INCREASED RECRUITMENT RATES INDICATE RECOVERING POPULATIONS OF THE SEA URCHIN *DIADEMA ANTILLARUM* ON CURAÇAO

Mark J. A. Vermeij, Adolphe O. Debrot, Noam van der Hal, Judith Bakker, and Rolf P. M. Bak

ABSTRACT

Recruitment of the sea urchin *Diadema antillarum* Philippi, 1845 was studied on artificial recruitment panels along the leeward coast of the island of Curaçao, southern Caribbean. Data were compared with historical data from the same coast that were collected before (1982–1983) and after (1984) the Caribbean-wide mass mortality of *Diadema* in October 1983. Average recruitment rates observed in 2005 were equal to 2.2 times lower compared to those observed before the *D. antillarum* die-off (1982 and 1983), but 56.5 times higher than those observed after the die-off in 1984. The increase in recruitment rates between 1984 and 2005 was 5–51 times greater than the increase in abundance of adult individuals over the same period. This suggests that despite the largely recovered recruitment rates of this important reef herbivore, unknown sources of high post-settlement mortality currently prevent a similar recovery of its adult population.

The long-spined sea urchin *Diadema antillarum* Philippi, 1845 used to be a common species that occurred in mean densities of 3–20 ind m^{-2} on the shallow fore-reef along the leeward coast of Curaçao (Smith, 1969; Bak and van Eys, 1975; Bauer, 1980; Bak et al., 1984), a relatively small island (444 km^2) in the southern Caribbean. In 1983, an unidentified disease caused *Diadema* to become almost extinct on Curaçao (Bak et al., 1984) and elsewhere in the Caribbean (Lessios, 1988). Mass mortality was first observed in October 1983 and locally 97.3%–100% of all urchins died (Bak et al., 1984). *Diadema antillarum* was an important benthic herbivore (Sammarco et al., 1974; Hughes et al., 1999) and turf/macroalgae increased in abundance after the *Diadema* die-off (De Ruyter van Steveninck and Bak, 1986; Lessios, 1988; Carpenter, 1990; Hughes, 1994). Because algae compete for space with juvenile corals, the *D. antillarum* die-off indirectly caused a reduction in the number of juvenile corals once algae had become more abundant (Edmunds and Carpenter, 2001). Therefore, many authors consider the *D. antillarum* die-off as one of the main factors contributing to the overall decline of Caribbean reef ecosystems (Hughes, 1994; Knowlton, 2001).

As of 2000, recovering *D. antillarum* populations have been observed throughout the Caribbean; e.g. Barbados (Hunte and Younglao, 1988), Jamaica (Edmunds and Carpenter, 2001; Haley and Solandt, 2001; Moses and Bonem, 2001), Dry Tortugas (Chiappone et al., 2001), St. Croix (Miller et al., 2003), Costa Rica (Alvarado et al., 2004), Puerto Rico (Weil et al., 2005), and Curaçao (Debrot and Nagelkerken, 2006). Local increases in *D. antillarum* density have been attributed to migrating adults (Hughes et al., 1987), influx of larvae from (local) refuge habitats where *D. antillarum* survived during the mass mortality (Debrot and Nagelkerken, 2006), and local population growth. Local increases in adult population density are important to future population recovery as increased adult density (a) overcomes Allee effects that arose after the species' die-off (Bak, 1985); (b) induces settlement of pelagic *D. antillarum* larvae (Hunte and Younglao, 1988), and (c) provides recruits with shelter from the

adult spine canopy (Miller et al., 2007). Hence, it can be expected that once adult density increases, positive feedback mechanisms will arise, creating conditions for increasingly greater recruitment success.

In 2002, adult *D. antillarum* densities in Curaçao were higher (0.08–0.28 ind m^{-2}; Debrot and Nagelkerken, 2006) than those observed immediately after the die-off (0.01–0.05 m^{-2}; Bak et al., 1984). This suggests that adult populations are recovering, but densities are still an order of magnitude lower than those reported pre die-off (2.9–4.2 m^{-2}; Bak et al., 1984). Because information is available on recruitment rates of *D. antillarum* before and immediately after the die-off (Bak, 1985), we aimed to investigate if the slow recovery of adult *D. antillarum* populations on Curaçao was related to low recruitment rates.

