

Temporal and spatial distribution of early larval stages
and post-larval recruitment of the long-spined sea
urchin *Diadema antillarum* in La Parguera, Puerto
Rico

by

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Abstract

This study describes temporal variations of early larval stages of the long-spined sea urchin, *Diadema antillarum* in neritic waters of La Parguera, Puerto Rico. Early larval stages were sampled by oblique plankton tows between the new and full moons at monthly intervals from April 2005 to July 2006, and September 2006. Early pluteus stages (< 5 days old) were found in 13 out of the 16 months of sampling, indicating that *Diadema* spawns throughout the year. Higher reproductive activity occurred during April and July 2005. Larval abundances were variable between years and successive months possibly reflecting the inconsistency of sampling aggregated or patchy distributions of larvae. Drogues released during the April spawning season from an area of high aggregations of mature adults indicated that a neritic, topographically steered flow fringing the inner shelf forereef platforms confined the early larval stages of *Diadema* within the insular shelf of La Parguera.

Spatial and temporal trends of *Diadema* post-larval recruitment were examined during two recruitment studies at three reefs at La Parguera, Puerto Rico from September 2005 to September 2006, and at six reefs from February to April 2008 and from July to September 2008. Settling plates built out of astroturf were used to measure recruitment at monthly intervals. Plates were placed at various depths on individual mooring lines. During the first study a total of 277 recruits of *Diadema* were collected. Post-larvae were mostly collected from the shelf-edge reef, with the exception of two recruits collected at the midshelf reef during October 2005. There was a significant difference in recruitment among months at the shelf-edge site (ANOVA, $F_{12, 38} = 9.94$, $p < 0.0001$) with the highest value (1,067 ind/m²) occurring in July 2006. The spatial and temporal trend of the 2008 study was similar to the 2005-2006 recruitment study. From a total of 221 *Diadema*

recruits, 218 were collected from the shelf-edge reefs (Old Buoy and El Hoyo) during 2008. The remaining three recruits were collected at Media Luna. Peak recruitment of *Diadema* (265 ind/m²), was observed during late summer at Old Buoy. Overall, the maximum recruitment rates observed at the La Parguera shelf-edge are higher than those measured in Curacao, Florida Keys and Canary Islands. Since surveys in the La Parguera region have demonstrated higher densities of *Diadema* at inshore reefs than at the shelf-edge, the higher recruitment observed at the shelf-edge reefs suggest that recruitment is not a major determinant of the spatial distribution of the adult population in La Parguera. The relatively high recruitment rates of *Diadema* at the shelf-edge, is evident that upstream sources of larvae are available. Assuming that recruitment on the plates is representative of recruitment on the reefs themselves, the inverse relationship between recruitment and adult densities raises an important issue about the population dynamics (mortality) of this species. Post-settlement processes, such as predation pressure by microinvertebrates may have an influence on the distribution of *Diadema* settlers.

Resumen

Este estudio describe los patrones de abundancia espacial y temporal de las etapas larvales tempranas del erizo de espinas largas *Diadema antillarum* en aguas costeras de La Parguera, Puerto Rico. Las larvas se obtuvieron mediante una serie de arrastres oblíquos entre la luna nueva y luna llena, desde abril, 2005 a julio, 2006 y en septiembre, 2006. Se encontraron las etapas pluteus de las larvas (< 5 días) en 13 de los 16 meses del muestreo, indicando que *Diadema* desova todo al año. La abundancia larval varió entre años y meses sucesivos posiblemente demostrando una distribución irregular. La abundancia promedio fue significativamente más alta durante abril y julio 2005, en comparación con los otros meses lo que puede sugerir una actividad reproductiva alta durante este periodo. Los flotadores lanzados en la temporada de mayor desove en una área de alta agregación de adultos fueron indicativos de un flujo costero, topográficamente dirigido incidiendo en las plataformas interiores del arrecife frontal, lo que mantiene las larvas juveniles dentro del litoral insular de La Parguera, Puerto Rico.

La distribución espacial y temporal del reclutamiento post-larval de *Diadema* fue examinada en tres arrecifes desde septiembre, 2005 a septiembre 2006, y en seis arrecifes desde febrero a abril, 2008 y desde julio a septiembre, 2008 en La Parguera, Puerto Rico. Se construyeron placas de asentamiento de grama artificial para medir el asentamiento mensual de las larvas. Las placas se colocaron a diferentes profundidades en sogas de anclaje independientes. En el primer estudio se colectaron un total de 277 reclutas de *Diadema*. La mayoría de los reclutas se colectaron en el beríl, con la excepción de dos individuos que se encontraron dentro del beríl durante octubre, 2005. Se observó una alta abundancia de reclutas durante julio 2006 (1,067 ind/m²). El patrón espacial y temporal observado en el estudio de 2008 fue similar al patrón del primer estudio de reclutamiento.

Durante el 2008, de un total de 221 reclutas, 218 se colectaron en los arrecifes que se encuentran en beríl (Old Buoy y El Hoyo). Tres reclutas se colectaron a Media Luna. Se observó un pico de reclutamiento de *Diadema* (265 ind/m²) tarde en el verano en el arrecife Old Buoy. La tasa de reclutamiento máxima durante estos dos estudios fue más alta que la tasa de reclutamiento antes del evento de muertes en masa de *Diadema* y también mayor que los reportados en los Cayos de la Florida e Islas Canarias. Debido a que inventarios en La Parguera han resultado con alta densidad de adultos de *Diadema* en los arrecifes cerca de la costa, la alta tasa de reclutamiento en arrecifes de mar afuera sugiere que esto no es un factor determinante en la distribución espacial adulta del erizo. La alta tasa de reclutamiento en el beríl, es indicativo que fuentes de larvas están presentes corriente arriba. Los procesos de post-reclutamiento, como depredación, pudieran afectar la distribución poblacional de *Diadema* más que el reclutamiento porque las fuentes de reclutamiento en este estudio se encontraron en áreas donde los individuos adultos eran muy escasos.

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Dedication

**To my family
Dad, Mom and Matt
You have always been there for me
Your support and love has helped me get to where I am now
&
Loved Ones which were with me in spirit
Grandma B and Grandpa Williams**

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Preface

The following dissertation has been written in four chapters. The first chapter has been published in Caribbean Journal of Science. I was a co-author on the second paper, which has been published as a Note in Coral Reefs. The third chapter has been accepted as a Note in Coral Reefs and is in the process of being published. Lastly, the fourth chapter has been submitted to the Journal of Experimental Marine Biology and Ecology.

General Introduction

Mass Mortality of *Diadema antillarum*

Lessios (1995) stated that the 1983-1984 mass mortality of *Diadema antillarum* was the most extensive and severe die-off ever recorded for a marine invertebrate. Before 1983, the presence of this organism was common (22 ind/m²) on coral reef habitats (Lessios 1995). After the massive die-off, populations were drastically reduced by 95-100% in many Caribbean locations (Lessios 1995). It was theorized that a water-borne pathogen transported by surface currents was the main cause of this mass mortality (Lessios et al. 1984, Phinney et al. 2001). In addition, one report stated that ballast water from ships was also linked with the spread of the urchin-killing pathogen (Bak et al. 1984). The spread of the massive mortality is believed to have originated from Punta Galeta, Panama and proceeded in two different fronts. The first front went east from Panama to Tobago. The second front was faster and traveled east of Costa Rica, North of Cayman Island, Belize, Mexico, Jamaica, Gulf of Mexico, Florida, and to Bermuda. In February of 1984, an area of 3.5 million square kilometers was affected by this mass mortality (Lessios 1988a). After the mass mortality drastic shifts occurred in the benthic community structure of Caribbean reefs such as a significant increase in abundance of benthic algal cover (Hughes et al. 1987, Levitan 1988, Carpenter 1990a).

Effects of the Mass Mortality

Adult *D. antillarum* play an important role in structuring coral reef communities by controlling algal abundance (Carpenter 1981, Carpenter 1986, Carpenter 1990a, Carpenter 1990b, de Ruyter van Steveninck and Bak 1986, Odgen et al. 1973, Robertson 1987, Sammarco 1982) and are one of the principal agents of bioerosion on reefs (Bak et

al. 1984, Scoffin et al. 1980). Also, *D. antillarum* is a commensal for many organisms, such as juvenile fishes, crustaceans, and echinoderms (Randall et al. 1964, Craft 1975, Steiner and Williams 2006a).

Diadema is a keystone herbivore that can exert control on the benthic algal populations on coral reef communities. Within the first week after the die-off, Bak et al. (1984) witnessed ubiquitous filamentous algae increasing significantly in density and length on the reefs of Curacao. In Jamaica, where the density of *D. antillarum* was reduced from 6.6 ind/m² to 0.0 ind/m², Liddell and Ohlhorst (1986) stated that the algal cover of noncrustose algae increased in reefs from 30.7 to 49.7%. In some reef locations, benthic algal cover increased between 100% and 250% (Phinney et al. 2001). The absence of *D. antillarum* did not only influence the increasing primary productivity on coral reef communities, but it also impinged on the settlement of sessile recruits like corals and the growth of adult corals.

Edmunds and Carpenter (2001) stated that *D. antillarum* might regulate coral abundance and diversity by keeping a top-down control of algal presence. Coral planulae and recruits are not able to settle and mature without algal-free zones (Raloff 2001). The mass mortality of *D. antillarum* not only affected coral recruitment but also the adult coral population. Some adult corals are more susceptible to algal overgrowth than others based on their morphology. For example, in Jamaica, corals with morphology prone to algal overgrowth, such as *Agaricia agaricites* suffered the highest mortality with the loss of this main herbivore (Lessios 1988b).

Diadema acts as a microhabitat for many organisms, thereby influencing reef community structure. Many organisms such as mysid shrimps, juvenile fishes,

crustaceans, and juvenile *D. antillarum* depend on adult *D. antillarum* for their survival. Steiner and Williams (2006a) found that when *D. antillarum* were collected for test measurements, the decapod *Percnon gibbesi* (Grapsidea), the cleaning goby, *Gobiosoma genie* and other juvenile fish that were commensals, were preyed upon by the wrasse *Thalassoma bifasciatum* (Labridae) and the damselfish *Stegastes fuscus* (Pomacentridae). Craft (1975) described the biology of *P. gibbesi* and its commensal association with *D. antillarum*. Craft (1975) observed that slippery dicks (*Halichoeres bivittatus*) became increasingly aggressive during the collection and relocation of *P. gibbesi* and would attack the crabs immediately after the diver uncovered them. After the post-die off, the reefal communities were characterized by greater algal abundance, less bioerosion, decreased survival of coral recruits and adults.

Present Abundance of *Diadema antillarum*

Twenty years after the mass mortality the recovery of *D. antillarum* has been very slow, while some areas show no signs of a recovery. *Diadema* densities at present remain far below pre-mortality densities (Hughes et al. 1987, Karlson and Levitan 1990, Forcucci 1994, Moses and Bonem 2001) in St. John, Dry Tortugas, Florida Keys, and Jamaica. Some believe that the effects of the mass mortality are irreversible (Karlson and Levitan 1990). However, signs of a slow recovery have been reported in Barbados (Hunte and Younglao 1988), St. Croix (Miller et al. 2003, Miller et al. 2007), Puerto Rico (Weil et al. 2005), Panama (Lessios 2005) and Dominica (Steiner and Williams 2006b). At present, abundance of *D. antillarum* in Puerto Rico is still low (0.83 to 1.39 ind/m² Weil et al. 2006) compared to pre-die off numbers (12 ind/m², Craft 1975). Lugo (2004) described the population status of *D. antillarum* in La Parguera and found that the mean

densities ranged from 0.01 to 0.82 ind/m². In La Parguera, Puerto Rico the *D. antillarum* populations are commonly found in shallow reef habitats. The past 5-10 years adult distributions have been variable in sea grass areas, high aggregations from 1.09 to 1.30 ind/m² can be found (Weil et al. 2006). While their abundance at shelf-edge locations rarely exceeds 0.02 ind/m². Lugo (2004) observed densities of medium-big urchins in shallow waters and higher densities of small individuals at deeper reefs. *Diadema* densities from recovering locations are still lower than that of the pre-die-off records.

Problems of Recovery

Because of their high fecundity (Levitan 1988, Levitan 1989), the recovery of *D. antillarum* could be expected to be quicker. There is a positive relationship between fertilization success and the population size of a free-spawning invertebrate (Levitan 1991). Lessios (2005) stated that the lack of recruitment in Panama could be caused by the lack of enough adults at upstream areas to reproduce at a rate that would overcome the natural mortality rates. Low larval supply has been identified as a factor limiting the recovery in the Florida Keys (Lessios 2005, Miller et al. 2009). Larval predation may also be an important factor hindering larval replenishment of downstream islands. Cowen et al. (2000) stated that even though a large amount of fish larvae may be released from a given population, significant numbers quickly decrease when realistic levels of diffusion and mortality are added.

A third reason for the lack of recovery is that there is not enough suitable reef substrate for settlement. Bak (1985) found that as the degree of fouling of the substrate increased, the settlement of *D. antillarum* decreased. Algal biomass increased on reefs after the mass mortality. Presently, many locations still have high algal biomass at reefal

sites, which is constraining recruitment of coral planulae (Raloff 2001) and perhaps, recruitment of *D. antillarum* on the reef. The fourth reason for the lack of recovery is post-larval predation. Szmant (The *Diadema* Workshop, 2004) stated that predation on *D. antillarum* juveniles is another factor influencing the recovery in the Florida Keys.

