Arrested recovery of *Diadema antillarum* population: Survival or recruitment limitation?

Ruber Rodríguez-Barreras [a],[*], María E. Pérez [b], Alex E. Mercado-Molina [a], Alberto M. Sabat [a]

[a] Department of Biology, University of Puerto Rico, Rio Piedras, PO Box 23360, San Juan 00931-3360, Puerto Rico
[b] Department of Mathematics & Center of Applied Tropical and Conservation, University of Puerto Rico, Rio Piedras, PO Box 23355, San Juan 00931-335, Puerto Rico

A B S T R A C T

Densities of the long-spined sea urchin *Diadema antillarum* remain significantly below pre mass-mortality levels at most Caribbean localities. The arrested recovery of this formerly abundant herbivore has been attributed to low supply of recruits and high post settlement mortality. There is, however, some debate as to which of these factors is determinant of the local dynamics of this echinoid. In this study, we use demographic modeling to analyze the contribution of recruitment and post settlement survival on the dynamics of *D. antillarum* in four localities of Puerto Rico Archipelago. Our results indicate relatively high adult survival, and low stasis but high growth transition in the small individuals. Recruitment rates were low and exhibited high spatial and temporal variability. The four populations exhibited asymptotic growth rates (λ) below 1.0, with λ varying from 0.918 to 0.964. The elasticity analysis showed that the survival of large-sized *Diadema* can potentially contribute most to the changes in λ for all sites. Numerical projections of the populations indicate that no site would exhibit an increase in density under current recruitment rates, but doubling recruitment would produce an increase in sea urchin density in three of the four sites. Recovery of *D. antillarum* populations would require the spatial and temporal co-occurrence of high recruitment and survival rates.

1. Introduction

Caribbean reefs systems have deteriorated dramatically over the last decades (Gardner et al., 2003; Hughes et al., 2010; De'ath et al., 2012). This decline has been associated with the cumulative effect of natural and human-induced disturbances such as, hurricanes, disease outbreaks, bleaching, pollution, and overfishing (Hughes, 1994; Bythell et al., 2000; Kramer et al., 2003). One of the most significant shifts in benthic community structure of Caribbean reefs occurred after the mass-mortality event of the sea urchin *Diadema antillarum* (Philippi 1845) between 1983 and 1984, which caused mortality rates of up to 99.9% at some Caribbean localities (Hughes et al., 1985; Hunte et al., 1986; Liddell and Ohlhorst, 1986; Lessios, 1988; Lessios, 2013).

During the thirty years since this region-wide collapse, abundance of the formerly abundant *D. antillarum* has remained below pre-mortality levels (Lessios, 1988; Karlson and Levitan, 1990; Levitan et al. 2014). Most studies report densities that still remain around or below 1 urchin. m^{-2} (Carpenter and Edmunds, 2006; Miller et al., 2007; Chiappone et al., 2008, Ruiz-Ramos et al., 2011; Rodríguez-Barreras et al., 2014). The lack of recovery has been attributed to low supply of recruits, or to high post settlement mortality (Lessios, 1988; Rogers and Lorenzen, 2008; Harborne et al., 2009; Mercado-Molina et al., 2014). Recruitment measurements, before and after the die-off, indicate a decrease of settlement in the Caribbean after 1984 (Bak, 1985; Vermeij et al., 2010). This decrease has been attributed either to reduced fertilization success (Lessios, 1988; however see Williams et al., 2010), or the lack of suitable conditions for larvae settlement (Rogers and Lorenzen, 2008). After the collapse of *D. antillarum* populations, fleshy-algae became overabundant in reef systems in the Caribbean potentially compromising settlement and recovery (Carpenter, 1985, Liddell and Ohlhorst, 1986; but see Bruno et al., 2009). Seaweeds produce tannins, phenols, and other secondary metabolites against herbivores that may affect fertilization success, larvae survival and settlement (Pennington, 1985; Hay and Fenical, 1988).

The evidence in support of the role of post-settlement mortality in controlling the dynamics of *D. antillarum*, is the observation that lower abundances have been reported inside no-take reserves (Chiappone et al., 2002; Brown-Saracino et al., 2007; Harborne et al., 2009), whereas overfished areas have reported higher *Diadema* densities (see Sellers et al., 2009; Idjadi et al., 2010). This sea urchin has multiple predators, including fish of the families Balistidae, Haemulidae, Labridae and Sparidae, lobster of the genus *Panulirus* spp., and gastropods of the genus *Cassis* spp. (Randall et al., 1964; Serafy, 1979; Carpenter, 1984). There is also evidence that physical factors can contribute to explain differences in *D. antillarum* abundance. The species is susceptible to hydrodynamic forces because its long spine canopy does not allow a large adhesive area to attach to the surface (Tuya et al., 2007). Therefore, areas with low wave energy tend to support higher abundances of *Diadema* (Debrot and Nagelkerken, 2006; Clemente et al., 2011; Rodríguez-Barreras et al., 2014).

Populations of *D. antillarum* are considered open in the sense that larvae produced at a given locality drift away from the local population due to water hydrodynamics and settle at other localities (Karlson and Levitan, 1990). Teasing apart the relative effect of recruit supply and post settlement mortality on the local dynamics and structure of open marine populations is not a trivial task. For instance, Caley et al. (1996) suggested multifactorial field experiments as a means of unraveling the effect of recruitment versus post-settlement mortality. Another approach towards the same end is demographic modeling. Pfister (1996) and Hughes and Tanner (2000) successfully used this approach to analyze the effect of survival (among other vital rates) and recruitment on the open populations of tide pool fishes and three Caribbean corals, respectively. In this study we follow the demographic modeling approach to examine the apparent lack of recovery in *D. antillarum*.

