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***Diadema antillarum* populations in Panama twenty years following mass mortality**

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Introduction

The ecology of Caribbean reefs experienced profound changes after 1983, when the black sea urchin, *Diadema antillarum* Philippi, a major herbivore and bioeroder (Ogden et al. 1973; Scoffin et al. 1980; Sammarco 1982; Hay and Taylor 1985; Carpenter 1986), suffered mass mortality due to an unidentified pathogen, which reduced its populations by more than 93% (Lessios et al. 1984a; Lessios 1988a). *Diadema*'s demise contributed to reef degradation by shifting the community dominance from live coral to macroalgal cover (Liddel and Ohlhorst 1986; Hughes et al. 1987; Lessios 1988a; Levitan 1988; Hughes 1989, 1994; Carpenter 1990; Ostrander et al. 2000; Aronson and Precht 2001; Edmunds and Carpenter 2001), was correlated with population increases of herbivorous fish (Robertson 1991) (but not other sea urchins) (Hughes et al. 1987; Lessios 1988b), and caused predators to switch their diets to other prey items (Reinthal et al. 1984; Robertson 1987).

Despite a respectable number of studies documenting ecological effects of the *Diadema* demise after the mass mortality event, there is a paucity of reliable data on the fate of its populations in the last two decades, relative to the situation before 1983. The mass mortality began suddenly, so pre-mortality population density data, essential for determining the degree of any subsequent

recovery, were available from only a few areas in the Caribbean (review in Lessios 1988a). What is more, quantitative comparisons of *Diadema* abundance through time require data obtained by the same methods at exactly the same location, because the patchy distribution of this sea urchin can produce widely different estimates, depending on the area that is included in the sampling. Few studies have combined the two requirements of pre-mortality densities and continuous monitoring at the same location to determine the degree of population recovery. One such study is that of Lessios (1995), which followed population densities of *D. antillarum* on 11 reefs in the San Blas area of Panama from points before the 1983 mass mortality until 1993. The present report extends the data from the same reefs to February 2003, for a record of 20 years of *Diadema* densities since the mass mortality occurred.

Materials and methods

The pre-mortality data were collected either in 1980 or in 1982. Each reef was monitored with the same methods used for the pre-mortality density determinations for a period of 20 years, starting immediately after the mass mortality in 1983 and in yearly intervals thereafter, except for 1998–1999, when the Kuna Indians did not permit access to the San Blas (Alper 1998). Five to twelve transects per reef were laid down from the shallowest point at which *Diadema* occurred before the mass mortality to the base of the reef, or to a depth of 17 m if the base of the reef occurred deeper. *Diadema* were counted in a corridor approximately 2 m wide along these transects (Lessios et al. 1984b; Lessios 1988b, 1995).

Results and discussion

The *Diadema* mass mortality started in Panama in January 1983, and took about a year to cover the entire

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tropical West Atlantic (Lessios et al. 1984a). Since that time, a modest recovery was noted in some areas of the Caribbean. Hunte and Younglao (1988) reported that 2 years after mass mortality reached Barbados, population densities of *D. antillarum* had increased to 37% of their pre-mortality levels. Miller et al. (2003), citing CARICOMP data, state that this increase at Barbados has been sustained to the year 2000, but (underscoring the importance of monitoring the same sites) Williams and Polunin (2001) did not find any *Diadema* at the reef they studied on the same island in 1997–1998. Hughes (1994) found that in many locations in Jamaica, *Diadema* populations remained consistently sparse from 1983 to 1994. However, after 1996 there was a local increase in shallow water, which was correlated with renewed coral recruitment (Aronson and Precht 2000; Edmunds and Carpenter 2001; Moses and Bonem 2001). Miller et al. (2003) reported that at St. Croix population densities of *D. antillarum* increased by > 100% between June 2000 and June 2001, but remained one order of magnitude less than their pre-mortality levels. Even these modest population increases did not appear to have occurred in Florida by 2000 (Chiappone et al. 2002a, b), despite relatively higher densities in the Dry Tortugas (Chiappone 2001).