Larval Biology of *Diadema antillarum*

Free-spawning is a mechanism that organisms utilize to disperse their genes and increase their population success. Fertilization of eggs of free-spawning individuals is difficult because of the rapid diffusion and limited life span of gametes in a dynamic ocean (Levitan 1995). The fertilization of the egg is critical for population survival and there are many mechanisms that organisms use to increase fertilization success. Some of these techniques are simultaneous spawning, aggregation, and large population size (Levitan 1995).

The minimum reproductive size of *D. antillarum* was found to be 3.8 cm in diameter (Lugo 2004). *Diadema* reproduction follows a lunar cycle, peaking during the new moon (Eckert 1998, Iliffe and Pearse 1982, Lessios 1981, Lessios 1991). However, Levitan (1988) found that *D. antillarum* spawned 25 days out of the 29 day in the lunar month, while also indicating that *D. antillarum* exhibits asynchronous spawning. Levitan (1988) noted that there was a slight increase of aggregative behavior throughout the lunar month. This aggregative behavior may increase fertilization success even if *D. antillarum* exhibit asynchronous spawning. In La Parguera *D. antillarum* reproduces yearlong with a reproductive peak between the spring and summer (Lugo 2004).

Echinopluteus

Echinoids display a complex life-history, which involves external fertilization of pelagic eggs, planktonic larval development and recruitment into a benthic habitat where it reaches an adult stage and reproduces (Smith 1997). The mean egg diameter of *D. antillarum* is $72.7 \pm 2.4 \mu\text{m}$, which is relatively smaller than other echinoids (Amy 1983). McEdward (1986a) predicted that species with larger eggs and larger initial larvae would either remain larger at each stage of development or develop to a given stage faster than species with small eggs. The time span that it takes a zygote to develop into an early plutei varies with species. Amy (1983) found that it takes 1,803 min. for a *D. antillarum* early plutei to develop. While, *Echinometra viridis* takes 1,205 min. to develop into an early pluteus. Therefore, compared with other tropical echinoids, *D. antillarum* fertilization and larval development are relatively slow.

In the course of its development, the echinoplutei undergoes remarkable changes in body (McEdward 1986b). The echinoplutei are characterized by bilateral symmetry, a complete gut; a convoluted ciliated band composed of short simple cilia that is used for swimming and feeding; 1-6 pairs of larval arms; nervous system closely associated with the ciliated band; paired, tripartite coeloms; and a calcareous endoskeleton (Wray 1992, Pearse and Cameron 1991). This endoskeleton develops into three major rods (body rod, postoral arm rod, and anterolateral arm rod), which support the arms. The rate of development and number of rods depends on the species. *D. antillarum* produces their first pair of long postoral arm rods by the fourth day after fertilization. By the eighth day, a pair of anterolateral arm rods developed (Eckert 1998). *Diadema* larvae only develop four arms compared with other echinoplutei, which develop typically eight arms (Okazaki 1975).

Larval size and shape are also important determinants of larval functional performance through influence on susceptibility to predation (Eckert 1998), swimming speeds (Emlet 1983), metabolic requirements (McEdward 1984) and clearance capacity (Hart and Strathmann 1995). The *D. antillarum* pluteus arm-span is larger than most tropical echinoid larvae. *Diadema* larval arm can grow to over 4.5 mm long, for a total arm span of over 9 mm (Eckert 1998). In addition, *D. antillarum* larva has the ability to move both arms 90°. Therefore, *D. antillarum* can maximize its arm span by having both arms parallel or vertical to each other. Eckert (1998) stated that with this large arm span, *D. antillarum* larvae might not be as vulnerable to predators as other echinoid larvae. Hart and Strathmann (1994) studied the positive association between the size of the larval arms and ciliated band length. Larval echinoids with larger arms will contain extensive ciliate bands. Ciliated bands are pertinent for feeding and locomotion.

The distribution of larvae is influenced by the dynamics of water motion in the coastal ocean in relation to the location of the spawning sites. Motility depends both on internal, physiological processes and on the physical properties of the fluid environment. The physical properties of water (e.g. density and dynamics viscosity) have a predominant influence on an organism's motion and are considered to be a major force in the evolution of their various modes of locomotion and feeding (Podolsky and Emlet 1993). A ciliated band around the echinoplutei arms is one mechanism that counteracts the physical properties of water. Ciliary locomotion occurs when the Reynolds number is below unity and where viscous forces control fluid behavior (Vogel 1994). For an actively swimming organism, the velocity increases from free-stream velocity to some maximum at or near the tips of the cilia and then decreases approximately linearly when

reaching the stroke region (Emlet 1983). Drag counteracts the velocity of the ciliary bands in the echinoplutei. Vogel (1994) defines drag as the rate of removal of momentum from a flowing fluid. Drag increases with arm length, arm number and arm orientation in a planktonic larva (Emlet 1983). Drag on the arms may decrease the sink rates of the larvae. *D. antillarum* exhibits arm flaring which can also increase drag and therefore decreases the sink rate. Therefore, the echinoplutei of *D. antillarum* may have some influence on its recruitment. Arm flaring does not alone increase drag, it also increases the diameter of the larva, which may prevent it from being eaten by predators in the water column. Conversely, predation on *Diadema* echinoplutei may be high since the size of the larvae may make them more visible.

Diadema metamorphosis is slow (4-6 weeks in a laboratory) compared to other tropical echinoderms, such as *Lytechinus variegatus*, that metamorphose in two weeks or less (Boidron-Metairon 1988). *Diadema* metamorphosis may be delayed for a longer time until suitable settlement sites are found since the larvae is planktrophic. It has been suggested that with this long larval stage, *D. antillarum* can be subject to predation and/or offshore transport for a longer period (Eckert 1998). The duration of larval development helps to understand the recruitment dynamics and estimates how long the larvae are planktonic (Eckert 1998).

The metamorphosis from larvae to demersal adult in echinoderms is extreme, involving extensive tissue absorption and the transformation from bilateral to pentaradial symmetry as the adult form develops from a rudiment on the larval body (McEdward 1986b).

Diadema metamorphosis is similar to other sea urchins. The juvenile (settler) is yolky

colored with red pigment spots and has small spines and five tube feet. The test diameter of a *D. antillarum* juvenile is approximately $515 \pm 17 \mu\text{m}$.

Recruitment

The colonization of benthic habitats by marine organisms with planktonic life stages involves three phases: planktonic development and dispersal, habitat selection and settlement (Keough and Downes 1982). Settlement rate is defined as the rate at which planktonic larvae of benthic organisms establish permanent contact with the substrate (Jenkins et al. 2000). Recruitment, which is the fourth phase, includes the survival of the organism until counted by an observer (Keough and Downes 1982). Bak (1985) defines *D. antillarum* recruits as individuals $< 3 \text{ mm}$. Recruitment is a key mechanism shaping and structuring reefal communities (Cameron and Schroeter 1980). Recruitment rather than reproductive output is the key concept for marine species demography and is one of the main determinants of spatial and temporal variations in population sizes (Cowen et al. 2000). Trying to identify sources and/or sinks of larvae is important to understanding supply to populations (Miller and Emlet 1997). Marine invertebrate larvae may navigate to suitable settlement sites by responding to gradients of environmental stimuli (Kingsford et al. 2002). Larval availability, substrate selection and juvenile mortality are factors that influence recruitment to a population.

Bak (1985) carried out the first documented *D. antillarum* settlement experiment. Bak (1985) used experimental substrate, such as plastic crates to compare settlement at two different reefs that were characterized by high and low adult sea urchin densities. The smallest recruits found in this study were between 0.9-1 mm. Bak (1985) found that in Curacao there was continuous but sparse settlement throughout the year with two

pronounced peaks (March/April and September/October) and two less distinct peaks (June/July and December and January). More recruits settled at the reef site that had the greater adult densities, maximum density reaching 102- 188 ind/m². In addition, the degree of fouling of the experimental substrate affected the settlement of *D. antillarum*. Settlers were more attracted to the relatively clean surfaces, such as those produced by *D. antillarum* grazing. This may explain why there was a significant amount of recruits at the site with more *D. antillarum*.

More recently, there has been *D. antillarum* recruitment experiments carried out in the Canary Islands (Hernández et al. 2006) and the Florida Keys (Miller et al. 2008). There has been no other reported settlement experiments in the Caribbean. Hernández et al. (2006) found a monthly maximum of 24-26 *D. antillarum* recruits/sampler with each sampler containing 100 pieces of experimental larval collectors (small plastic balls with a very high surface exposed area). Also, Miller et al. (2008) found that the overall rates of recruitment in the Florida National Marine Sanctuary were variably low, with the highest rates being below 2 settlers/m² and monthly counts of zero were common.

Temporal Variation of Early Larval Stages of the Long-Spined Sea Urchin *Diadema antillarum* in La Parguera, Puerto Rico

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ABSTRACT.—This study describes temporal variations of early larval stages of the long-spined sea urchin, *Diadema antillarum* in neritic waters of La Parguera, Puerto Rico. Larvae were sampled with oblique plankton tows between the new and full moons at monthly interval from April 2005 to July 2006, and September 2006. Early pluteus stages (< 5 days old) were found in 13 out of the 16 months of sampling, indicating that *Diadema* spawns throughout the year. Mean abundances were significantly higher during April and July 2005 compared to the other months, suggesting higher reproductive activity during these months. Larval abundances were variable between years and successive months possibly reflecting a patchy distribution of larvae. Drogues released during the April spawning season from an area of high aggregations of mature adults indicated that a neritic, topographically steered flow fringing the inner shelf forereef platforms confined the early larval stages of *Diadema* within the insular shelf of La Parguera.

KEYWORDS.—*Diadema antillarum*, pluteus larvae, temporal distribution, La Parguera, Puerto Rico, Caribbean

INTRODUCTION

Diadema antillarum (Echinodermata, Echinoidea) suffered massive die-offs from a possible water-borne pathogen during the early 1980's in the Caribbean Sea (Lessios et al. 1984). More than twenty years after the mass mortality, the recovery of *Diadema* populations in Caribbean reefs has been very slow, while some areas show no signs of recovery. Recovery has been reported in Barbados (Hunte and Younglao 1988), St. Croix (Miller et al. 2003), Panama (Lessios 2005), Jamaica (Carpenter and Edmunds 2006) and Puerto Rico (Weil et al. 2005).

In La Parguera, Puerto Rico, the present *Diadema* populations are commonly found in shallow reef habitats. Weil et al. (2005) found average densities in six sampled reef sites ranging from 0.83 to 1.39 ind. m⁻² and from 1.09 to 1.30 ind. m⁻² in sea grass plains. During the past 4 yrs, an absence of adult *Diadema* has been noted at shelf-edge locations in La Parguera (S. M. Williams, pers. obs.). Considering their high fecundity (Levitan 1988, 1989), the population recovery of *Diadema* would have been expected to be quicker. Possible reasons for the slow recovery of this sea urchin may be associated

with: 1) low fertilization success due to the low density of adult *Diadema*, 2) insufficient larval supply due to higher mortality rates, 3) high predation on recruits and/or 4) the lack of suitable reef substrate for settlement.

Planktonic larval dispersal is difficult to measure due to small larval size, behavior and the dynamic conditions in which they live. The distribution of planktonic larvae is influenced by the velocity and direction of water currents from spawning sites. Questions about larval transport focus largely on: (1) where they go, (2) dispersal and (3) where they came from (Levin 2006). At present, there is a lack of information on *Diadema* larval behavior, abundance and distribution in the water column. Estimates of larval duration from laboratory studies range from 4-5 wks (Eckert 1998) to 52 days (Carpenter 1990). Levitan (1988) found that *Diadema* were more likely to spawn on the new moon versus the full moon although spawning was observed on 25 of the 29 lunar days.

This study focused on the temporal abundance and dispersal of early *Diadema* larvae in La Parguera, Puerto Rico. The main

objectives of this study were to (1) characterize the temporal patterns of the abundance of *Diadema* larvae and (2) describe transport trajectories of early larval stages from an adult spawning site in La Parguera.

MATERIALS AND METHODS

Study site

La Parguera is located on the southwest coast of Puerto Rico (Fig. 1). Two lines of emergent reefs run roughly parallel to the mangrove shoreline and a submerged reef fringes the shelf edge. The insular shelf extends approximately 11 km offshore. Adult *Diadema antillarum* densities were measured from 10 randomly distributed belt transects (2 X 25 m) on patch reefs on the backreef of

Media Luna, a mid-shelf emergent reef (17° 56.500'N, 67° 02.482'W; Fig. 1) where up to 3.28 ind. m⁻² of adult *Diadema* were observed in preliminary surveys.