Methods

Between March and July 2005, we measured recruitment rates of *D. antillarum* at 7 reef sites along the leeward coast of Curaçao, Netherlands Antilles (Grote Knip, St. Martha, Daaibooi, Slangenbaai, Buoy One, Piscaderabaai and Water Factory; Fig. 1). This time frame was chosen to cover a period starting just before and ending right after a seasonal peak in *D. antillarum* recruitment (Bak, 1985). At 2-wk intervals the number of newly arrived *D. antillarum* recruits was counted on grated plastic panels placed at depths of 3–5 m following the methods described in Bak (1985). Recruits were defined as newly arrived individuals with tests smaller or equal than 3 mm in diameter.

The grated plastic recruitment panels consisted of two panels of white plastic egg crate (57 × 27 cm) with a thin (3 mm) Formica sheet sandwiched in between. Each side of the panel consisted of 780 cells measuring 10 × 10 × 10 mm. At each site two such recruitment panels were attached to a metal frame 20 cm above the reef. Recruitment panels require biofouling before they attract *Diadema* settlers, and recruitment rates of *D. antillarum* are affected by the amount of time that panels have been submerged (Bak, 1985). Because recruitment was only observed after panels had been submerged for 3 wks (Bak, 1985), we placed our panels on the reef three weeks prior to the first surveys in March to ensure that they were sufficiently conditioned before our surveys began. All panels were placed in shallow water coral communities, dominated by *Montastraea* spp., *Diploria* spp. and *Madracis mirabilis* Duchassaing and Michelotti, 1860 that are common along the entire leeward coast of Curaçao (Van Duyl, 1985). Additional observations were made daily for 2 wks at one site (Piscaderabaai) to describe the early development of new *D. antillarum* recruits on the aforementioned panels.

For our 2005 dataset, differences in recruitment rates among sites and through time were analyzed using a non-parametric Kruskal-Wallis (KW) ANOVA. To compare the recruitment rates observed in this study to those of Bak (1985), recruitment rates from both datasets were averaged across all sites to produce island-wide, rather than site-specific, estimates of *D. antillarum* recruitment rates. This procedure yielded more comparable estimates of *D. antillarum* recruitment through time as different sites were visited during both studies and could not be directly compared. Both studies quantified *D. antillarum* recruitment at 2-wk intervals. Recruitment rates were subsequently analyzed using a KW-ANOVA using "year" (1982, 1983, 1984, and 2005) as a grouping variable. Note that 1982 and 1983 represent "pre-die-off" years. All post hoc comparisons were conducted by pair-wise KW-tests based on Least Significant Differences (LSD). LSD allows for non-parametric multiple group comparisons (Portney and Watkins, 1993). The difference between any two groups calculated by KW-tests must exceed the Least Significant Difference before that difference can be considered as statistically significant.
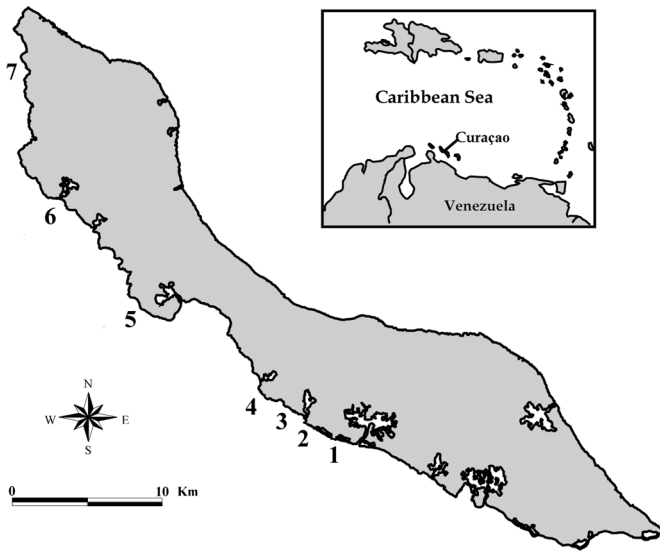
Figure 1. Map of Curaçao showing the seven sites at which recruitment of *Diadema antillarum* was monitored: (1) Water Factory, (2) Piscaderabaai, (3) Buoy One, (4) Slangenbaai, (5) Daaibooi, (6) Sta. Martha, and (7) Grote Knip.

Results

General Observations.—*Diadema antillarum* recruitment was first observed on May 13, 2005, 2 mo after the first grate panels were placed on the reef. The recruits measured ≤ 3 mm in test diameter. Observations made in addition to the two-weekly surveys showed that the recruits initially had a red coloration that changed to black in less than a week. Another sea urchin species, *Echinometra lucunter* (Linnaeus, 1758), recruited to the panels in extremely low densities and was not further considered in this study.

