 1. Map of the study sites. Sunset Point is 0.5km southwest from Smithsonian Tropical Research Institute facilities. The mangrove island is less than 0.5 km away from STRI to the south east. Locations of transects is approximate.

Sunset Point, Isla Colón, Bocas del Toro, Panamá

Sunset Point, located 0.5 km southwest of the Smithsonian Tropical Research Institute dock was studied on the south, seaward side from the tip of the point in the southeast to 150 m to the west. It is characterized by three types of environments: coral reefs, sea grass beds, and mangroves. Average water depth was <1m to 1.5m deep. Total area observed at Sunset Point equals 2700m^2.

Coral Reefs

Coral reefs dominated the site for the first 75m of study in the eastern section of the point. Reefs at Sunset Point consisted for the most part of branching coral, especially finger coral, *Porites porites*, both dead and alive. Two sets of transects were taken in live coral, one set was taken in mostly dead finger coral. Lettuce coral (*Agaricia agaricites*) and branching fire coral (*Millepora alcicornis*) were also present but not dominant. Finger coral, both live and dead, were heavily covered in filamentous and macro- algae; some areas had more than 50% coverage. Genera of algae present include *Dictyota* spp., *Padina* spp., *Halimeda* spp., *Caulerpa* spp., *Ventricaria* spp., and *Jania* spp. Coral was inhabited by other species of urchins, especially *Echinometra vidris*, which was very abundant, even in areas with *Diadema*. Also *Eucidaris tribuloides* and the *Lytechinus variegates* were present, but these species existed in low numbers in the reefs. Areas surrounding the reefs were characterized by sea turtle grass, *Thalassia testudinum*, covering the substrate composed of sand and broken pieces of coral. There were few small scattered colonies of brain coral (*Diploria* spp.). Water depth in these transects started at approximately 1.5m deep on the eastern end, but became shallow, less than one meter, over the coral beds. Total area covered in the coral reefs equals 900m^2.

*Sea Grass (*Thalassia testudinum*)*

The westernmost 75m of transects were taken in the area considered sea grass beds. The substrate consisted of sand and broken coral, mostly broken finger coral, and a few single colonies of brain coral (*Diploria* spp.). There were infrequent patches of massive encrusting corals (*Siderastrea* spp.) throughout the sea grass beds around which the *Diadema* congregated. Some colonies reached diameters up to one meter. The majority of the corals were more than 50% dead, usually missing the top center giving the coral a ring-shaped appearance. The dead portions of coral were covered with a film of algae. Algae in the sea grass beds surrounding the coral were of the same genera as mentioned above. Many of the *Diadema* were found under the sides of overhanging sides of the coral. Coral was also inhabited by reef urchins (*Echinometra vidris*). Water depth in these transects was less than one meter deep. Total area covered in sea grass equals 900 m^2.

*Mangrove (*Rizophora mangle*)*

Mangroves were measured from the easternmost tip of Sunset Point heading west for 450m (equal to the length of three sets of transects). Visibility in the mangrove roots ranged from very murky to very clear and very calm water to moderate wave action. Some portions of roots were inaccessible for snorkeling, making it difficult to find *Diadema*. Some portions of the roots, especially in the first two sets of transects, were well established and formed a dense network of roots. They were lined by fields of sea grass, as characterized in the above section. The third set of transects in the western portion of the site were less dense with murkier water.

There was less sea grass surrounding the mangroves in the third transect and more trash. Total area covered in sea grass equals 900 m^2.

Mangrove Island, Isla Colón, Bocas del Toro, Panamá

The unnamed mangrove island covers approximately 6 ha and is located less than 0.5km southeast of the Smithsonian Tropical Research Institute dock and approximately 0.5km east of Sunset Point. The south and west sides of the island, the seaward sides, are surrounded by coral reefs, whereas the north and east sides, the inland sides, are surrounded by still, sediment covered sea grass beds. The south and west sides were those studied. Total area studied equals 2700 m^2.

Coral

The coral reefs around the mangrove island were more diverse than those on Sunset Point, especially in the first two sets of transects on the western side of the island. In addition to finger coral (*Porites porites*.), lettuce coral (*Agaricia agaricites*), and branching fire coral (*Millepora alcicornis*), which were found at Sunset Point, there was also blade fire coral (*M. complanata*), staghorn coral (*Acropora cervicornis*), massive coral (*Siderastrea* spp.), boulder coral (*Montastraea* spp.), and brain coral (*Diploria* spp.) in large quantities all within the same reef rather than one dominant species as at Sunset Point. This reef covered a much larger area, uninterrupted by large patches of sea grass, and had a larger profile, standing almost one meter deep in some sections. The reef on the southern side of the island was more similar to that at Sunset Point. It was largely dominated by *Porites porites* but other species of coral, mentioned above, were common in the sea grass beds in the surrounding area. Water depth averaged 1.5m deep on the western reef to less than one meter in the southern reef. Coral along the majority of transects was heavily covered with algae, especially in the crevices between coral and from there spreading out to the main coral body. Many coral were 50% covered in algae and some greater than 75%. The dominant types of algae were those mentioned for Sunset Point.