Water current velocities and directions

Fluorescent dye and drogues were used as indicators of the potential dispersal trajectories of early larval stages of *Diadema* from the mid-shelf reefs of La Parguera. On April 15, 2005, one week after the new moon and the previously reported peak month for increased gonad indices of *Diadema* in La Parguera (Lugo, 2004), approximately 40 adult *Diadema* were injected with 0.5M of KCL at the backreef of Media Luna. At 1:00 PM fluorescent dye was

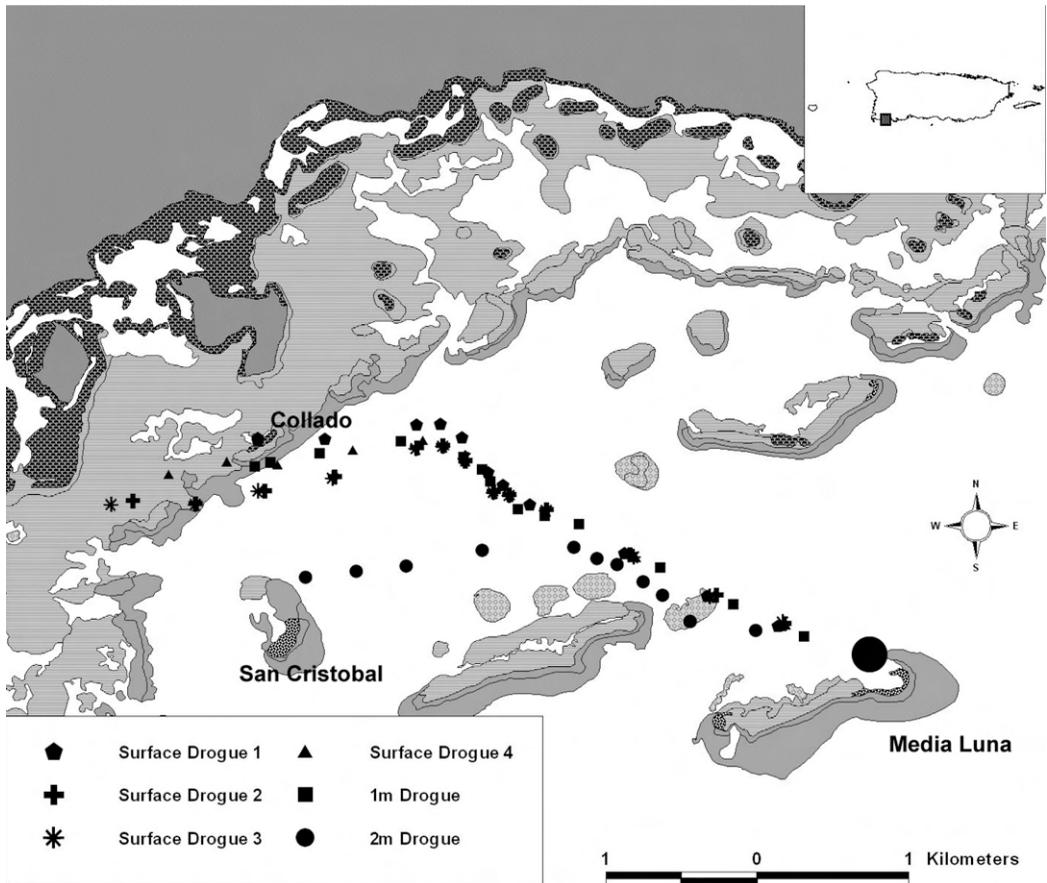


FIG. 1. Drogue trajectories during a 14 hour sampling period at the study location in La Parguera, Puerto Rico. Symbols depict different drogues. The large darken encircled point indicates point of release.

released in the area where most of the injected urchins were observed spawning. About 5 min after the release of the dye six drogues were placed around the perimeter of the dye patch. Each drogue consisted of four perpendicular vanes with a cross-sectional area of 0.36 m² and shaped as a cruciform. The vanes were suspended by a cable from a single, numerically marked central buoy. Lights and marking tape were attached to the top of the buoys for tracking at night. Four surface drogues, one drogue that extended over a depth of 1 m and another at a depth of 2 m. Positions for each drogue were obtained approximately every hour using GPS. The drogues were only tracked for a total of 14 h due to rough sea conditions.

An Acoustic Doppler Current Profiler (ADCP – RD Instruments) was deployed April 5, 2005 at a depth of ~18 m depth in the channel between Media Luna and Turumote reefs (17° 55.893'N, 67° 02.313'W) near the adult *Diadema* spawning site. Data on water current velocity and direction was obtained from 1 m bins of the water column every 15 min for one month.

Plankton surveys

Diadema larvae were sampled with a 0.5 m diameter plankton net with a 64 µm mesh in the area where the drogues were last marked, between Cayo Collado (17° 57.250'N, 67° 04.682'W) and Cayo San Cristobal (17° 56.525'N, 67° 04.582'W). An Ocean Test flowmeter (MF315) and pressure/temperature sensor were attached to the net. Three oblique one minute tows were taken between the surface and 15 m approximately at monthly intervals between the new and full moon from April 2005 to July 2006, and September 2006. Plankton tows were always taken during the mid-morning to early afternoon and samples were preserved in 3% formalin.

All stages of *Diadema* larvae were counted using Eckert's (1998) manuscript for identifying and aging the early larvae. Also, R. Emler helped in the identification of these larvae to the family level. The only other species of sea urchin in the Diadematae family in Caribbean waters is *As-*

tropyga magnifica and its incidence is rare, especially in Puerto Rico.

Statistics

A one-way Analysis of Variance (ANOVA) test was applied to examine differences of velocity between the drogues with the Statistica 7 package. A nested ANOVA test was applied to evaluate temporal and yearly patterns of larval abundance. The months were nested within the appropriate years. The Pearson correlation coefficient was used to examine the temporal larval abundances vs. surface temperature measurements. Sea surface temperature (SST) data was obtained from the NOAA's Tide and Current website (<http://co-ops.nos.noaa.gov/>) for Magueyes Island (9759110), Puerto Rico. Monthly temperature measurements were averaged between the new moon and the sampling date.

Cassie (1963) index of patchiness, P , was calculated in order to measure the spatial patchiness of larvae among replicate samples. Cassie's index was calculated as

$$P = (s - \bar{x})/\bar{x}^2,$$

where \bar{x} is the mean larval count per sample divided by the average volume filtered (Ind/9.9m³) and s , the variance. Cassie's index is useful because it represents a measure of the intensity of pattern (e.g. degree of aggregation) that is independent of the mean. Therefore, it is possible to compare spatial patterns when means differ among samples. $P > 0$ indicates patchy larval distribution (assuming the Poisson).

RESULTS

The mean trajectory of the drogues followed a west-northwest direction (Fig. 1). The overall velocity of the drogues was 7.6 cm s⁻¹ (range: 1.3 – 17.3 cm s⁻¹). Average overall velocities of the surface, 1m and 2m drogues were 8.1, 7.1 and 5.9 cm s⁻¹, respectively. The mean flow was mostly tidally driven (Fig. 2). There was a change in speed of the mean flow but not in direction.

Only early larval stages (4-8 day-old) of *Diadema antillarum* were collected in this study (Fig. 3). These larval stages were found

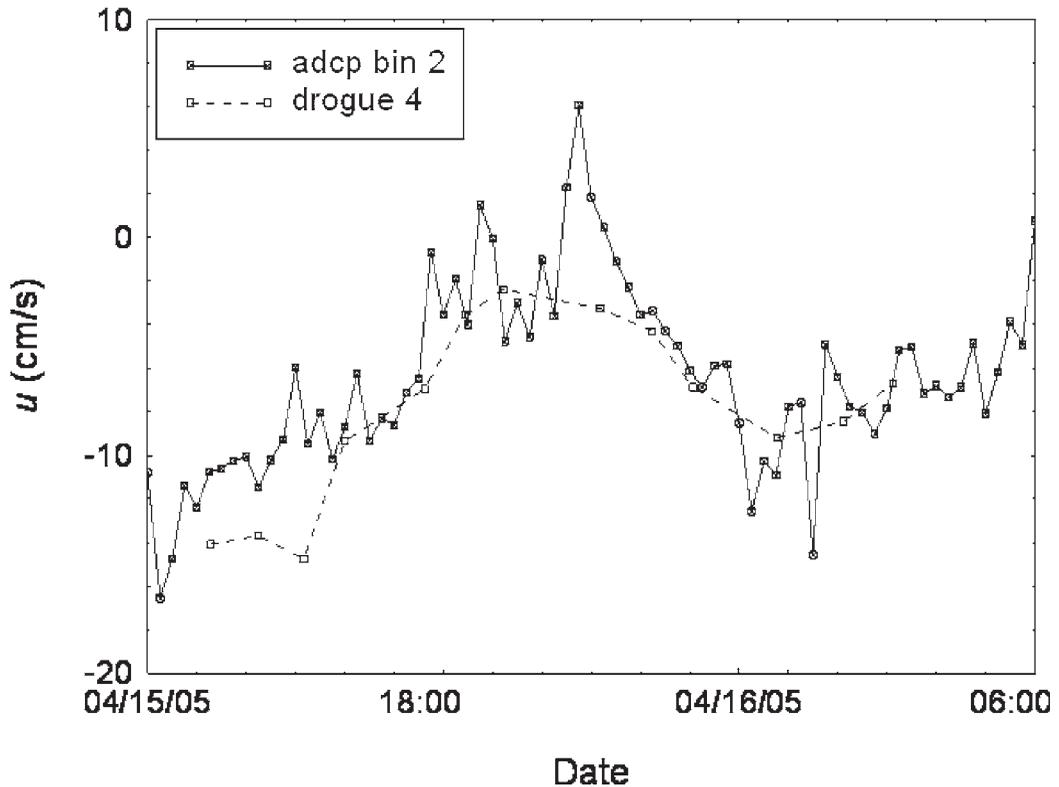
Parguera Media Luna Drogues: u Time Series

FIG. 2. Hourly mean flow of a surface drogue (#4) and the ADCP time series at 2.6 m during April 15th and 16th, 2005.

in 13 out of the 16 months of sampling, indicating that *Diadema* spawn throughout the year (Fig. 4). There was a significant difference (nested ANOVA; $df = 15, 32$ $F = 11.895$; $p < 0.0001$) among the monthly *Diadema* larval abundances. Mean larval abundances (Ind/100m³ \pm SD) ranged from $1,239 \pm 309$ in April and $1,078 \pm 648$ in July to 0 individuals in September and October of 2005 and January 2006 (Fig. 4). Mean abundances during April and July of 2005 were significantly higher than the rest of the sampling months (Tukey HSD, $df=34$, $p < 0.0001$). Larval abundances also differed significantly between 2005 and 2006 (ANOVA; $df = 1, 22$; $F = 6.154$; $p = 0.018$). Smaller peaks in mean larval abundances occurred in February (387 ± 130 , Ind/100m³ \pm SD) and September (166 ± 107 , Ind/100m³ \pm SD) of 2006.

In this study there was no significant relationship between monthly larval abundances and SST (Pearson, $r=0.03$). However, a peak in larval abundance coincided with the lowest temperature (26.37 °C) recorded in February 2006.

The inconsistent peaks of abundance between the two years may be a result of the patchiness distribution of these larvae (Fig. 5). Patchiness index ranged from 0.01 on May 9, 2006 to 2.97 on April 30, 2006 (Fig. 5).

DISCUSSION

The temporal pattern of early *Diadema antillarum* larvae suggests year-round reproduction. This observation coincides with most other *Diadema* studies conducted in the Caribbean (Randall et al. 1964, Lewis

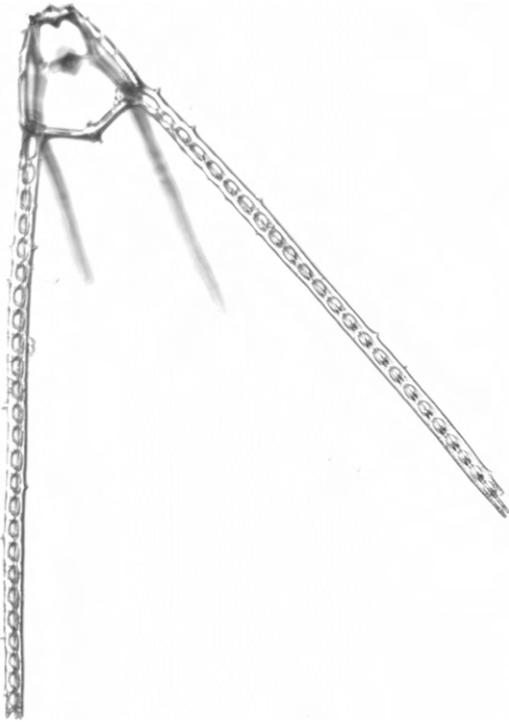


FIG. 3. Ventral side of an early larva of *Diadema antillarum* collected in this study.

1966, Bauer 1976, Lessios 1981, Iliffe and Pearse 1982, Garrido et al. 2000, Lugo 2004). Superimposed over the seemingly continuous reproductive pattern there appears to be a peak spawning season as indicated by high larval abundances during April and July 2005 and February 2006. Lugo (2004) also recognized a spring spawning peak in La Parguera based on gonad indices. This reproductive pattern also follows spawning cycles described for the U.S. Virgin islands (Randall et al. 1964), Barbados (Lewis 1966) and Curacao (Bak 1985). The lowest larval abundances recorded in this study were observed from September 2005 through January 2005, which differs from the Florida Keys where peak spawning occurs in November (Bauer 1976).