Diadema Recruitment.—*Diadema antillarum* recruitment rates did not differ among sites around the island (KW-ANOVA, $H_{6,60} = 6.24$, $P = 0.40$). Highest mean recruitment rates were observed at Grote Knip (average: 21.0 recruits 2 wk^{-1}; SE: 7.8), whereas recruitment rates were lowest at Buoy One and Slangenbaai (0.17 recruits 2 wk^{-1}; SE: 0.17). When data from all sites were combined, recruitment differed significantly through time (KW-ANOVA, $H_{8,60} = 39.37$, $P < 0.01$). Rates gradually increased from May 6, 2005 to June 3, 2005 when recruitment peaked and then gradually decreased towards the end of the study on July 16, 2005.

Comparison with Historic Pre- and Post-Die-off Recruitment Rates.— The 2005 data showed a peak in *D. antillarum* recruitment rates around early June similar to that observed in 1982 and 1983 (Bak, 1985). Although recruitment rates differed among years (KW-ANOVA, $H_{3,24} = 13.96$, $P < 0.01$), subsequent post-hoc analyses showed that recruitment rates of *D. antillarum* in 2005 were (a) significantly higher than recruitment after the die-off (1984) (pair-wise KW-test; $P < 0.05$); (b) significantly lower than recruitment rates in 1983 (pair-wise KW-test; $P < 0.01$) and,
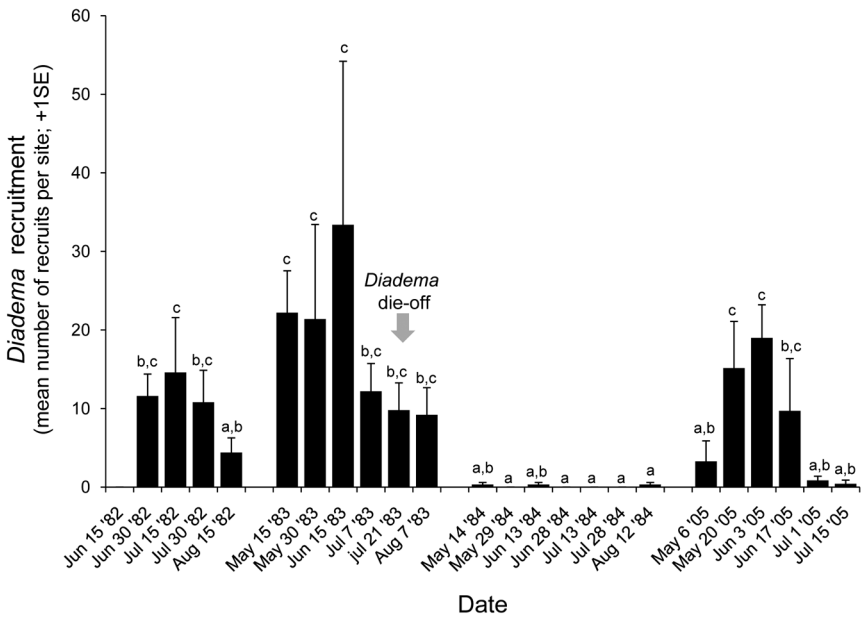
Figure 2. Mean bi-weekly recruitment rates of *Diadema antillarum* (± SE) through time for all sites pooled during the summer recruitment peak of *Diadema* in Curaçao for 2005 (present study) and pre- (i.e., 1982–1983) and post die-off (i.e., 1984) periods (recalculated from Bak [1985]'s original data). Letters above each bar indicate significant groupings based on post-hoc analyses (pair-wise KW test; P < 0.05).

(c) similar to those observed in 1982 (pair-wise KW-test; P = 0.23). Hence, recruitment rates in 2005 were similar (1982) to 2.2 times lower (1983) compared to those observed before the *D. antillarum* die-off, but were on average 56.5 times higher than the rates reported after the *D. antillarum* die-off in 1984 (Fig. 2).

Discussion

Our data demonstrate that recruitment rates of *D. antillarum* showed obvious signs of recovery in Curaçao in 2005. Recruitment of *D. antillarum* in 2005 was 44.8%–97.5% of the recruitment rates observed before the die-off (compared to 1983 and 1982 respectively; Bak, 1985). Available data for 2002 show that adult densities remained low, ranging between 0.08–0.28 ind m^{-2} in 2002 (Debrot and Nagelkerken, 2006) compared to 2.93–4.16 ind m^{-2} before the die-off (Bak et al., 1984). Following the die-off in the fall of 1983, adult densities had decreased to 0.01–0.05 ind m^{-2} (Bak et al., 1984). Adult densities in 2002 were slightly higher, but only at 1.9%–9.6% of their pre die-off density. No evidence was found to suggest that their densities had noticeably increased between 2002 and 2005, the year that we conducted our recruitment surveys (van der Hal, unpubl. data). While adult density and recruitment had both increased, the increase in *D. antillarum* recruitment rates far exceeded the increase in adult abundance, i.e., 5–51 fold, assuming that adult densities in 2005 were approximately similar to those in 2002. Positive feedback mechanisms, where increased adult density promotes recruitment, seem unlikely to explain the high re-

cruitment rates observed in 2005 given the minimal increase in adult density since the *D. antillarum* die-off. An increase in the availability of pelagic larvae, and/or a reduction in pre- and/or early post-settlement mortality could alternatively explain the increased abundance of young recruits of *D. antillarum* on Curaçaoan reefs.