*Sea grass (*Thalassia testudinum*)*

Sea grass surrounded the mangrove island. Substrate consisted of sand and broken pieces of coral. For the most part it was very similar to the sea grass beds at Sunset Point without the high frequency of encrusting corals.

*Mangrove (*Rizophora mangle*)*

The mangroves that made up the island were for the most part well established with dense roots. The surrounding sea grass beds and sand flats were very murky with lots of sediment and garbage accumulated. Water was not as clear as at Sunset Point.

***Sampling* Diadema antillarum**

To measure *Diadema* in this investigation, transects were made using a 30m long meter tape. However, before the first transect was put down, a survey was taken of the area using a kayak to identify areas with *Diadema* and to help facilitate the placement of transects. When patches of *Diadema* were found, the transects were laid haphazardly around each patch, including as much of the patch and surrounding area as possible. In reefs, the first transect was laid along the inland edge of the reef. In the sea grass beds, the transects were laid down in no specific pattern. After placing the first transect, the investigation was conducted using a length of PVC pipe 2m long to measure one meter on either side of the transect. The locations of each

Diadema encountered along the transects were noted and the body size of each individual, without spines, was measured using centimeter calipers. Qualitative observations about the environmental conditions were recorded also, including estimated percent algae cover, species of algae, species of urchins, and types of coral present. After one transect was finished, the tape was moved two meters farther toward the outer reef and the same procedure was followed. A total of five transects were completed, each transect covering an area of $60m^2$, for a total of $300m^2$ per set. Three sets of transects were completed per habitat per site, three in coral, three in sea grass, three in mangroves. To measure the mangroves, however, the transects were laid end to end covering a distance off 150m for each set. The total area for each habitat was $900m^2$ and the total area investigated per site was $2700m^2$.

Additionally, a sample of ten *Diadema*, 6 from Sunset Point and 4 from the mangrove island, was randomly collected to test for the sex ratio. Individuals were measured using calipers and opened using a scalpel. Information recorded included the site collected from, size, and sex. Sex was determined by the presence of eggs or sperm.

RESULTS:

The only variation from the original methods proposed was to leave out the use of quadrats and instead measure algae cover qualitatively. In addition to the coral reefs at these sites, sea grass beds and mangrove roots were also inspected for *Diadema*. Only two sites near the Smithsonian Tropical Research Institute were visited rather than STRI point and the other proposed study site at Hospital Point on Isla Solarte due to time limitations. In addition to measuring test sizes, a sample was taken (6 from Sunset Point, 4 from the mangrove island) to check for sex ratio. Individuals were opened using a scalpel.

Sunset Point, Isla Colón, Bocas del Toro, Panamá

Coral

Sizes of the patches of *Diadema* in the coral reefs at this site ranged from one square meter to 57 square meters. The three largest patches contained 65, 53, and 43 *Diadema* respectively. Overall there were 195 *Diadema* in the coral environment or 70.9% of the total *Diadema* sampled at Sunset Point (Table 1, Figure 2), but one was unable to be removed from its hiding spot and was therefore not measured. Test sizes (n=194) ranged from 28-95mm, but were most frequent in the range of 70-79mm (27.3%), while 76% of test sizes were within 60-89mm (Table 2, Figure 3a). The average test size was 67.5mm (SD=15.4). The total area studied was $900m^2$. The density of *Diadema* at Sunset Point in the coral habitat was $0.22/m^2$ (Table 3).

Sunset Point—Isla Colón, Bocas del Toro, Panamá			
	Coral	**Sea Grass**	**Mangrove**
Transect 1	77	8	24
Transect 2	66	28	0
Transect 3	52	11	9
TOTAL	195	47	33
Site Total	275		

Mangrove Island—Isla Colón, Bocas del Toro, Panamá			
	Coral	**Sea Grass**	**Mangrove**
Transect 1	5	0	0
Transect 2	1	0	0
Transect 3	11	0	0
TOTAL	17	0	0
Site Total	17		

Table 1. Absolute numbers of *Diadema antillarum* encountered by site, environment, and transect number.