The lunar cycle (Hunte and Younglao 1988, Lessios 1988, Levitan 1988) and change in temperature may be factors that regulate spawning of *Diadema* (Hugo 2004). In this study the peak in larval abundance concurred with the lowest temperature

recorded during February 2006. Lugo (2004) found a significant negative relationship between the gonad indices and mean sea surface temperatures (SST) from La Parguera. Garrido et al. (2000) found that in the Canary Islands the spawning season coincides with a period of the most rapid temperature increase. In addition, there was a generally high abundance of *Diadema* larvae in samples with high-suspended dissolved organic matter (murky samples) during this study (S. M. Williams, pers. obs.).

Zooplankton patchiness influences the variability in the estimates of distribution and abundances of zooplankton communities (Cassie 1968). The inconsistent patterns of larval abundance between the two years and the equivalent months during this study reflect the patchiness in the distribution of these larvae (Fig. 5). Patchiness has been reported for other echinoderm larvae studies (Lavitra et al. 2006, Greenwood et al. 2000). In these studies the echinoplutei were patchy within sample replicates, which was also the case for *Diadema* larvae. Greenwood et al. (2000) stated that a small mouth diameter plankton net and limited haul time might be factors that influence the patchiness of echinoderm larvae in their study.

Drogues released in the backreef of Media Luna and the ADCP time series indicated that the circulation of coastal waters at La Parguera is towards the west-northwest. This flow along the coast seems to be influenced by the boundary layers of the coastline and the coral reefs. The mean magnitude of the drogue trajectories, approximately 7.6 cm s^{-1} , would have allowed *Diadema* larvae to travel $\sim 26 \text{ km}$ in a period of four days, assuming that the larvae were positioned near the surface layer and behaved as passive particles. The prevailing current speed and direction suggests an early dispersal of *Diadema* larvae within the insular shelf of La Parguera during the first two days, but it is uncertain if the older larvae will continue offshore out to the Mona Passage, or follow the shelf contour towards the north along the west coast of Puerto Rico. Rojas (2002) suggested that there was a prevailing northward flow on the west

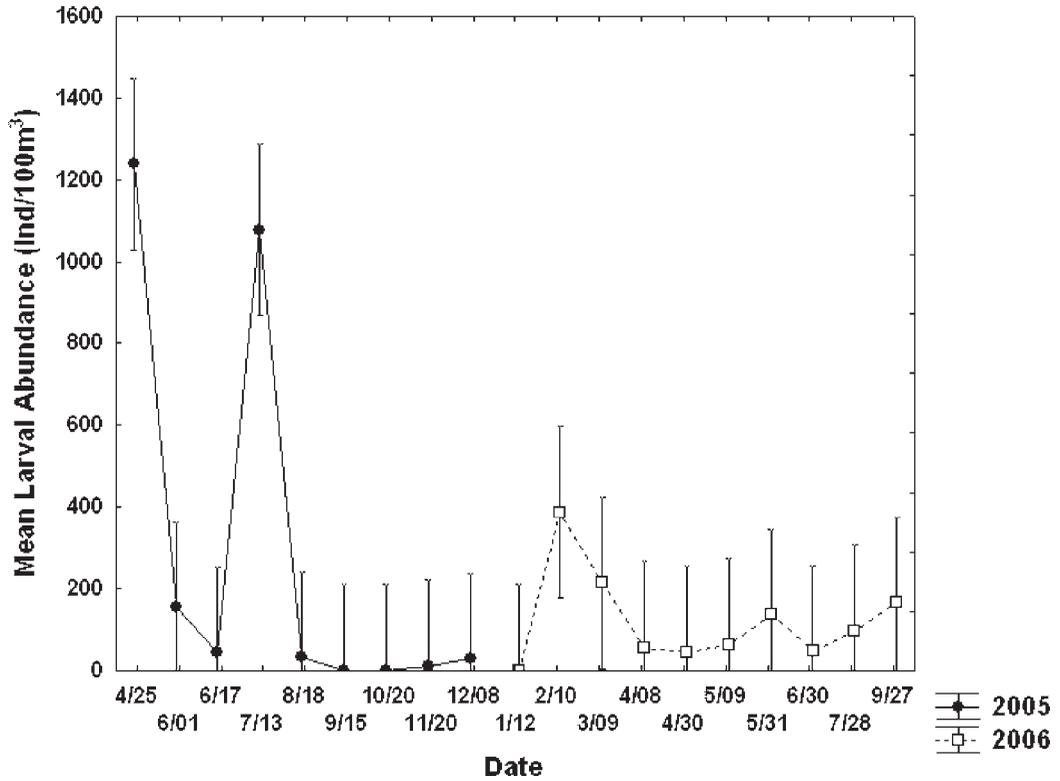


FIG. 4. Larval abundances and Standard Deviation (SD) of *Diadema antillarum* (Ind/100m³) during the different sampling times. Vertical bars denote 0.95 confidence intervals.

side of the island. Appeldoorn et al. (1994) studied the egg dispersal of a coral reef fish from inshore reef spawning site in La Parguera and concluded that a prevailing current similar to that described in this study for *Diadema*, resulted in an early neritic larval distribution. No *Diadema* larvae were collected from offshore stations sampled (S. M. Williams, unpubl. data). Presence of early pluteus larvae of *Diadema* from our plankton collections within-shelf stations in La Parguera supports the early neritic dispersal pattern inferred from the drogue study.

In this study, the early-staged larvae of *Diadema* represented 22% of the total echinopluteus assemblage counted, 5,704 larvae (S. M. Williams, unpubl. data). Caley et al. (1996) stated that the local production of offspring for many benthic invertebrates and demersal fishes has little or no direct role in setting local population size

because larval recruitment from other places provides the input of new individuals. Therefore, the recovering *Diadema* populations of Puerto Rico may be an important source of larval replenishment for downstream islands. A more intensive spatial sampling needs to be performed during the summer (peak time for larval presence) within the La Parguera shelf and offshore waters in order to provide a more comprehensive characterization of the pelagic life cycle and distribution of *Diadema* larvae.

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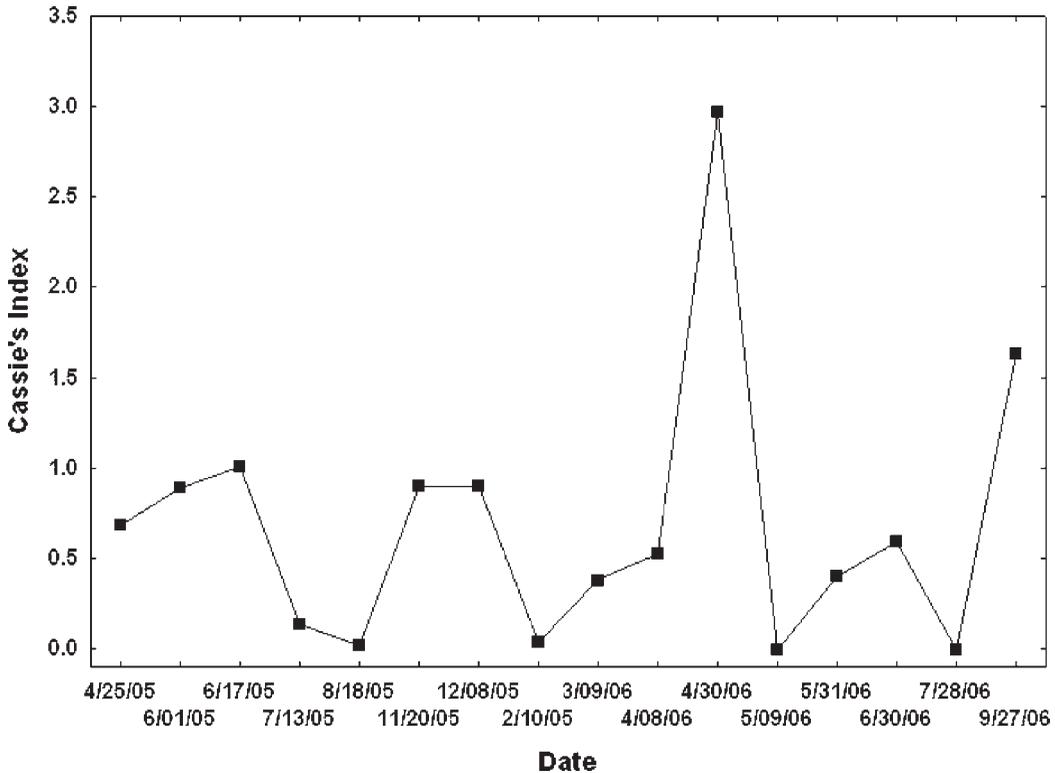


FIG. 5. Index of patchiness of *Diadema antillarum* larval abundance (Ind/9.9m³) during sampling events off La Parguera.

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Assessment of current rates of *Diadema antillarum* larval settlement

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Abstract The generally slow and incomplete recovery of the long-spined sea urchin, *Diadema antillarum*, from the 1983–84 Caribbean-wide die-off, particularly in the Florida Keys, USA, raises the question of factors limiting population recovery. This study sought to quantify larval settlement rates as an indicator of larval supply at two sites in the Florida Keys, utilizing methods comparable to an

historic study. Settlement at two sites in southwest Puerto Rico was also examined as a comparison of present-day settlement rates at a site where *D. antillarum* recovery has been moderate. Monthly settlement rates were low ($\max < 2 \text{ m}^{-2}$) and did not differ between the two sites examined in the Florida Keys. Settlement was significantly higher at only one of the Puerto Rico sites ($\max 16 \text{ m}^{-2}$), but still an order of magnitude lower than that reported for historic populations in Curaçao (1982–83). Results are consistent with the hypothesis of low larval supply limiting *D. antillarum* recovery in the Florida Keys.

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Keywords Florida Keys · Recovery · Puerto Rico ·
Settlement · Larval supply

Introduction

The massive, region-wide die-off of the keystone grazing sea urchin, *Diadema antillarum*, that occurred in 1983–84 throughout the Caribbean is among the most profound (Hughes et al. 1987; Carpenter 1988; Lessios 1988) and persistent (Carpenter 1990; Hughes 1994; Lessios 2005) ecological disturbances of shallow coral reef ecosystems observed to date. Abundances in many areas remain reduced by orders of magnitude decades after the die-off event (Lessios 2005; Debrot and Nagelkerken 2006), with severe consequences in terms of ecological function and reef health (e.g., Lessios 1988; Knowlton 1992; Mumby 2006).

Although limited to moderate *D. antillarum* recovery has been reported in many areas of the Caribbean, this is not the case in the Florida Keys where adult density remains extremely low (Chiappone et al. 2002; Lazar et al. 2005). Anecdotal observations of small individuals in reef

rubble and other back reef habitats, however, suggest that post-settlement mortality due to predation and/or physical scouring may be important limitations on population recovery in this region (Chiappone et al. 2002; Lazar et al. 2005, MWM pers. obs.). The degree to which limited larval supply may contribute to lack of recovery in the Keys is not known. Indeed, the only published reports of *D. antillarum* settlement rates are from the eastern Atlantic population (Hernandez et al. 2006) or from pre-die-off era in Curaçao (Bak 1985). We sought to characterize *D. antillarum* settlement patterns in the Florida Keys as a means to inform the consideration of sea urchin restocking strategies as a potential reef restoration measure. To place current Florida Keys settlement rates in modern context (i.e., with another Caribbean location where a significant degree of population recovery has been observed (Weil et al. 2005)), we also examined settlement rates in southwest Puerto Rico.

Methods

Settlement of *Diadema antillarum* was quantified over a 1-year period from August 2005 to July 2006 at two sites in the upper Florida Keys (Table 1). One site was located in a former large ship grounding within the fore reef at Molasses reef (where adult *D. antillarum* are never observed), while the other was a high-flow back reef area behind Pickles reef where adult *D. antillarum* are occasionally observed and juvenile *D. antillarum* are observed to recruit regularly (M. Miller pers obs.; K. Nedimyer pers. comm.). Experimental settlement plates were modeled on those used by Bak (1985) in Curaçao; namely, two plates of polystyrene “eggerate” grid with a transparent panel of plexiglass sandwiched in between. Each grid plate was 23 × 18 cm and plates were attached with cable ties to buoyed lines (four plates each attached between 0.5 and 2 m above the reef substrate), or to an adjacent stainless steel stake (one plate each ~ 10 cm above the reef; Fig. 1). Settlement plates were deployed above the reef substrate to help ensure that settlers came from the water column rather

than from the benthos. A total of 25 plates were deployed at each site (i.e., five mooring lines with adjacent stakes) for a total of ~ 2 m² sampling area (including both sides of the plates) per reef. At monthly surveys (range: 25–36 days), each plate was scrutinized in the field, any *D. antillarum* settlers were recorded and removed, and all plates were exchanged with clean ones.

To compare observed settlement rates in the Florida Keys with a geographic location where *D. antillarum* recovery has occurred to a greater extent (Weil et al. 2005), we deployed the same design of settlement plates at two sites in southwest Puerto Rico (Table 1) and made four (monthly) observations between June and October 2006. A total of 36 plates were deployed at each site, attached to mooring lines (none to stakes), surveyed, and replaced monthly as in the Florida Keys sites.

For both geographic regions, total monthly settlement counts (all plates combined) were standardized to density (# per m⁻²) and to 30-day intervals. These monthly rates were compared qualitatively between Florida and Puerto Rico and with the historic data from Curaçao (Bak 1985).