The recovery of source-populations for Curaçao's *D. antillarum* population could explain the return to pre die-off recruitment rates on the island. Similar to observations made after the die-off, recruitment rates of *D. antillarum* can vary independent of the local adult population. After the die-off, adult populations on Curaçao had effectively disappeared, but recruitment continued for another 4–5 mo (Bak, 1985). It is now assumed that *D. antillarum* populations up-current from Curaçao, which had not yet succumbed to the disease, continued to provide larvae to downstream locations. Recruitment to down-current locations ceased when the upstream source populations were also decimated by the disease (Bak, 1985; Lessios, 1988). Similarly, but vice versa, *Diadema* recruitment rates could increase independent of the status of the local adult population, when recovery of adult populations progresses faster in up-current populations. For Curaçao, such locations could include Barbados where recovery of *D. antillarum* progressed extremely fast, i.e., some reefs had already returned to 57.4% of their pre die-off adult densities by 1985 (Hunte and Younglao, 1988).

The reefs of Curaçao are heavily overfished (Van't Hof et al., 1995; Debrot and Sybesma, 2000; Debrot and Nagelkerken, 2000). Densities of fish that prey on *D. antillarum* (mainly triggerfishes; *Balistidae*; Randall et al., 1964; Lessios, 1988; Forcucci, 1994) were already too low to support their commercial taking around the 1960s (Debrot and Nagelkerken, 2006) and have since then further decreased (Bruckner and Bruckner, 2003; Nagelkerken et al., 2005). While the low abundance of documented *D. antillarum* predators could contribute to the observed increase in recruitment rates, it is unknown which other fish species prey on recently recruited *D. antillarum* rather than on adult individuals. It is likely that wrasses, sparids, and haemulids prey on *Diadema* recruits resulting in increased post-settlement mortality of older recruits and lower effective recruitment into the adult population. An increase in such fish species could be the result of overfishing of their predators (Sandin et al., 2008). In this case, overfishing could indirectly hamper the recovery of *Diadema* populations due to increased post-settlement mortality of *Diadema* recruits caused by the taking of predatory fishes that normally eat predators of *Diadema* recruits.

We conclude that *D. antillarum* populations on Curaçao are recovering due to an increase in recruitment, with recruitment rates in 2005 comparable to those before the 1983 die-off. The adult population was also increasing in size (Debrot and Nagelkerken, 2006) albeit at a much slower rate, relative to the observed increase in recruitment rates. This suggests that while individuals settled successfully, poor post-settlement survivorship limited overall population growth. Predation, physical disturbance (Miller et al., 2009) and lack of suitable post-settlement habitat could all contribute to low post-settlement survival of *D. antillarum*. It is to be expected that the observed increase of recruiting and adult *D. antillarum* continues, or even accelerates, when positive feedback loops arise. It is presently unclear whether such feedback loops have started operating on Curaçaoan reefs. Nevertheless, our findings illustrate a positive aspect of Caribbean reef development showing that natural recovery of organisms that were once abundant is still possible.

Acknowledgments

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ADDRESSES: (M.J.A.V.) *Caribbean Research and Management of Biodiversity (CARMABI), Piscaderabaai z/n, PO Box 2090, Willemstad, Curaçao, Netherlands Antilles and University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics (IBED), PO Box 94766, 1090 GT, Amsterdam, The Netherlands.* (A.O.D.) *Caribbean Research and Management of Biodiversity (CARMABI), Piscaderabaai z/n, PO Box 2090, Willemstad, Curaçao, Netherlands Antilles.* (N.H., J.B.) *University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics (IBED), PO Box 94766, 1090 GT, Amsterdam, The Netherlands.* (R.P.M.B.) *University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics (IBED), PO Box 94766, 1090 GT, Amsterdam, The Netherlands and Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands.* CORRESPONDING AUTHOR: (M.J.A.V.) *Telephone: +5999 5103067, E-mail: <m.vermeij@carmabi.org>.*