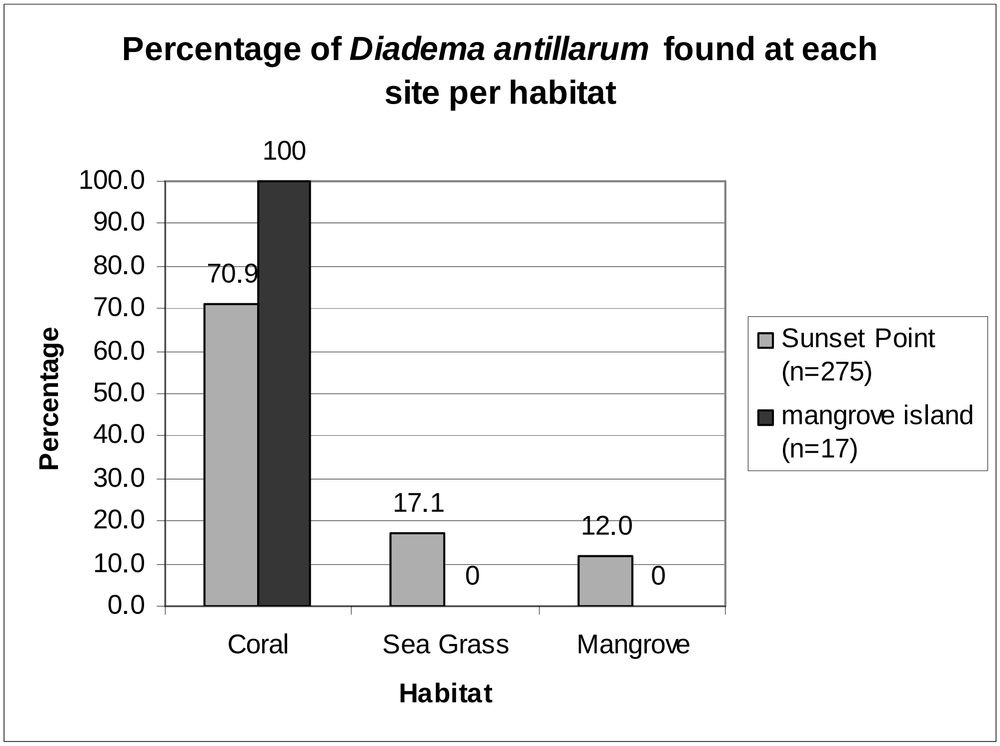

Figure 2. Percentage of the total number of *Diadema antillarum* found in each habitat at both Sunset Point (n=275) and Mangrove Island (n=17). Values correspond to those in Table 1.

Sea grass

Patches of *Diadema* ranged from less than one square meter to six square meters. No *Diadema* were found more than one meter away from the *Siderastrea* spp. encrusting corals in the sea grass beds. The largest patches of *Diadema* were found around large clusters of *Siderastrea* (more than 5 colonies, average colony size 0.5m diameter) whereas the smaller patches were found around clusters of one or two colonies of coral. The largest patch covered an area of 6 square meters and contained 20 *Diadema*. There were a total of 47 *Diadema* in this environment, or 17.1% of the total sample, at Sunset Point; however, one was unable to be removed and measured (Table 1, Figure 2). Test sizes (n=46) ranged from 24-90mm. Test sizes were most frequent within the range of 70-79mm (26.1%), while 50% were in the range from 60-79mm (Table 2, Figure 3a). Average test size was 59.0mm (SD=15.9). The total area measured was 900m^2, and the density of *Diadema* observed was 0.05/m^2 (Table 3).

Mangrove

In total, 33 *Diadema*, or 12.0% of the total sample, were counted along the mangroves (Table 1, Figure 2). Unfortunately, accessibility to the majority of the *Diadema* was limited by the mangrove roots. For this reason, no *Diadema* test sizes in the mangrove roots were measured. Total area observed was 900m^2, with a density of 0.04/m^2 (Table 3).

Overall, at Sunset Point 275 *Diadema* were counted (Table 1), and 240 were measured. Average test size was 65.4mm (SD=16.7) across all individuals sampled in the site. Total area observed at Sunset Point was 2700m^2, and density of *Diadema* overall at Sunset Point was 0.10/m^2 (Table 3).

Sunset Point						Mangrove Island		
Size (mm)	Absolute number Diadema Coral	Percentage of size class-Coral	Absolute number Diadema Sea Grass	Percentage of size class-Sea Grass		Size (mm)	Absolute number Diadema-Coral	Percentage of size class-Coral
20-29	2	1.03	2	4.35		20-29	0	0.00
30-39	9	4.64	6	13.04		30-39	0	0.00
40-49	26	13.40	6	13.04		40-49	1	5.88
50-59	6	3.09	6	13.04		50-59	4	23.53
60-69	51	26.29	11	23.91		60-69	3	17.65
70-79	53	27.32	12	26.09		70-79	7	41.18
80-89	44	22.68	2	4.35		80-89	2	11.76
90-99	3	1.55	1	2.17		90-99	0	0.00
Unknown	1		1			unknown	0	
TOTAL	195		47			TOTAL	17	0

Table 2. Absolute number of *Diadema antillarum* per size class (range=10mm) and the corresponding percentage of total number of *Diadema* per size class for coral and sea grass at Sunset Point and coral at the mangrove island.