Results and discussion

Diadema antillarum settlement was variable among sites and months (Fig. 2, Table 2). Zero monthly settlement was commonly observed at all sites except The Buoy (Table 2). The maximum monthly settlement at the Florida Keys sites was <2 individuals m⁻², while The Buoy in Puerto Rico displayed a maximum monthly settlement rate of ~ 16 m⁻² (Table 2). Enrique Reef had the lowest settlement among the study sites, with 75% of observations yielding zero settlers and maximum monthly settlement of 0.3 m⁻², despite having substantially higher adult *D. antillarum* density (Table 1). Maximum settlement observed at the current study sites was up to an order of magnitude less than the biweekly maxima reported by Bak (1985) at two fringing reef study sites in Curaçao prior to the 1983–84 die-off (Table 2). *D. antillarum* settlement was also much

Table 1 Characteristics of study sites

| Site | Habitat | Depth (m) | Coordinates | Adult <i>Diadema</i> ? |
|------------------|-------------------------------------------------------|-----------|----------------------------|-----------------------------------------------------|
| Molasses, FK | Grounding site (low relief) within offshore fore reef | ~ 7 | 25°00.35' N 80°22.38' W | Nil |
| Pickles, FK | Back reef, mixed hardbottom with outcrops and rubble | ~ 3 | 24°59.36' N 80°24.81' W | Rare (<0.1 m ⁻² , pers. obs.) |
| The Buoy, PR | Shelf edge, drowned reef | 19 | 17°53.30' N 66°59.89' W | Extremely rare (<0.01 m ⁻² , pers. obs.) |
| Enrique Reef, PR | Nearshore bank reef | ~ 3 | 17°57.29' N 67°02.60' W | Moderate (1.5 m ⁻² ^a) |

^a Weil et al. (2005)

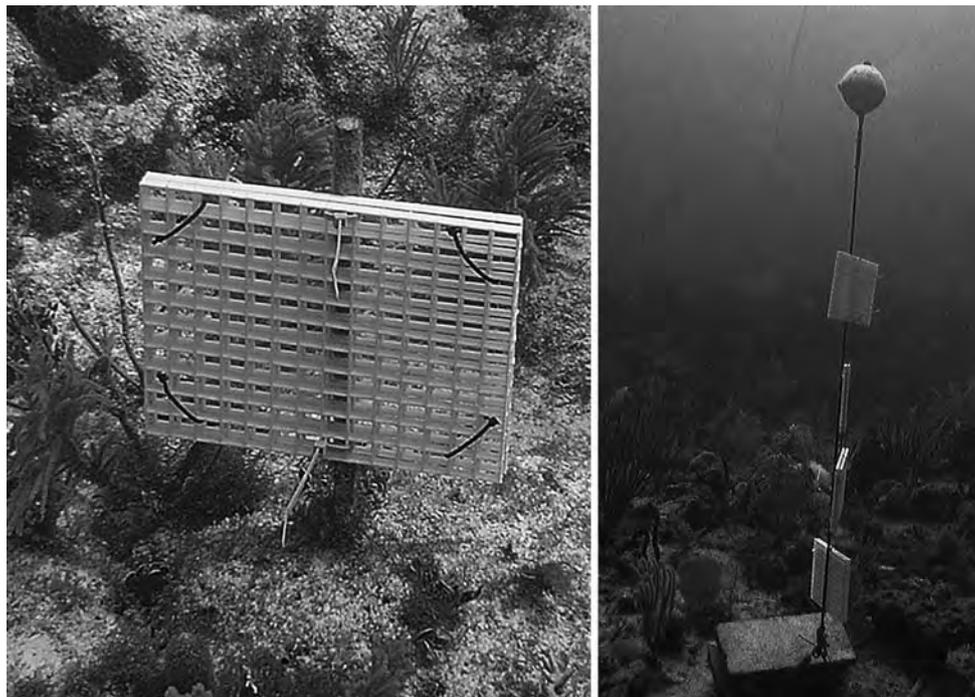


Fig. 1 *Diadema antillarum* settlement plates, modeled after those used by Bak (1985), as deployed to a stake (~ 10 cm from benthos, left panel) and on a buoyed line (right panel)

Table 2 Summary of *Diadema* settlement from current study compared with historical observations

| Time | Region | Site | Observation interval | <i>N</i> | Maximum (# settlers m^{-2}) | Proportion observations with \sim zero settlement |
|----------|--------------|--------------|----------------------|----------|--------------------------------|-----------------------------------------------------|
| 2005–6 | Florida Keys | Pickles | Monthly | 13 | 1.9 | 0.538 |
| 2005–6 | Florida Keys | Molasses | Monthly | 13 | 1.6 | 0.462 |
| 2006 | Puerto Rico | The Buoy | Monthly | 4 | 16.3 | 0 |
| 2006 | Puerto Rico | Enrique Reef | Monthly | 4 | 0.3 | 0.750 |
| 1982–84* | Curaçao | Buoy III | Biweekly | 46 | 188 | 0.108 |
| 1982–84* | Curaçao | Ava Blancu | Biweekly | 42 | 45 | 0.238 |

N = number of observations

* Data from Bak (1985), period of study prior to April 1984 when settlement ceased due to regional die-off

more consistent in the earlier data from Curaçao, where $<25\%$ of observations yielded no settlers.

The current study varied somewhat in methodology from Bak (1985), but in ways that make the conclusion of higher and more consistent settlement in the historic study a robust one. Bak (1985) utilized two or three larger plates (27×57 cm) per reef, for a total sampling area (<1 m^2 per reef) of approximately half that used in the current study (>2 m^2 per reef). This author surveyed settlement biweekly (i.e., half the interval between our surveys) and indicated that (biweekly) settlement rates declined over time with fouling of the settlement plates (Bak (1985) left individual plates deployed over periods of 3 to 5 months) with peak settlement rates observed over the period from 4 to 8 weeks of submergence (see Bak 1985, Fig. 5). In the

current study, we surveyed every 4 weeks and all plates were replaced with clean ones each time, which, according to Bak (1985) should have yielded maximum settlement. Overall, our higher replication (i.e., dispersion of observed surface over a greater area of the reef at each site), higher total sampling area, and optimal timing of replacement of clean substrates suggests that the comparison of our maximum observed settlement rate of 16 m^{-2} to Bak's (1985) maximum of 188 m^{-2} is a conservative one.

Though the number of sites was limited, the current study showed a lack of qualitative correspondence between adult presence/absence or density and observed settlement (an indicator of larval supply). Rather, similar settlement at sites with adults both present and absent (Florida Keys), or significantly higher settlement at a site with low versus

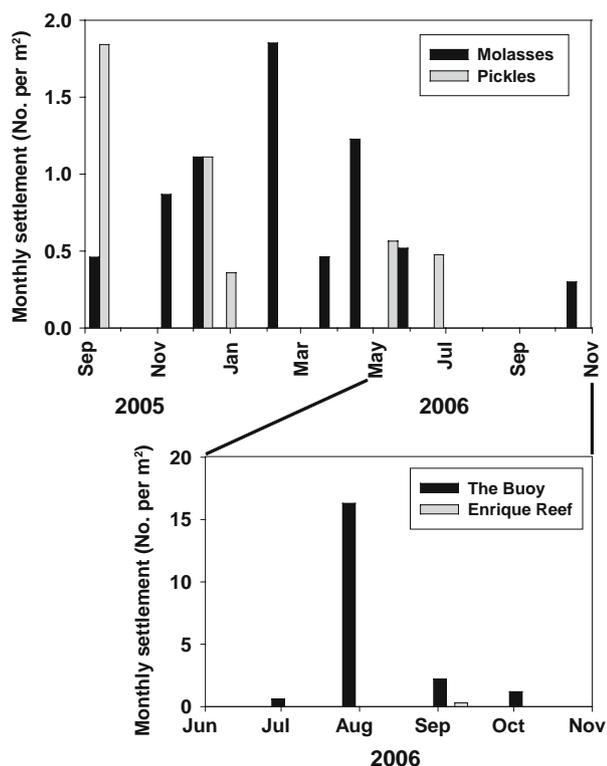


Fig. 2 Monthly settlement density (pooled for all settlement plates, standardized to 30-day intervals) of *Diadema antillarum* at two sites in the upper Florida Keys (upper panel) and two sites in southwest Puerto Rico (lower panel). Note different y-axis scales in each panel

moderate adult *D. antillarum* density (Puerto Rico) was observed. This pattern is not consistent with the hypothesis of positive density-dependent recruitment in *D. antillarum* (Miller et al. 2007), perhaps because the mechanism of density dependence is unrelated to larval supply with density-dependent facilitation of *D. antillarum* recruitment likely operating at post-settlement stages. Earlier studies of settlement (Bak 1985) and recruitment of small juveniles (Hunte and Younglao 1988) in the Eastern Caribbean, in contrast, did find a positive correspondence of these early life stages with adult density.

Results of the current study are consistent with the hypothesis that low larval supply in the Florida Keys, relative to current levels of larval supply in an area of moderate *D. antillarum* recovery (southwest Puerto Rico) and, especially, relative to historic levels in Curaçao, constrains *D. antillarum* recovery in the Florida Keys. The low abundance of *D. antillarum* in the Florida Keys is characterized by size distribution skewed to small (dominantly juvenile) animals (Chiappone et al. 2002). This suggests that individuals that do settle successfully also have poor survivorship potentially due to high predation and/or physical disturbance. The relative importance of pre- versus post-settlement limitation of *D. antillarum*

recovery in the Florida Keys remains a difficult question. Larval supply and post-settlement limitation are not independent from each other; obviously a larger larval supply is required for recruitment success when post-settlement survivorship is low, and vice versa. These are important factors to consider in discerning the feasibility of potential proactive restocking actions (e.g., The Nature Conservancy, The *Diadema* Workshop, 2004; available at http://conserveonline.org/docs/2004/09/Diadema_Workshop_Full_Repor.pdf) aimed at enhancing important grazing functions and/or facilitating coral recruitment on Florida Keys reefs. Such anticipated benefits of *D. antillarum* recovery have been documented in other areas with natural *D. antillarum* recovery (Carpenter and Edmunds 2006; Myhre and Acevedo-Gutierrez 2007) or enhancement via translocation (Macia et al. 2007).

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Recruitment pattern of *Diadema antillarum* in La Parguera, Puerto Rico

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Keywords *Diadema antillarum*, Recruitment, Spatial and temporal variability, Puerto
Rico, Caribbean

Abstract

Recruitment success is one of the factors that may be influencing the slow population recovery of *Diadema antillarum* at many locations in the Caribbean. *D. antillarum* recruitment was measured with recruitment plates at monthly intervals from September 2005 to September 2006 at three reefs along an inshore-offshore gradient in La Parguera, Puerto Rico. A total of 275 recruits of *D. antillarum* were collected at the shelf-edge reef during this 13-month study. Two recruits were collected at the mid-shelf reef and no recruits were collected at the inner shelf reef. Recruitment varied among months at the shelf-edge, with the highest value (1,067 ind/m²) occurring in July 2006. Previous benthic surveys in the La Parguera region have demonstrated higher densities of adult *D. antillarum* at inshore reefs. The higher recruitment at the shelf-edge suggest that recruitment is not a major determinant of the spatial distribution of the adult population. Recruitment occurring in this study is indicative that sources of larvae were available upstream and larval survival was occurring.

Introduction

Diadema antillarum populations declined by 95-100% in many Caribbean locations in 1983 (Lessios 1995). Karlson and Levitan (1990) suggested that since the mass mortality occurred over such a large scale it would be difficult for *D. antillarum* to recover to pre-mass mortality numbers. Since these predictions 20 years ago, signs of a slow recovery are apparent in Barbados (Hunte and Younglao 1988), St. Croix (Miller et al. 2003; Miller et al. 2007), Puerto Rico (Weil et al. 2005), Jamaica (Carpenter and Edmunds 2006) and Dominica (Steiner and Williams 2006). The present abundance of *D.*

antillarum in Puerto Rico is still low compared to pre-die off densities (12 ind/m²; Craft 1975). Adult *D. antillarum* populations are mostly confined to shallow reef habitats in La Parguera, Puerto Rico (Weil et al. 2005), and abundances at shelf-edge locations rarely exceed 0.02 ind/m² (Miller et al. 2008).

Larval mortality and/or recruitment have been suggested as the main factors regulating the adult population size of *D. antillarum* (Karlson and Levitan 1990). Balch and Scheibling (2001) defined recruitment as occurring some time after settlement when individuals can be reliably counted and some post-settlement mortality or migration may have occurred. Recruitment of *D. antillarum* has been recently measured in the Canary Islands (Hernández et al. 2006) and in the Florida Keys (Miller et al. 2008). Hernández et al. (2006) found a monthly maximum of 24-26 *D. antillarum* recruits/sampler with each sampler containing 100 pieces of experimental collectors (small plastic balls with a very high surface area, 0.04 m²/ball). Also, Miller et al. (2008) found that the overall rates of recruitment in the Florida National Marine Sanctuary were variably low, with the highest rates being below 2 ind/m² and monthly counts of zero were common. The objective of this study was to examine spatial and temporal trends of *D. antillarum* recruitment in La Parguera, Puerto Rico, and to assess its relationship to the distribution of the adult populations.