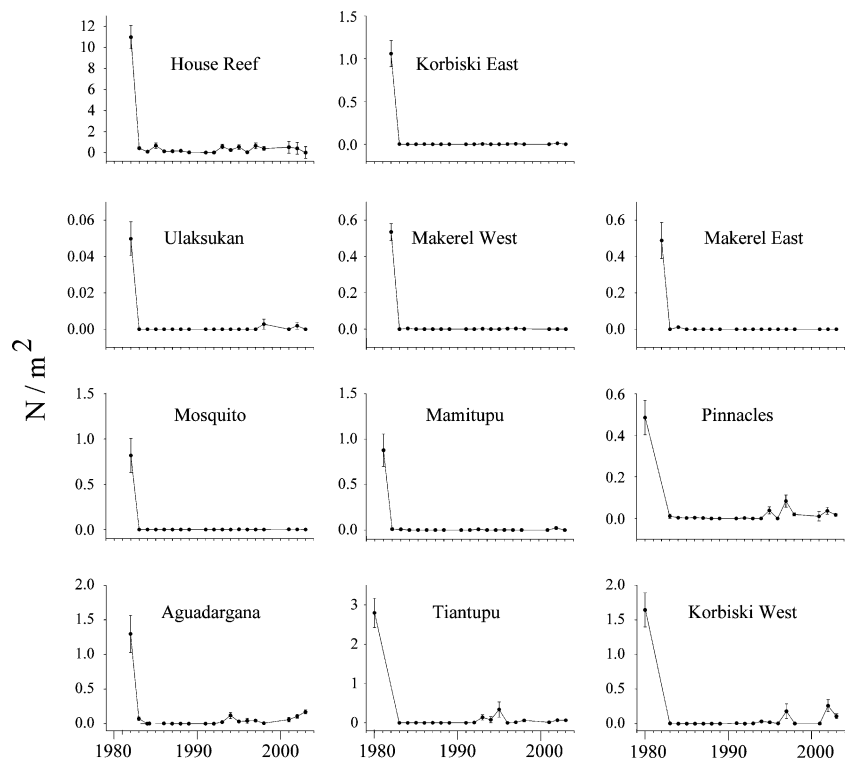
Even though populations in Panama had more time to recover than in other areas, the long-term series of data from the San Blas Archipelago indicates that 20 years after the mass mortality they remain at less than 6.5% of their pre-mortality levels (Fig. 1). Increases in point density at some reefs, caused by single events of successful recruitment, were not sustained; the

resultant cohorts of adult individuals soon diminished, indicating that such recruitment events were the result of chance convergence of factors that contribute to larval survival.

The lack of apparent recruitment could have been caused by too few adults in upstream areas to reproduce at a rate that would overcome the normal sources of mortality (the Allee effect), or by the continuing presence of the pathogen that devastated the populations in 1983–1984. Of the two possibilities, the former is more likely. Isolated incidents of mortality with symptoms similar to the ones noticed in 1983 have occurred in Panama (Lessios 1988b) and in Florida (Forcucci 1994), but otherwise the existing individuals on each reef are healthy, even in areas at which densities have been artificially increased to simulate pre-mortality conditions (Lessios 1988b).

Whatever the actual reasons for the lack of *Diadema* recovery in the last 20 years, it is possible that the population increases seen in Barbados, Jamaica, and St. Croix will gradually register in other areas as well. Evidence from mitochondrial DNA (Lessios et al. 2001a) indicates that *D. antillarum* populations from the entire Caribbean constitute a single gene pool, which suggests a high degree of larval mixing in each generation. This, in turn, means that the offspring of adults establishing themselves after local events of successful recruitment will be spread widely, requiring many generations before they produce observable sustained increases in any one locality. Genetic evidence of historically high population densities of this sea urchin in the last 100,000 years (Lessios et al. 2001b) suggests

Fig. 1 Means and standard errors of *Diadema antillarum* population density in 5–12 transects per reef on 11 reefs in the San Blas Archipelago, Panama between 1980 and 2003. See Lessios et al. 1984b for reef locations



that, if the past is any guide, this may be a passing phase in evolutionary time, from which *D. antillarum* will recover in centuries, even if it has failed to do so to any appreciable extent in decades.

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