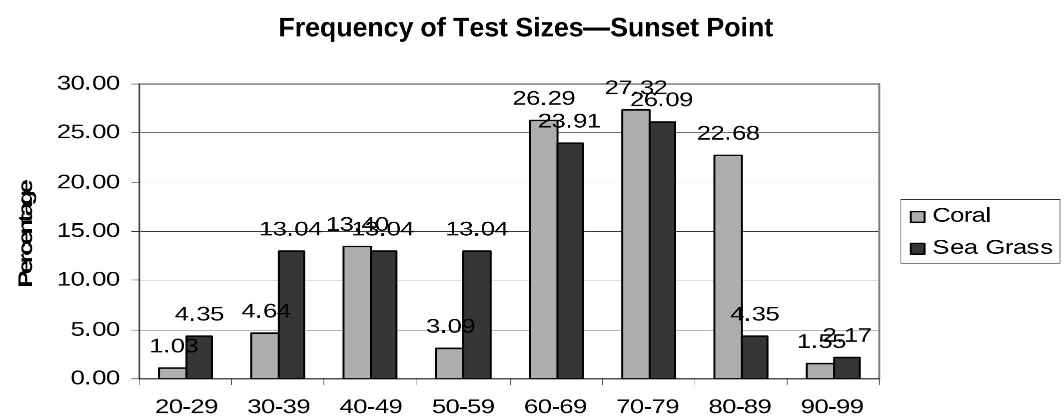

Figure 3a

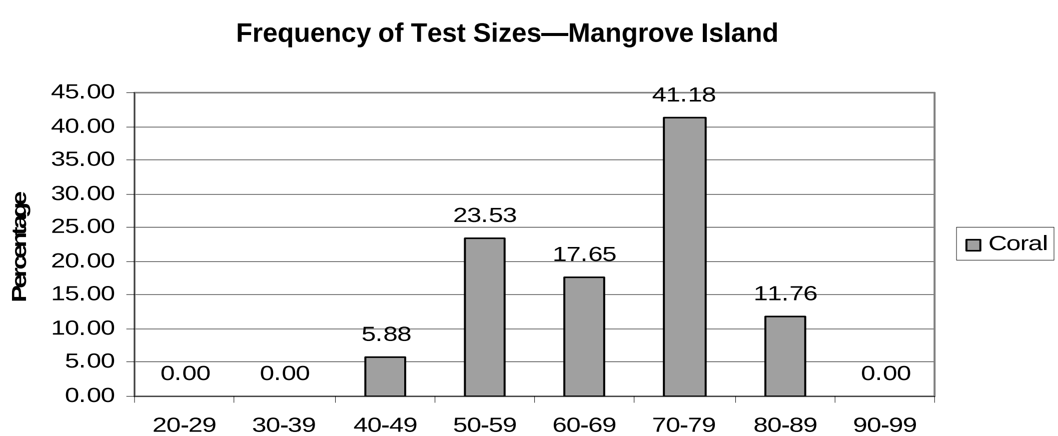

Figure 3b

Figures 3 a and b. Frequency of test sizes by size class, represented as percentages of the total number of *Diadema antillarum* measured at Sunset Point (3a) and Mangrove Island (3b) in each environment. Note: no data from mangroves in Sunset Point (Figure 3a), because they were inaccessible. No data for sea grass or mangrove at Mangrove Island (3b) because no *Diadema* found in these habitats.

Mangrove Island, Isla Colón, Bocas del Toro, Panamá

Coral

In total, 17 *Diadema* were found in the coral at the mangrove island (Table 1, Figure 2). Of those, 11 were found in the set of transects on the south side of the island where the dominant coral was *Porites porites*. Only 6 *Diadema* were found in the more diverse reef on the western side of the island. Density in the coral at this site was 0.02 *Diadema*/m^2. Test sizes range from 47-85mm. The frequency of test sizes was highest in the range of 70-79mm (46.2%) (Table 2, Figure 3b). However, average test size was 67.8mm (SD 11.3)

Sea grass and Mangrove

No *Diadema* were observed in either the sea grass or mangrove environments at the mangrove island making density in these two habitats 0.

Overall density at the mangrove island across the three types of habitats was 0.01 *Diadema*/m^2 (Table 3).

Both sites combined

Density of *Diadema* in the coral reefs, from both sites is 0.12/m^2, in sea grass density is 0.03/m^2, and in mangroves, density is 0.02/m^2 (Table 4). Density throughout the whole study area, both Sunset Point and the mangrove island, an area of 5400m^2, is 0.05/m^2.

Subset Point—Isla Colon, Bocas del Toro, Panamá					**Mangrove Island--Isla Colon, Bocas del Toro, Panamá**			
	Coral	**Sea Grass**	**Mangrove**			**Coral**	**Sea Grass**	**Mangrove**
TOTAL Diadema per habitat	195	47	33		TOTAL Diadema per habitat	17	0	0
Density (m^{-2})	0.22	0.05	0.04		**Density (m^{-2})**	0.02	0	0
Overall Density at Sunset Point (m^{-2})	0.10				**Overall Density at Mangrove Island (m^{-2})**	0.01		

Table 3. Density of *Diadema antillarum* per habitat by site as well as the overall densities of *Diadema* /m^2. Area per habitat is 900 m2. Total area per site equals 2700 m2.

	Coral	**Sea Grass**	**Mangrove**
Number Diadema	212	47	33
Density (m^{-2})	0.12	0.03	0.02

Table 4. Density of *Diadema antillarum* by habitat across both Sunset Point and Mangrove Island.

Sex Ratio

Of the 10 individuals sampled, all ten were female. Sizes ranged from 67-83mm. One of the females had been recently fertilized, as was determined by the presence of sperm in addition to eggs (Table 5). Additionally, one male was observed at the coral reef in the mangrove island on May 10, 2008 releasing sperm.

Site	Size (mm)	Sex
Sunset Point	75	Female
Sunset Point	76	Female
Sunset Point	80	Fertilized female
Sunset Point	83	Female
Sunset Point	83	Female
Sunset Point	83	Female
Mangrove island	67	Female
Mangrove Island	75	Female
Mangrove Island	82	Female
Mangrove Island	82	Female

Table 5. Size and sex of individuals from Sunset Point and mangrove island (n=10).

