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NOTE

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 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 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.

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

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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 "eggcrate" 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 m^2 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 *Diadema*?
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	*N*	Maximum (# settlers m^{-2})	Proportion observations with ~ 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

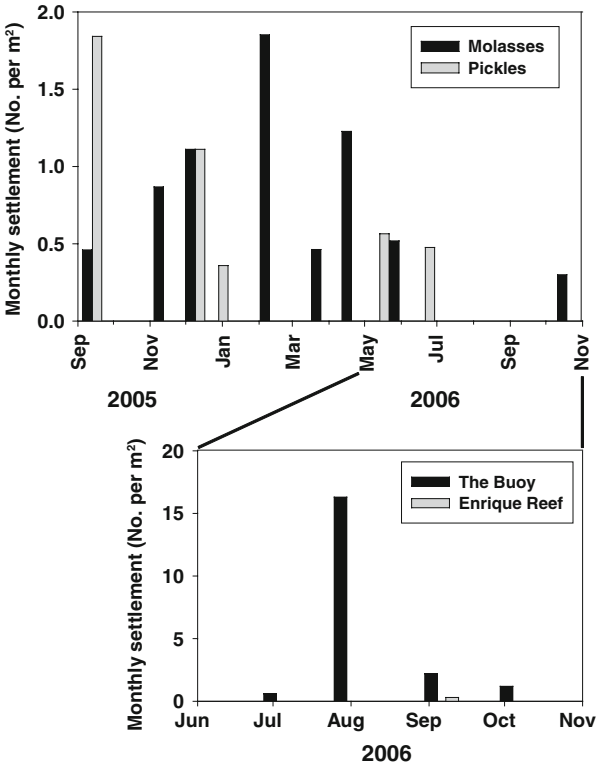

Fig. 2 Monthly settlement density (pooled for all settlement plates, standardized to 30-day intervals) of *Diadema antillarum* at two sites in the upper Florida Keys (upper panel) and two sites in southwest Puerto Rico (lower panel). Note different *y*-axis scales in each panel

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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