Materials and methods

We examined *D. antillarum* recruitment at three reefs in the vicinity of La Parguera on the southwest coast of Puerto Rico (Fig. 1): an inshore reef (Las Pelotas, 17°57.42' N; 67°04.19' W), a mid-shelf reef (Media Luna, 17°56.08' N; 67°02.91' W)

and a shelf-edge reef (Old Buoy, 17°53.29' N; 66°59.88' W). Las Pelotas is an emergent reef with *D. antillarum* densities ≤ 0.15 ind/m² (Benavides 2006). Media Luna is also an emergent reef with *D. antillarum* densities ≤ 0.50 ind/m² (Benavides 2006). Old Buoy is a submerged reef on the edge of the continental shelf located about 9 km from the coastline. Coral cover (41%, García-Sais et al. 2001) is higher at Old Buoy than the two other reefs, but adult *D. antillarum* are rare at this site.

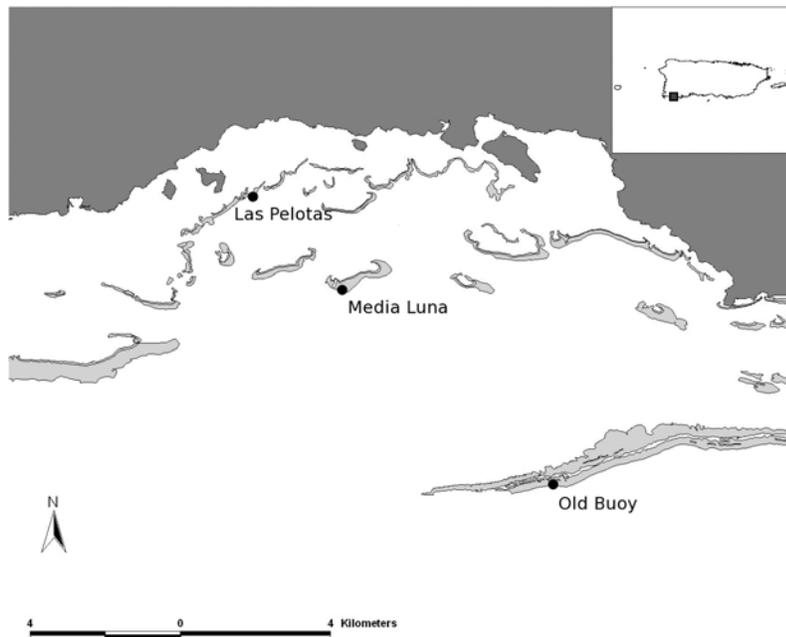


Fig. 1 Map of study sites for settlement experiments in La Parguera, Puerto Rico.

Three mooring lines were placed at each reef. Mooring lines were placed in sandy areas next to each reef, in a north to south pattern, perpendicular to the main reef axis, approximately 2 meters apart. Pieces of artificial turf were used as the recruitment plates for this study. A 128 cm² piece of artificial turf was placed horizontally on the top of a

cement block (Fig. 2a) that anchored each mooring line. Also, two 64 cm² pieces of artificial turf (Fig. 2b) were placed vertically back to back from each other at different depths on each mooring line. At Old Buoy, plates were placed at 19 m, 12 m and 6 m, at Media Luna at 10 m, 8 m and 5 m and at Las Pelotas at 3 m and 2 m. Plate depths differed due to the different water depths at each reef. The purpose of the vertical plates was to determine if ‘settlement ready’ larvae were in the water column during this study. Buoys were placed 2.5 meters below the water surface in order to reduce the movement of the mooring lines by surface waves.



Fig. 2a,b Horizontal (a) and vertical (b) recruitment plates made out of astroturf at the shelf-edge site in La Parguera, Puerto Rico.

Artificial turf plates were initially deployed during the first week of September 2005. The plates were collected and replaced with a new plate at monthly intervals until September 2006. Mooring lines were also cleaned each month with a knife. In the laboratory the retrieved plates were washed with seawater and inspected for *D. antillarum* recruits. Sea urchins with a test diameter < 3.0 mm were counted as a recruit.

A one-way Analysis of Variance (ANOVA) test was applied to examine the temporal variance of *D. antillarum* recruitment at just the shelf-edge site, since there was a lack of recruitment at Media Luna and Las Pelotas. A Sign test was carried out in order to determine differences in recruitment of *D. antillarum* between sites. The Statistica 7 package was used for these statistical analyses.

Results and discussion

Newly recruited *D. antillarum* (~0.4 mm) exhibited a reddish color with tiny unbanded spines. Larger recruits (> 0.6 mm) displayed a red test but had longer spines that were banded with colors of white and red. The test size of recruits collected during this study ranged from 0.4 mm to 2.4 mm. *D. antillarum* recruits were found during 12 out of the 13 mo (Fig. 3) as might be suggested given the year-round reproduction in La Parguera, Puerto Rico (Lugo 2004; Williams et al. 2009). Significant temporal variations of recruitment were observed at the shelf-edge site (ANOVA, $F_{12, 38} = 9.94$, $p < 0.0001$), with peak recruitment occurring in July (Fig. 3). Recruitment at Old Buoy station was high (overall mean of 183 ind/m²) compared to previous reports (Hernández et al. 2006; Miller et al. 2008). Therefore, seasonal effects occurring during the mid- to late summer, possibly sudden increases in temperature and/or food availability on the reefal substrate, may serve as a cue for larval settlement of *D. antillarum* at the shelf-edge.

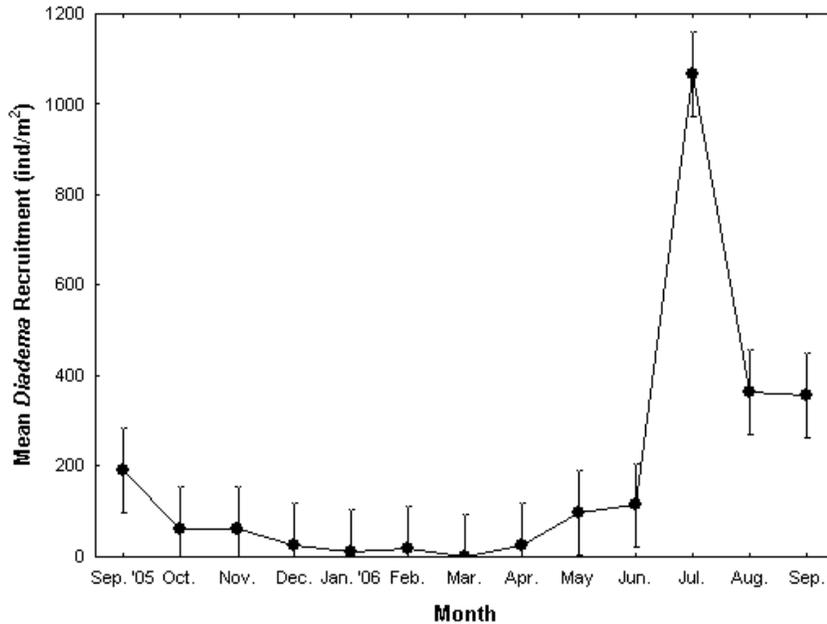


Fig. 3 Mean monthly recruitment of *Diadema antillarum* per m² at Old Buoy. Vertical bars denote standard errors (n=9).

Spatial variations of recruitment by *D. antillarum* were evident. Recruitment was greater at Old Buoy than at Media Luna or Las Pelotas (Sign Test, $p < 0.01$). A total of 275 recruits were found at the shelf-edge site, 14 recruits were collected at 19 m, 122 at 12 m and 139 at 6 m plates. Two recruits were found at the mid-shelf reef and no recruits were collected at the inner shelf reef, La Pelotas. Three non-mutually exclusive explanations for the low recruitment at the inner and mid-shelf reefs compared to the shelf-edge site include (1) stochastic variation, (2) a shelf-edge reef larval ‘filtering effect’ (Gaines et al. 1985), settlement of *D. antillarum* at the shelf-edge caused a large drain on the larval population as water mass passed over inner and mid-shelf reefs and 3) that high abundance of fleshy macroalgae colonizing the artificial turf plates precluded recruitment at inshore reefs (unpublished). Bak (1985) noted that *D. antillarum*

recruitment was enhanced when the settlement plates were un-fouled. At the inner and mid-shelf reefs the artificial turf plates were difficult to locate due to the fleshy algae, compared to the relatively clean plates at the shelf-edge where the original color of the artificial turf was still visible.

If mortality of recruits is constant in space and time, the adult distribution should match the distribution of recruits (Gotelli 1988), but in this study the greatest recruitment of *D. antillarum* in Puerto Rico was concentrated at the shelf-edge, where adult urchins are rare. Therefore, *D. antillarum* recruitment in La Parguera may be independent of local adult density (Lessios 1988). Assuming that recruitment on the plates is representative of recruitment on the reefs themselves, the inverse relationship between recruitment and adult densities raises an important issue about the population dynamics of this species. Post-settlement mortality on *D. antillarum* at the shelf-edge may be high, explaining the absence of these adult urchins at this location.

Lessios (2005) and Miller et al. (2008) argued that low larval supply was the limiting factor inhibiting the recovery of *D. antillarum* in Panama and the Florida Keys. The high recruitment reported at the shelf-edge in this study is indicative that upstream sources of *D. antillarum* ‘settlement ready’ larvae are available and these larvae were capable of surviving through the planktonic stage. The shelf-edge may act as a ‘sink’ for settling larvae and the habitat dynamics of this reef may play an important function in understanding the recovery and future reef restoration efforts of *D. antillarum*.populations.

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Recruitment dynamics of *Diadema antillarum* in La Parguera, Puerto Rico.

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Abstract

Spatial variations in the recruitment of sessile marine invertebrates may be due to: larval supply, mortality and/or dispersal, habitat selection and/or mortality of the settler. Recruitment of *Diadema antillarum* and was studied at six reefs along an inshore-offshore gradient in La Parguera, Puerto Rico from February to April 2008 and from July to September 2008 with settling plates at monthly intervals. Recruitment plates built out of artificial turf were used to measure recruitment. Plates were placed at various depths on individual mooring lines. Factors that could possibly be influencing *Diadema* recruitment such as, plate fouling and the presence of microinvertebrates, “potential predators” were examined. From a total of 220 *Diadema* recruits collected, 217 were collected from the shelf-edge reefs (Old Buoy and El Hoyo). The remaining three recruits were collected at Media Luna, a mid-shelf reef. In this study, fouling of the substrate was shown not to be regulating the recruitment of *Diadema* at inshore and mid-shelf reefs. An inverse relationship was found between *Diadema* and microinvertebrate recruitment (Pearson, $r=-0.67$, $p<0.0001$). Significant differences between recruitment of microinvertebrates and *Diadema* were found between sites (Factorial ANOVA, $F_{20,95}=9.8$, $p<0.0001$), with the inner and mid-shelf reefs displaying higher recruitment of microinvertebrates. Post-settlement processes, such as predation pressure by microinvertebrates may have an influence on the recruitment pattern of *Diadema* in this study.

Key words: *Diadema antillarum*, Recruitment, Microinvertebrates, Predation, Puerto Rico, Caribbean

1. Introduction

More than twenty years after its Caribbean wide mass mortality the recovery of *Diadema antillarum* has been very slow, while some areas show no signs of a recovery. The abundance and recovery of this important keystone herbivore depends on: 1) sufficient number of fertile adults upstream, 2) plankton survival and dispersal 3) recruit survival, and 4) suitable reef substrate (Lessios, 2005; Szmant, pers comm). Szmant (per comm) recognized that post-recruitment predation is one of the main factors regulating the recovery of *Diadema* in the Florida Keys. In addition, low larval supply has been proposed as a limiting factor in the Florida Keys and also in Panama (Lessios, 2005; Miller et al., 2008). Williams et al. (in review) concluded that upstream sources of *Diadema* larvae are available in La Parguera and that these larvae are capable of surviving the planktonic stage.

Recruitment is a key mechanism shaping and structuring reefal communities (Cameron and Schroeter, 1980). Recruitment rather than reproductive output is the key concept for marine species demography and is one of the main determinants of spatial and temporal variations in population sizes (Cowen et al., 2000). However, in La Parguera, recruitment of *Diadema* is not the major determinant of the spatial distribution of the adult populations (Williams et al., in review). Post-settlement mortality may be shaping the distribution of adult *Diadema* in La Parguera (Williams et al., in review) Predation shapes the community structure and diversity on a coral reef structure. Urchin abundance is regulated and temporal and spatial distribution maintained by predation, especially juveniles, which are more vulnerable. Post-settlement mortality in the early life

of a marine invertebrate can be extremely high and can have strong modifying effects on patterns of recruitment (Jenkins, 2005). In the case of *Diadema*, mortality is density independent but highly variable and patterns of recruitment will be modified by mortality (Caley et al., 1996).

Puerto Rico appears to be one of the few locations where the *Diadema* population is slowly recovering (Weil et al., 2006), thus providing an ideal setting to study the recruitment dynamics influencing population recovery. The experimental setup in this study was based on Williams et al. design (in review), with the addition of three new reef sites. The main objectives of this study were to determine if plate fouling and the presence of microinvertebrates, “potential predators” are factors inhibiting recruitment at the inner and mid-shelf reefs of La Parguera, Puerto Rico.