DISCUSSION:

Test Sizes

Test sizes at both sites were much more frequent in the larger class sizes. At both Sunset Point and the mangrove island more than 50% of *Diadema* were between 60-79mm. However, Sunset Point showed a greater tendency toward larger urchins with 22.6% having test sizes 80-89mm whereas *Diadema* at the mangrove island showed a higher tendency toward smaller test sizes with 23.5% having test sizes 50-59mm (Figures 3a and 3b). Test sizes, between sites in coral habitats only, showed no statistical difference between test sizes (Sunset Point mean test size 67.52mm SD=15.37, mangrove island mean test size 67.76mm SD=11.34, $t = 0.99$). Unfortunately, no other studies have been done around the Caribbean comparing populations in the various types of habitats (coral, sea grass, mangroves). Though there was no significant difference in test sizes across sites within the coral habitat, there was a significant difference between test sizes at Sunset Point across habitats (i.e. coral vs. sea grass; $t = 0.001$). Overall, average test sizes in sea grass at Sunset Point was 58.96mm (SD=15.92) while in the coral at the same site mean test size was 67.52 (SD=15.37). The smaller test sizes in the sea grass may have been due to a smaller sample size. It may also be a result of *Diadema* in sea grass being young recruits from the nearby larger populations in the coral. Young *Diadema* often settle near the population from which they came (Knowlton 2001).

Around the Caribbean, mean test size in St. Croix (Miller et al. 2003) is 48.6mm with the frequency of test sizes dominated by the size class 31-40mm. In Dominica (Steiner 2006) mean test sizes ranged from 45.4-67.7mm across various study sites, while the overall average test size was 60.0mm. Levitan (1988), five years after the mass mortality of *Diadema*, found mean test size to be increasing, probably as a result of high food availability that was caused by the dramatic decline in the main herbivores in the area. In his study at St. John, where pre-mortality test size was 34mm, mean test size in June 1987 had increased to 60mm diameter. Mean body size has been increasing at a rate of 11.3mm/year since the population crash in the St. John. Levitan expects growth rate to continue until the populations reaches these predicted mean body size for the current population density (i.e. for a density of 0.25-0.75 individuals/m^2 the mean body size is predicted to end in the range of 80-110mm). However, Levitan's observation is in contrast to a study in Kuna Yala, Panamá (Lessios 1984a) where mean test size reduced from 48mm to 25mm following mortality. Compared to recent studies in other locations, *Diadema* at Sunset Point and the mangrove island have relatively large average body sizes. In the case of the sites on Isla Colón in this study, the large average test size may indicate that populations on Isla

Colón in Bocas del Toro have recovered to a mature, stable population density and are likely to continue growing. Unfortunately, without knowing pre-mortality mean test size it is difficult to support that assumption.

Overall, the commonly observed strong bimodal distribution of test size frequency that was suggested by Lewis's (1966) pre-mortality *Diadema* population study was not observed in the population in this study. Miller et al. (2003) observed the *Diadema* populations in St. Croix in 1983 to have a bimodal size frequency distribution with peaks focused in the size classes 21-40mm and 61-80mm, but from 1984-1986, shortly after the die-off, Miller et al. observed a large majority of *Diadema* within the size classes 61mm to greater than 80mm, while at the same time very few *Diadema* with test sizes less than 60mm. In 2000, he observed the size frequency focused around test sizes 31-50mm. He also observed recently that, small *Diadema* (20-40mm) are becoming more common in St. Croix, perhaps suggesting recovery is near at hand because there is such a high concentration of juveniles. Hunte and Younglao (1988) in 1985 in Barbados observed a range of test sizes from 60-98mm with an average test size 60mm at one site and 40mm at another site. The population surveyed on Isla Colón does not have a high frequency of individuals in the size classes observed by either Miller et al. (2003) or Hunte and Younglao (1988). The high percentage of larger individuals indicates a population of individuals likely to be over two years old, a demographic that will be sexually mature and reproducing (Ogden & Carpenter 1987). Therefore, the potential for successful reproduction by these highly fecund animals is very high at this study site on Isla Colón.

An additional observation of *Diadema* has been that average body size changes according to food availability making large test sizes more frequent in areas with more available food sources. However, food availability is also related to population density. Areas with high population density are likely to be overgrazed, thus restricting average test sizes (Levitan 1988). Levitan (1988) showed algal cover in the study area to be 70.0-96.2% while mean test size was 60mm and population density was approximately 0.25-0.75 individuals/m^2. Though there was no quantitative analysis of algae cover in this study, the estimated percentage of algae cover was also very high, especially at the reefs on the western side of the mangrove island. Interestingly, the study area at the mangrove island had the lowest population density (0.003/m^2 for the two sets of transects on the western side of the island in this type of reef) and the most available food, yet without a significant difference in average test size compared to Sunset Point, which had a higher population density (0.22/m^2) with a lower percentage of algal cover. This difference may be the result of the preference of *Diadema* larvae to settle in moderately grazed areas (Knowlton 2001). Additionally, grazing of algae in this type of habitat may be limited because most of the algae growing in crevices between coral is inaccessible and may exclude *Diadema* from grazing (Ogden & Carpenter 1987). Therefore, *Diadema* recruitment at the mangrove island may be limited for the same reason that population density should be highest, the over-abundance of algae. Even though the heterogeneous reef environment on the west side of the mangrove island provides lots of good quality crevices for juvenile *Diadema* to hide, *Diadema* larvae may be unable to settle as a result of otherwise unfavorable conditions. Feedback loops such has this have played a significant role in the cause of slow *Diadema* recovery throughout the Caribbean. Areas with lower population density, in the case of this study the mangrove island reef, recruit and keep fewer juveniles (Miller et al. 2007).