Unstructured models have been used in *D. antillarum* to simulate its dynamics (Karlson and Levitan, 1990; Rogers and Lorenzen, 2008; Levitan et al., 2014). These models, however, do not allow dividing the population into discrete classes and analyze the contribution of each size class to the overall population growth. Structured models allows the partition of the contribution of each class to population growth rate; thus, providing more biological meaningful management decisions. We analyze the contribution of recruitment and post settlement survival to the dynamics of the species by constructing, parameterizing and analyzing size-based matrix population models for four localities of northeastern Puerto Rico Archipelago. We use the equations to numerically simulate the effect of different rates of recruitment on the local dynamics of the species. Thus, we evaluate the relative contribution of all matrix transitions (including survivorship) to population asymptotic growth rate (λ) through the elasticity analysis.

2. Methods

2.1. Site description and data collection

The study was conducted in four shallow-water fringing reefs (<3.0 m depth) located in northeastern Puerto Rico Archipelago: Cerro Gordo (CGD- 18°16′51.40″N, 65°17′12.21″W), Luquillo (LQY- 18°23′18.46″N, 65°43′5.52″W), Tamarindo (TMD- 18°18′55.29″N, 65°19′5.82″W), and Melones (MLN- 18°18′15.70″N, 65°18′42.27″W), see Fig. 1. The geological composition of TMD and MLN is characterized by volcanic and intrusive rocks, with some limestone deposits, whereas LQY and CGD are made up by carbonate rocks. Structural complexity varies from sites with relatively high rugosity indexes (CGD and MLN), to less complex fringing reefs (TMD and LQY). Fleshy macroalgae average cover is less than 10 ± 6.37 % in the four localities, whereas live coral cover was greater than 15% at all

sites, peaking at TMD with 29.09 ± 12.15%. See more details in Rodríguez-Barreras et al. (2014). Surveys were conducted during August of 2011, 2012, and 2013 (three censuses). Mean density was estimated using the belt-transect methodology (Sellers et al., 2009). Eight transects of 10 m^2 (5 m $\times$ 2 m) were established per site parallel to the coast and separated by 10 m each. All individuals within the transects were counted. Size frequency data were also collected during this period by measuring the test diameter of fifty sea urchins selected at random (caliper error ± 0.05 mm). See more dataset details in Rodríguez-Barreras et al. (2014), where all sites acronyms coincide, except TMD that is named TM1.

2.2. Demographic model

The life cycle of *D. antillarum* was summarized into three size classes: small, medium, and large individuals (Fig. 2). The small size class includes urchins with a horizontal test diameter between 10 and 40 mm; the medium size class includes those larger than 40.1 and smaller than 60 mm, and the large ones are those with diameters in excess of 60.1 mm (Karlson and Levitan, 1990; Miller et al., 2003; Rodríguez-Barreras et al., 2014). Data on larval stage of *D. antillarum* is scarce, and the few available studies have focused in measuring abundance in the pelagic stage, but not of survival or settlement success in natural reef substrate (Vermeij et al., 2010; Williams et al., 2010), therefore the dynamic of the larval stage was not included in the model. Early recruits were also excluded because of their cryptic behavior and small size does not allow an accurate estimate of their abundance. Thus, the simplified life cycle we were analyzing in this study excludes the pelagic phase, and the initial 3 months after settlement (assuming a growth rate of between 6 and 7 mm. month^{-1} (Levitan et al., 2014)). We assumed in this analysis that the number of individuals entering the population at a test diameter of 10 mm is more strongly influenced by the number of larvae successfully settling at each site, than the number removed by predators during the first 3 months after settlement. We understand that mortality due to predation is relative low during this period because of their cryptic behavior, and refugee availability according to Levitan et al. (2014).

The demographic model in Equation (1) presents five transitions: the probability of surviving and remaining in the same size class (P_x), and the probability of surviving and growing (G_x) from a given stage to the next one. The real dominant eigenvalue and the corresponding right and left eigenvectors of the 3×3 projection matrix were calculated to obtain the asymptotic population growth rate (λ), plus the stable stage and reproductive value vectors. The stable stage and reproductive value vectors were used to calculate the elasticity matrices (Caswell, 1996). Asymmetric 95% confidence limits of λ were estimated from the 2.5th and 97.5th percentiles with a bootstrapping routine 1000 times (Caswell, 2001).

$$\begin{bmatrix} S \\ M \\ L \end{bmatrix}_{t+1} = \begin{bmatrix} P1 & 0 & 0 \\ G1 & P2 & 0 \\ 0 & G2 & P3 \end{bmatrix} \times \begin{bmatrix} S \\ M \\ L \end{bmatrix}_t + \begin{bmatrix} R \\ 0 \\ 0 \end{bmatrix}_t \quad (1)$$

Initially we had planned a capture-mark-recapture study to estimate the life cycle transitions. However, this was not possible because three tested tagging methodologies failed due to low retention and/or high mortality (see Rodríguez-Barreras and Sabat, 2015). Instead, life cycle transitions were estimated using the quadratic programming routine (QP); a mathematical algorithm that minimizes quadratic forms subjects to inequalities, using changes in the abundance of the three size classes, during the three censuses. This procedure takes as inputs the C matrix (constrain -non-negative), and the vector b = (0 0 0 0 0 1 1 1). A new matrix G and a new vector f are generated and used in the QP routine that