2. Materials and Methods

2.1 Study Area

The Natural Reserve of La Parguera, Lajas is located on the southwest coast of Puerto Rico between Guánica and Cabo Rojo (Fig. 1). The recruitment study included six reefs in La Parguera, these were Las Pelotas, Enrique, San Cristobal, Media Luna, El Hoyo and Old Buoy (Table 1).

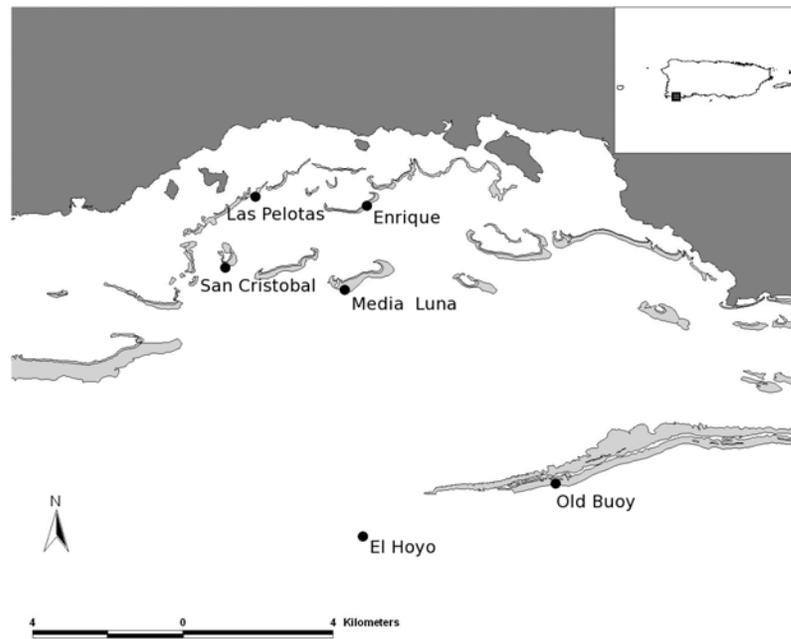


Fig. 1 Map of La Parguera, Puerto Rico, showing reefs sites where settling plate experiments were located.

Table 1 Characteristics of study sites

| Site | Reef Type | Depth(m) | Coordinates | Adult Diadema (Benavides, 2006) |
|---------------|-----------------------|----------|-----------------------------|--------------------------------------|
| Las Pelotas | emergent, inner shelf | 12 | 17°57.42' N 67°04.19' W | Low, $\leq 0.15 \text{ m}^{-2}$ |
| Enrique | emergent, inner shelf | 12 | 17°57.29' N 67°02.59' W | Low, $\leq 0.15 \text{ m}^{-2}$ |
| San Cristobal | emergent, mid-shelf | 15 | 17°56.40' N 67°04.62' W | Moderate, $\leq 0.50 \text{ m}^{-2}$ |
| Media Luna | emergent, mid-shelf | 19 | 17°56.08' N 67°02.91' W | Moderate, $\leq 0.50 \text{ m}^{-2}$ |
| Old Buoy | submerged, shelf-edge | 19 | 17°53.29' N 66°59.88' W | Rare |
| El Hoyo | submerged, shelf-edge | 19 | 17°52.53' N 67° 02.64' W | Rare |

2.2 Recruitment Experiment

Three mooring lines were deployed during the first week of September 2005 at each of the six reefs shown on Figure 1. Mooring lines were placed over the reef, or in sandy areas next to the reef, in a north to south pattern, perpendicular to the main reef axis, approximately 2 meters apart. Pieces of artificial turf were used as the recruitment plates for this study. Two 64 cm² pieces of artificial turf were placed back to back from each other at different depths on each mooring line. At the Old Buoy, El Hoyo and Media Luna, plates were placed at 17 m, 12 m, 9 m, 6 m and 3 m. Plates were placed at 12 m, 9 m, 6 m and 3 m at San Cristobal and at Las Pelotas, Enrique plates were placed at 9 m, 6 m and 3 m. Buoys were set 2.5 meters below the surface in order to reduce movement of the lines by surface waves.

Plates were deployed from February to April 2008 and from July to September 2008 (total of 6 months). Plates were retrieved and replaced at monthly intervals. Mooring lines were cleaned each month with a knife. At the laboratory, plates were washed with seawater and inspected for *Diadema* recruits. A recruit was defined in this study as a recently settled juvenile that had survived for a period of time after settlement (Connell, 1985). Newly settled *Diadema* were measured under a microscope and then either released if alive or preserved in 95% EtOH. Motile microinvertebrates such as crabs, shrimp, cowries and lobsters were also counted.

An additional experiment was performed during August 2009 in order to analyze if the temporal duration (one month) of the plates was playing a crucial factor hindering recruitment at mid-shelf and inner shelf reefs. Plates were collected and replaced every

week and every two weeks for a month at Media Luna and were placed for one month at Old Buoy. Plates were placed at all depths mentioned above.

2.4 Data Analysis

Factorial ANOVA test was performed to examine recruitment variations of *Diadema* between shelf-edge sites and depths. Also, differences of recruitment between microinvertebrates and *Diadema* at the different sites and at the different depths at the shelf-edge were examined with a Factorial ANOVA test. A Pearson correlation was carried out to establish the relationship between *Diadema* and microinvertebrate recruitment. Statistica 7 package was used for all statistical analyses.

3. Results

Newly settled *Diadema* (~0.4 mm) exhibited a reddish color with tiny unbanded spines. Recruits 0.6 mm-1 mm in test size also contained a red test but had longer spines that were banded with colors of white and red (Fig. 2). The older recruits (>1.0 mm) were characterized by a purplish-black test with banded spines colored black and white. The test size of recruits ranged from 0.4 mm to 2.4 mm.

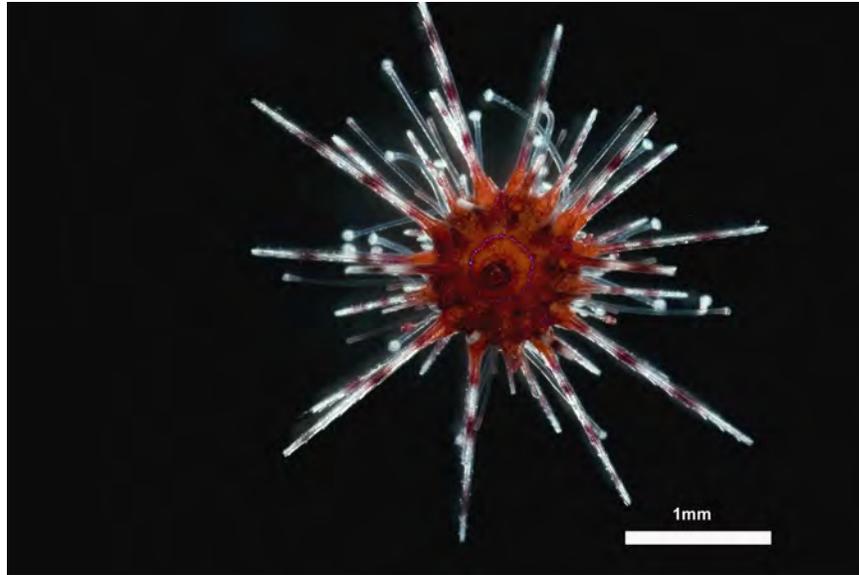


Fig. 2 *Diadema antillarum* recruit collected at Old Buoy.

A total of 220 *Diadema* recruits were collected within this 6-month study. Recruits were found mostly at shelf-edge stations with the exception of three recruits that were collected at Media Luna during April, July and August. No recruits were collected at other inner shelf reefs. Recruitment rates between shelf-edge stations, El Hoyo and Old Buoy were not significantly different (Fig. 3, Factorial ANOVA, $F_{1,178}=1.90$, $p=0.17$). The overall mean recruitment at both shelf-edge sites was 94 ind/m².

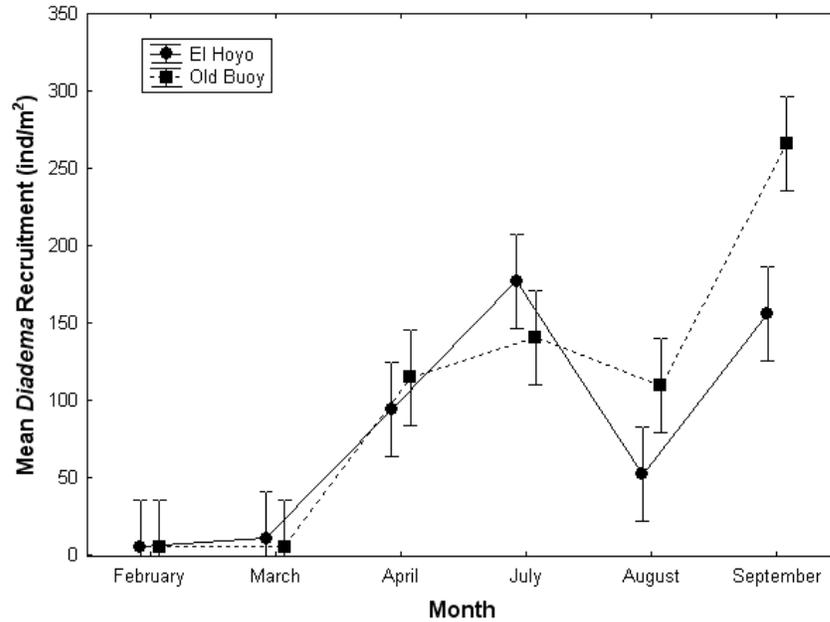


Fig. 3 Mean monthly recruitment (ind/m²) of *Diadema antillarum* at shelf-edge sites, Old Buoy and El Hoyo, La Parguera. Bars denote standard errors.

There was a significant difference of *Diadema* recruitment between depths at the shelf-edge stations (Fig. 4, Factorial ANOVA, $F_{4, 178}=5.69$, $p<0.0001$), with peak recruitment on 9 m plates (197 ind/m², Fig. 4). The lowest recruitment was found on 3 m plates (47.7 ind/m²) at El Hoyo.

In the experiment set to test for fouling effects, a total of 39 recruits of *Diadema* were collected at Old Buoy during August 2009. Only two recruits were collected at Media Luna during this time. No recruits were collected on the one-week plate intervals at Media Luna.

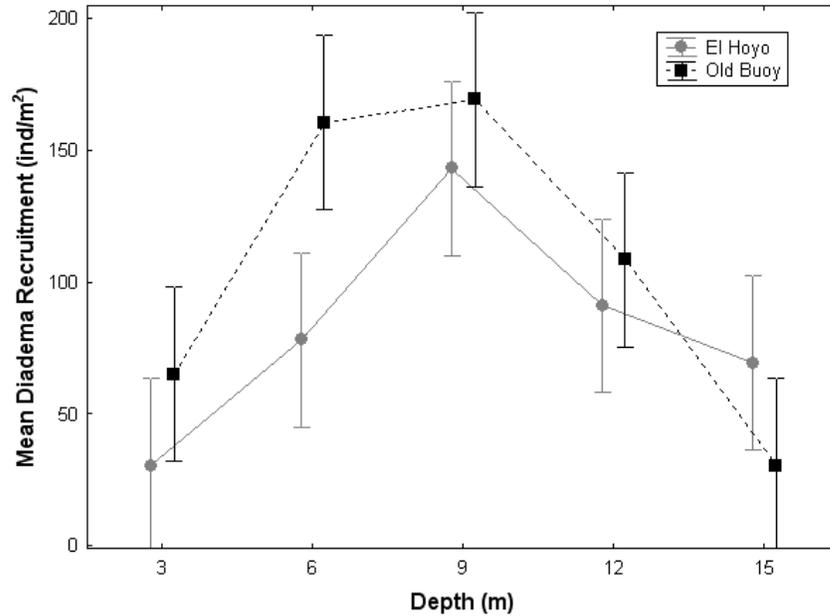


Fig. 4 Mean recruitment (ind/m²) of *Diadema antillarum* at different depths from shelf-edge sites, Old Buoy and El Hoyo, La Parguera. Bars denote standard errors.

There was a negative relationship found between *Diadema* and microinvertebrate recruitment (Pearson, $r=-0.67$, $p<0.0001$). Significant differences between recruitment of microinvertebrates and *Diadema* were found between sites (Factorial ANOVA, $F_{20,95}=9.8$, $p<0.0001$), with the inner and mid-shelf reefs displaying higher recruitment of microinvertebrates (Fig. 5). Also, at the shelf-edge sites there was a significant difference between recruitment of microinvertebrates, including *Diadema* between depths, with more microinvertebrates collected on the shallower plate depths (Fig. 6, Factorial ANOVA, $F_{16,875}=5.5$, $p<0.0001$).