Density

In addition to average test size, density was also highest in coral reefs environments in comparison to sea grass beds and mangroves in this study. Density in the coral at Sunset Point was 0.22/m^2 while in the sea grass and mangroves density was 0.05/m^2 and 0.04/m^2 respectively (Table 3). At the mangrove island density in the coral was 0.06/m^2 and 0 in the sea grass and mangroves studied. Over both sites density in coral was 0.12/m^2, sea grass was 0.03/m^2 and mangrove was 0.02/m^2 (Table 3). The overall density in both sites and all habitats was 0.05/m^2. Compared to recent studies in other sties around the Caribbean, population density in Kuna Yala, Panamá, the densities at most study sites was lower than 0.2/m^2 (Lessios 2005). In St. Croix, 2001, density was 0.2/m^2-0.8/m^2 at various sites, though they remained one order of magnitude less than the pre-mortality densities (Miller et al. 2003). In Dominica, 2004, density was 2.0/m^2 and 2.98/m^2 at the two study sites (Steiner 2006). In Puerto Rico, 2004, population densities at various sites ranged from 0.01-0.82/m^2 (Lugo 2004). Population densities at Sunset Point and the mangrove island on Isla Colón in Bocas del Toro, Panamá are lower than other locations throughout the Caribbean, but similar to those most recent studies on the eastern Atlantic shore of Panamá. However, even though Lessios (1984a) wrote that there are no known populations of *Diadema* that escaped the mortality, it is difficult to know what the populations pre- and post-mortality in the populations on Isla Colón at Sunset Point and the mangrove island were or how they have changed since 1983. Assuming conditions in both the archipelagos of Kuna Yala and Bocas del Toro are similar for *Diadema* and that populations in Bocas del Toro declined to similar population densities as in Kuna Yala, it could be postulated that recovery of populations on Isla Colón, Bocas del Toro has been slow and has been only minimal compared to other Caribbean populations of *Diadema*.

Sex Ratio

Few ecological studies have looked at the sex ratio within populations of *Diadema* around the Caribbean. One study observed the male to female sex ratio in a population of *Diadema* to be 1:2 (Birkelund 1997). Observation in Puerto Rico (Lugo 2004) found a sex ratio 0.89:1 male to female. The sample (n=10) taken in this population suggests the populations are heavily weighted toward females because all individuals were female (Table 5). However, it is very unlikely the population is entirely female because populations of that sex ratio would not persist. *Diadema* are not hermaphrodites and cannot self fertilize (Knowlton 2001). One female from Sunset Point was identified as having been recently fertilized by the presence of sperm when opened. Additionally, personal observation showed one *Diadema* on the southwest side of the mangrove island was releasing sperm. Males were present at both sites but in small numbers.

Though samples were taken randomly within large groups of *Diadema*, the results suggest that *Diadema* group together not only by size class (Steiner 2006) because all *Diadema* measured from Sunset Point were within a 9mm range but also group together by sex (Table 5). This habit may be to help increase the rates of successful fertilization if all eggs are released in a certain area at a particular time of the month. In the future, it will be important to take a bigger sample size to form a better understanding of the relationship between the sexes across the population.

Community

Congregation of *Diadema* in the coral reefs is not an uncommon behavior. *Diadema* are nocturnal animals, grazing between the hours of 3:00pm and 6:00am and then becoming inactive for the rest of the day (Ogden & Carpenter 1987). Congregation is largely an adaptation to protect against predators. However, many of the *Diadema* observed, particularly at Sunset Point, were found grazing on broken pieces of algae covered *Porites*. One investigation (Carpenter 1984) has shown the removal of predator pressure has often resulted in a change in the daytime cryptic habits of *Diadema* to spend more time feeding; therefore, the observed grazing during the day suggests low incidence of predators at Sunset Point. Population density is largely dependent on abundance of predators (Ogden & Carpenter 1987). This area, with a low observed abundance of *Diadema* predators, is likely to see continued increases in population density. There is likely also low competition from territorial, diurnal damselfish, other herbivorous fish, or other sea urchins.

Though *Diadema* populations are normally very patchy, in terms of density and recruitment (Lessios 1988a), there was a clear trend in the preference of habitat in the patches of *Diadema* in this study. A clear majority of *Diadema* were located in the coral at each site. At Sunset Point 195 *Diadema*, or 70.9% were found in the coral, and all 17 *Diadema* at the mangrove island were found in the coral. At Sunset Point only 47, or 17.1% of *Diadema* were found in the sea grass, and 33 or 12.0% were found in the mangroves (Figure 2). Randall (1964) noted *Diadema* could be found in high densities in rock, coral reef, mangrove roots, sea grass beds, and sand flats. Yet recent studies on *Diadema* populations post-mortality have only been conducted in reef environments—fringing reefs, patch reefs, and reef fronts (Miller et al. 2003; Lessios 2005; Steiner 2006) possibly implying *Diadema* are less common, or perhaps that these sea grass beds and mangrove roots are less important or less affected by *Diadema* than coral reef. Though *Diadema* were observed in reefs, sea grass, and mangroves at Sunset Point, densities in the latter two habitats were very low (0.05/m^2 for sea grass and 0.04/m^2 for mangrove [Table 3]). This observation may imply one of two situations, 1) populations before 1983 had low densities in sea grass beds and mangrove roots and were left unaffected by the mortality, but this situation is unlikely since no populations in the Western Atlantic are known to have been unaltered by the die-off, or 2) populations in these habitats were affected by the mass mortality and have only slightly recovered, a more probable situation due to comparisons with other *Diadema* populations in Panamá.

One surprising observation was the preference of *Diadema* at the mangrove island to inhabit relatively low profile, monospecific clusters of reef on the south side rather than the eastern reef with many species of coral and a large profile. Ogden and Carpenter (1987) suggested reef areas with higher spatial heterogeneity, such as the reef on the west side of mangrove island, provide greater protection from predators and as a result probably maintain higher population densities of *Diadema* regardless of the abundance of predators. However, the diverse reef at the mangrove island was an exception to this observation. The western reef offered both more areas to hide and more variety in algae as well as more overall algae cover, yet there was half the amount of *Diadema* as was found in the cluster of *Porites* on the south reef.

Diadema antillarum has been identified as a keystone herbivore in Western Atlantic marine environments (Lessios et al. 1984b, Randall & Starck 1964; de Rutyr van Steveninck & Bak 1986), and recent studies have showed the central importance of herbivory in reef health (Knowlton 2001) making healthy *Diadema* populations essential in reefs throughout the Caribbean. Two particularly important coral, *Acropora* spp. and *Montastraea* spp., were both identified at the mangrove island where *Diadema* density was low (0.01/m^2) and algal cover was high (often above 75%). All species of algae that have become very abundant across the Caribbean following the mortality (Ogden & Carpenter 1987), including *Dictyota* spp., *Padina* spp., *Halimeda* spp., and *Jania adherens* were present in the study reefs, in addition to other types of algae, *Caulerpa* spp. and *Ventricaria ventricosa*. Additionally, the frequency of small, single colonies of coral in the mangrove island was low indicating the coral present is most likely several decades old. This qualitative assessment makes the mangrove island appear unhealthy in both terms of live coral cover and recruitment rates, which could be the result of the low *Diadema* density on the reef. It could be predicted that increases in population at this reef will likely be slow because of the low frequency of adult *Diadema* that could recruit juveniles and unfavorable conditions for juvenile recruitment, in general, on the poorly grazed algae. The algae here are unlikely to be grazed because of the low population density of *Diadema* and the inaccessibility of much of the algae in hard to reach coral crevices. Additionally, there were large populations of damselfish (*Stegastes* spp.) in the area that could provide a source of competition for *Diadema*.

CONCLUSION:

Though there are no populations of *Diadema antillarum* in the Caribbean known to have escaped the mass mortality event of 1983-1984, it is difficult to assess the change in population at Sunset Point and the mangrove island on the south side of Isla Colón in Bocas del Toro without information from ongoing monitoring. In conclusion, it is possible to determine the current state of the population. Overall density at Sunset Point is 0.22 individuals /m^2 while at the mangrove island, where reefs are more diverse, density is less than 0.02 individuals /m^2. Though *Diadema* were present in all three types of habitats surveyed, coral, sea grass beds, and mangrove roots, they were found in higher densities in coral, particularly beds of live finger coral, *Porites porites*, in comparison to reefs of more diversity and a greater profile. In addition, *Diadema* in the finger coral had higher frequency of larger test sizes suggesting the populations in these areas are older and of sexual maturity. An analysis of the sex ratio provided interesting results showing the whole sample size to be female, with only one female having been recently fertilized. Sex ratio in this population is heavily weighted toward females who often congregate not only in groups according to size class but also by sex. Average test sizes of the populations in Sunset Point and at the mangrove island were lower than those of other sites around the Caribbean recently surveyed but are similar to the sizes recorded for *Diadema* in Kuna Yala on the eastern Atlantic coast of Panamá. Assuming the population has been recovering since 1983 in Bocas del Toro, it may be doing so at a similar rate as the populations in other parts of Panamá and may be nearing a stage of rapid recovery.

Unfortunately, these two sites, which were chosen because of their accessibility during a limited time period created many limitations for this study. The short duration of the study restricted the size of the study area, both in the number of transects, number of sites, and the overall area of Bocas del Toro covered by the sites. Therefore, the information concluded from this study does not indicate current status of the total *Diadema* population in Isla Colón or of Bocas del Toro, Panamá. In order to come to a better understand of the populations of *Diadema* in Bocas del Toro, it is essential to continue this type of study in more locations around the islands over an extended period of time. Though that information will still not show the whole picture of the change in *Diadema* populations since 1983, ongoing monitoring will provide information that can be extrapolated to provide a better assumption on population dynamics over the last 25 years.

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WORKS CITED:

AGRRA. Evaluación rápida de arrecifes del Atlanticos y del Golfo de México.