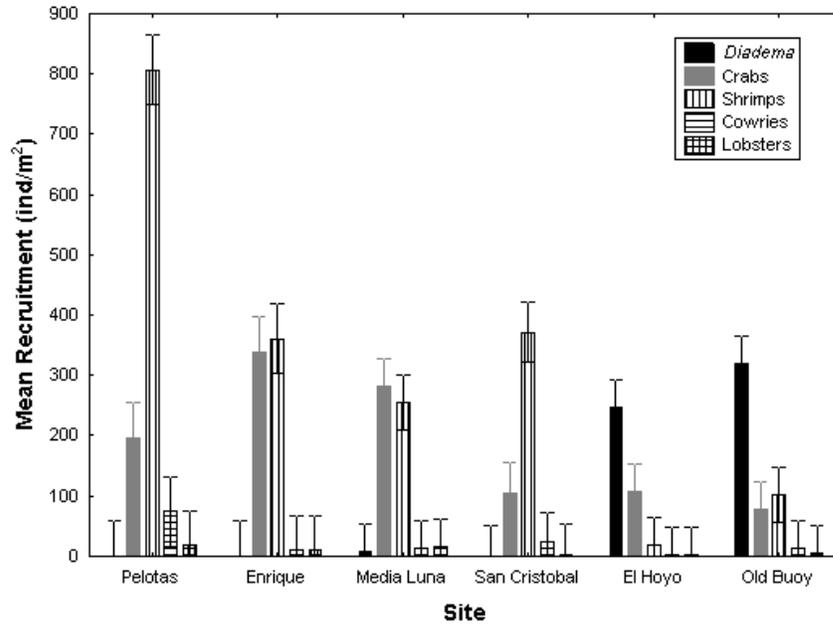


Fig. 5 Mean recruitment (ind/m²) of *Diadema antillarum* and microinvertebrates at the different sampling sites. Bars denote standard errors.

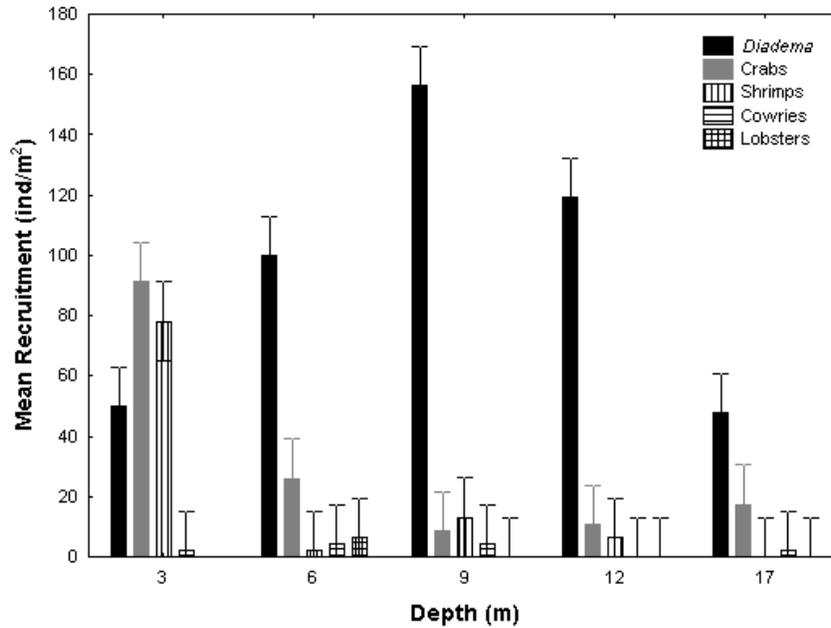


Fig. 6 Mean recruitment (ind/m²) of *Diadema antillarum* and microinvertebrates at different depths from shelf-edge. Bars denote standard errors.

4. Discussion

The spatial distribution in recruitment found in this study was very similar to Williams et al. (in review) study in 2005-06. Recruitment of *Diadema* in this study was mainly observed to occur at shelf-edge reefs, Old Buoy and El Hoyo, which are approximately 5.5 km apart. *Diadema* recruitment is not just occurring at Old Buoy (Williams et al., in review), but concentrated at the shelf-edge region of La Parguera. At both of these shelf-edge sites it is rare to witness an adult *Diadema*. This study confirms that *Diadema* recruitment is not a major determinant of the spatial distribution of the adult population in La Parguera (Williams et al., in review). At the shelf-edge reefs during the beginning of the study we witnessed larger juveniles (~1 cm test diameter) hidden in the spaces of the cement blocks of the mooring lines. A couple months later these juveniles disappeared and were no longer near the cement blocks. Some reported predators of adult *Diadema* are triggerfishes (*Balistes vetula* and *Canthidermis sufflamen*), jacks, grunts, wrasses (*Bodianus rufus* and *Halichoeres radiatus*), porcupinefishes (*Diodon hystrix*), helmet shells and lobster (Randall et al. 1964). Most reported predators of *Diadema* (Randall et al., 1964) were observed to have a higher abundance at the shelf-edge sites than at the inner and mid-shelf reefs of La Parguera, especially triggerfishes (Garcia Sais et al., 2001). It is assumed that *Diadema* at the shelf-edge survive to a certain size (<1-2 cm), until they are easily visible to fish and invertebrate predators. Post-settlement mortality shapes the adult populations at the shelf-edge region.

During this study, only three recruits were collected at Media Luna and no recruits were collected at San Cristobal, Enrique and La Pelotas. Williams et al. (in

review) also found low recruitment at Media Luna and collected no recruits at Las Pelotas. It should be noted that recruitment at Media Luna, observed during April, July and August 2008, although relatively lower (max 5 ind/m²) than at the La Parguera shelf-edge (max 265 ind/m²), was still comparatively higher or comparable than those reported in recent recruitment studies performed at the Florida Keys and Canary Islands (Hernandez et al. 2006; Miller et al. 2008). What was influencing the low and/or lack of recruitment of *Diadema* at inshore and mid-shelf reefs? Williams et al. (in review) noted Bak (1985) found that *Diadema* recruitment in Curacao was enhanced when the settlement plates were un-fouled. there was also a qualitative difference in the algal cover on the plates between the different shelf locations (Fig. 7a,b) and at the different depths. Inner, midshelf reefs and shallower depths (3 and 6 m) presented the most algal abundance when compared to shelf-edge reefs and deeper plates (pers observ). Fleshy benthic algae were observed in mats below, above and directly on the plates (Fig. 7b). The main algal species identified on these plates were *Ceramium spp.*, *Seirospora occidentals*, *Polysiphonia spp.* and *Pleonosporium spp.* During the fouling experiment in this study, *Diadema* recruitment was still considerably lower (total of 2 recruits) at Media Luna than at Old Buoy (39 recruits), even when plates were collected every week and/or every two weeks during August 2009. Algal cover on the one and two-week plates at Media Luna were relatively similar to those left out for a month at the shelf-edge site. Therefore, fouling of the substrate was shown not to be the major factor precluding the recruitment of *Diadema* at the inshore sites in La Parguera during this study.

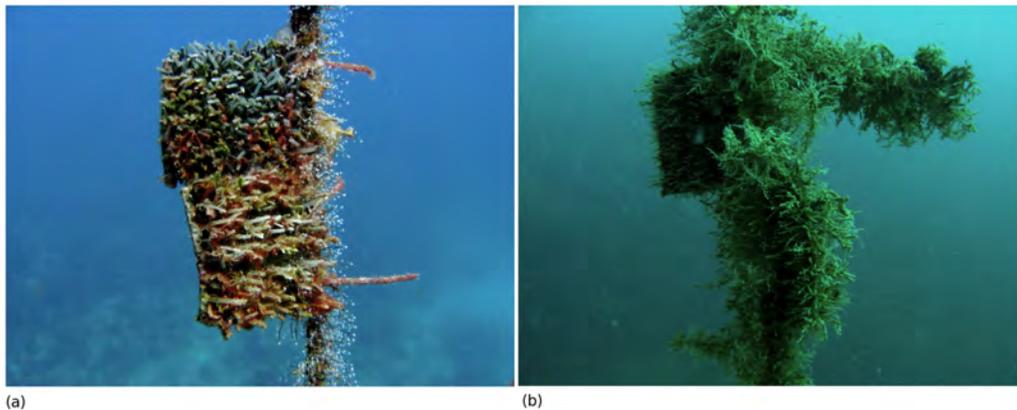


Fig. 7a,b Relatively clean plates (a) at Old Buoy and fleshy algae located on the plates (b) at Media Luna.

There are two other mechanisms that can be postulated that have possible a larger weight on the spatial distribution of recruitment found in this study. To begin with, low supply of larvae may be hindering the recruitment of *Diadema* at inner and mid-shelf reefs of La Parguera. Older larvae (~24 day old) of *Diadema* have not been found within the neritic waters (Williams et al., 2009) but have mainly been collected from the shelf-edge and offshore waters of La Parguera (Williams and García Sais, in review). *Diadema* settlement at the shelf-edge may have caused a large drain on the larval population as the water mass passes over the inner and mid-shelf reefs (Williams et al., in review). In addition, the low incidence of older stage larvae in neritic waters of La Parguera may also be due to be high larval mortality at the shelf-edge. Older stage larvae of *Diadema* are relatively large; larval arm can grow to over 4.5 mm long, for a total arm span of over 9 mm (Eckert, 1998). Sale (1991) affirmed that most diurnal planktivores are more numerous along the reef edges adjacent to deeper water and García-Sais et al. (2001)

observed this to be true in La Parguera. A higher abundance of zooplanktivorous fishes were identified more at the shelf-edge than at inshore reefs in La Parguera. Even some fishes are known to spawn offshore as a behavioral adaptation in order to avoid predation by neritic zooplanktivorous fishes (Johannes, 1978). However, a more intensive spatial sampling needs to be performed within the La Parguera shelf and offshore waters in order to provide a more comprehensive characterization of the pelagic life cycle and distribution of *Diadema* larvae.

Secondly, there is little known on the role micropredators play in regulating the juvenile and adult distributions of *Diadema*. Harrold et al. (1991) found that small crabs were predators of *Strongylocentrotus purpuratus* and *S. franciscanus* settlers and that the crabs influenced the distribution of sea urchin settlement in their study. The optimal depth for *Diadema* recruitment at the shelf-edge was on the 9 m plates with the lowest recruitment found on the shallower plates (Fig. 4). More microinvertebrates were identified on the 3 m and 6 m plates at shelf-edge stations (Fig. 6). There was a noticeable amount of microinvertebrates on plates that were collected from the inner and mid-shelf stations (Fig. 5), areas of little or no *Diadema* recruitment. Also, more lobster recruits were collected at the inshore sites and lobster adults are known predators of adult *Diadema* (Randall et al., 1964). High settlement mortality of *Diadema* at the inshore and mid-shelf reefs might also explain the low or absent recruitment recorded at these sites.

Spatial variation in recruitment of sessile marine invertebrates may be derived from a number of sources: events within the plankton, choices made by the settling larvae and mortality of juvenile organisms after settlement (Keough and Downes, 1982). Assessing the sources of spatial variation in recruitment of *Diadema* in La Parguera is

more complex than originally thought. We believe that settler mortality and/or low larval supply are two possible factors limiting a quicker recovery of *Diadema* populations at the inshore and mid-shelf reefs. If settlement mortality is high, large fluctuations in recruitment will translate into smaller fluctuations in the numbers of adults (Caley et al., 1996) and at the inshore sites that is what is happening in La Parguera. Slow recovery of *Diadema* populations is taking place at the inshore reefs of La Parguera and post-settlement survivorship seems to out weight the low larval supply and/or settlement mortality occurring at these sites. Harborne et al. (2009) observed that increased settlement rates are less important than increased predation pressure in the population dynamics of *Diadema*. We believe that factors affecting post-settlement survival, such as predation pressure are more accurate predictors of the distribution of *Diadema* populations. Future studies are needed to determine the role that microinvertebrates play on the recruitment survival of *Diadema*.

Settler survivorship needs to be increased in order to increase the recovery of *Diadema* densities at the inshore sites. Inshore reefs in La Parguera are more deteriorated and algal dominated than shelf-edge reefs. Macroalgal mats are usually occupied with more micro-predators. Macroalgal dominated reefs might contain more microinvertebrates as seen on the recruitment plates collected at the inshore sites. So, in order to decrease micro-predators and increase settler survivorship, macroalgal cover needs to be drastically reduced on the inshore reefs of La Parguera. In La Parguera, fishermen are now fishing out parrotfish since the commercial fish species are overfished. It seems that it will be a long and possibly a dead end road for the full recovery of *Diadema* population in La Parguera. Unless, there are management plans carried out that

would result in an increase of herbivorous fish species and decrease in terrigenous outputs (nutrient inputs) of the reefs of La Parguera.

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Conclusions

- *Diadema antillarum* spawns throughout the year in La Parguera
- Higher reproductive activity of *Diadema* in La Parguera occurs during April and July
- *Diadema* larval spatial distribution are aggregated or patchy
- *Diadema* populations in La Parguera may be an important source of larval replenishment for downstream islands
- There is a topographically steered flow which fringes the inner shelf foreereef platforms in La Parguera
- *Diadema* post-larval recruitment is greater during the summer months
- *Diadema* recruitment is greater at the shelf-edge region
- Recruitment rates in La Parguera are greater than those reported before the mass mortality in Curacao and also compared to recent studies in the Florida Keys and Canary Islands
- Inverse relationship between recruitment and adult urchin densities were observed in La Parguera suggesting that recruitment is not a major determinant of the spatial distribution of the adult population
- Upstream sources of *Diadema* larvae are available at La Parguera
- Post-settlement processes, such as predation pressure by microinvertebrates may have an influence on the recruitment pattern of *Diadema*

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