Bak, RPM. 1994. Sea urchin bioerosion on coral reefs. Coral Reefs 13:99-103.

Bak, RPM, MJE Carpay, ED de Rutyr van Steveninck. 1984. Densities of the sea urchin *Diadema antillarum* before and after mass mortalities in Curaçao. Marine Ecology Progress Series 17:105-108.

Bauer, JC. 1980. Observations on geographical variations in population density of the echinoid *Diadema antillarum* within the Western Atlantic. Bulletin of Marine Science 30:509-514

Bauer, JC. 1982. On the growth of a laboratory-reared sea urchin, *Diadema antillarum* (Echinodermata: Echinoidea). Bulletin of Marine Science. 32: 643-645.

Bellwood, DR, TP Hughes, C Folke, M Nystrom. 2004. Confronting the coral reef crisis. Nature 429:827-833.

Birkelund C. 1997. Life and death of coral reefs. Chapman & Hall, New York, NY.

Carpenter, RC. 1984. Predation and population density control of homing behavior in Caribbean echinoid *Diadema antillarum*. Marine Biology 82(1): 101-108.

Colin, PL. 1988. Marine invertebrates and plants of the living reef. T.F.H. Publications, Neptune City, NJ.

de Rutyr van Steveninck, ED and RPM Bak. 1986. Changes in the abundance of coral reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. Marine Ecology Progress Series 34:87-94.

Edmunds, PJ and RC Carpenter. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Science Early Edition pg 1-5.

Hendler, G, JE Miller, DL Pawson, PM Kier. 1995. Echinoderms of Florida and the Caribbean: Sea Stars, Sea Urchins, and Allies. Smithsonian Institution Press, Washington DC.

Hunte, W, D Younglao. 1988. Recruitment and population recovery of *Diadema antillarum* (Echinodermata; Echinoidea) in Barbados. Marine Ecology Progress Series 45: 109-119.

Jackson, JBC. 2001. What was natural in the ocean? Proceedings of the National Academy of Science 98(10):5411-5418.

Kaplan, EH. 1988. *Diadema antillarum*. Peterson Field Guides: Southeast Caribbean Seashores. Houghton Mifflin, Boston, MA.

Knowlton, N. 2001. Sea urchin recovery from mass mortality: New hope for Caribbean Coral Reefs. Proceedings of the National Academy of Science 98(9): 4822-4824.

Lessios, HA, JD Cubit, DR Robertson, MJ Shulman, MR Parker, SD Garrity, SC Levings. 1984a Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. Coral Reefs 3(4): 173-182.

Lessios, HA, DR Robertson, JD Cubit. 1984b. Spread of *Diadema* mass mortality throughout the Caribbean. Science 226(4672): 335-337.

Lessios, HA. 1988a. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? Annual Review of Ecology and Systematics 19: 371-393.

Lessios, HA. 1988b. Population dynamics of *Diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panamá. Marine Biology 99: 515-526.

Lessios, HA, MJ Garrido, BD Kessing. 2001. Demographic history of *Diadema antillarum*, a keystone herbivore on Caribbean reefs. Proceedings of the Royal Academy of London 268:2347-2353.

Lessios, HA. 2005. *Diadema antillarum* populations in Panamá 20 years following mass mortality. Coral Reefs 24(1): 125-127.

Levitan, DR. 1988. Density-dependent size regulation and negative growth of the sea urchin *Diadema antillarum* Philippi. Oecologia 76(4): 627-629.

Lugo Ascorbe, MA. 2004. Population status of the black sea urchin *Diadema antillarum* (Philippi) in La Parguera, Puerto Rico, 20 years after the mass mortality event. University of Puerto Rico, Mayaguez Campus, pp. 1-61.

Miller, RJ, AJ Adams, NB Ogden, JC Ogden, JP Ebersole. 2003. *Diadema antillarum* 17 years after mass mortality: is recovery beginning on St Croix? Coral Reefs 22(2): 181-187.

Miller, RJ, AJ Adams, JP Ebersole, E Ruiz. 2007. Evidence for positive density-dependent effects in recovering *Diadema antillarum* populations. Journal of Experimental Marine Biology and Ecology 349(2): 215-222.

Ogden, JC, RC Carpenter. 1987. Species profiles: Life history and environmental requirements of coastal fishes and invertebrates (South Florida)—Long Spined Sea Urchin. US Fish and Wildlife Service Biological Report 82(11.77): 1-17.

Phinney, JT, F Muller-Karger, P Dustan, J Sobel. 2001. Using remote sensing to reassess the mass mortality of *Diadema antillarum* 1983-1984. Conservation Biology 15(4): 885-891.

Randall, JE and WA Starck II. 1964. Notes on the biology of the echinoid *Diadema antillarum*. Caribbean Journal of Science 4(2): 421.

Shulman, MJ and DR Robertson. 1996 Changes in the coral reefs of San Blas, Caribbean Panama: 1983 to 1990. Coral Reefs 15(4): 231-236.

Smithsonian Tropical Research Institute (STRI). 2008. Bocas del Toro species database: Echinodermata. Accessed 25 May 2008. http://biogeodb.stri.si.edu/bocas_database/search/phylum/8/

Stenbeck, RS. 2003. Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978-1988). NOAA/RSMAS pg. C31-C38