

Recovery of *Diadema antillarum* and the potential for active rebuilding measures: modelling population dynamics

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Abstract. Recent studies suggest that population recovery of the long-spined sea urchin *Diadema antillarum* could help to reverse the phase shift observed on Caribbean coral reefs by reducing macroalgal cover and promoting coral recruitment. Interest has arisen around the potential for active rebuilding measures such as hatchery release and translocations to aid and increase the slow and patchy population recovery so far witnessed since the 1983 mass mortality event. We developed a population dynamics model for *D. antillarum* to gain insight into the key processes preventing population growth and assess the effectiveness of proposed rebuilding strategies. The model accounts for compensatory density-dependence in recruitment and growth and depensatory density effects associated with fertilization success, a possible refuge function of the adult spine canopy for juveniles and ‘cultivation’ of preferable habitat by grazing. Results show that the population can exist at low and high-abundance equilibria associated with high and low macroalgal abundance respectively. The switch to high abundance is hampered by high juvenile mortality due to the absence of refuges. Restoration may be aided by release of large urchins and by manipulation of macroalgal cover. Experimental work is suggested to test process models and quantify functional relationships used in this exploratory analysis.

Key words: Allee effect, cultivation effect, predation refuge, habitat modification, active rebuilding

Introduction

The long-spined sea urchin *Diadema antillarum* was once abundant on coral reefs of the Caribbean region, fulfilling a role as the keystone herbivore of macroalgae (Sammarco 1982; Carpenter 1986). Its functional extinction following the mass mortality event of the early 1980s had a profound effect on coral reef community composition and is thought to have played a major role in the subsequent phase shift from states dominated by live coral to states dominated by macroalgae (Aronson and Precht 2000). Recent studies have shown that population recovery of *D. antillarum* has the potential to reverse the phase shift, reducing macroalgal cover and promoting coral recruitment (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006). Widespread population recovery of *D. antillarum* may therefore be considered as a tool with which to aid coral reef restoration in the Caribbean.

While in some locations, *D. antillarum* abundance has recovered markedly (Carpenter and Edmunds 2006); in others the population has persisted at a low level of abundance (Lessios 2005; Chiappone et al 2002). The mechanisms underlying differential recovery and the potential for active rebuilding measures remain poorly understood. Hypotheses

relating to the negative impact of low population density on population growth may explain the slow and patchy recovery that has been observed across the region (Lessios 1988). *D. antillarum* is a dioecious species with broadcast spawning, a long larval stage and limited adult dispersal (Lessios 1988). Despite their long spines, *D. antillarum* are susceptible to predation by around 15 fish species and multiple invertebrates with the greatest risk being to smaller size classes (Carpenter 1984; Clemente et al 2007). Direct negative effects of low population density, referred to as Allee effects may be responsible for a reduction in fertilization success, larval settlement and post-settlement survival (Bak 1985; Levitan 1991; Miller et al 2007). At low population density the chances of adult urchins spawning synchronously and at close enough proximity to allow for successful fertilization is greatly reduced (Levitan 1991). Larvae in the water column may take settlement cues from conspecifics and it is thought that the spine canopy of adult urchins may act as an important predation refuge for susceptible juveniles (Nishizaki and Ackerman 2007; Miller et al 2007). Both larval settlement and post-settlement survival may be further reduced at low population density through an indirect effect which we will refer to as the cultivation effect.

As prolific grazers and bioeroders, *D. antillarum* are associated with habitats low in macroalgal cover and high in reef topographic complexity (Lee 2006). Evidence suggests that surfaces clear of macroalgae are preferred for larval settlement (Bak 1985) and we hypothesize that reefs that lack macroalgae and have greater topographic complexity will naturally have more reef cracks and crevices that provide effective predation refuges. Few studies have set out to test hypotheses relating to Allee and cultivation effects and none have aimed to quantify their impact at a demographic level. In this study we synthesize data from the literature and use it to produce a combined population dynamic and grazing impact model for *D. antillarum*. The aim of the modeling process is to gain a quantitative understanding of the recovery dynamics of this keystone species and inform the best avenues for future empirical studies and rebuilding strategies.

The model was explored to assess the impact of Allee effects and cultivation effects on the critical densities and sizes of urchins required for population persistence and population growth. The model was run under circumstances of both initial high macroalgal cover and low macroalgal cover to examine the impact of potential habitat modification.

Methods

We produced a combined population dynamics and grazing impact model for *D. antillarum*. Population dynamics are described by a size-structured, projection matrix model (Shepherd 1987; Lorenzen 1995) in which, the urchin population is divided into size classes such that the population density at time t is represented by a vector, n of densities-at-size. The equation that computes this vector for time $t + dt$ is:

$$n_{t+dt} = GS(n_t + r_t) \quad (1)$$

Where G is a growth projection matrix, S is a survival matrix and r is a vector of new recruits obtained from the stock-recruitment relationship described below. Both G and S are dependent on population density and habitat state.

Growth

Due to conspecific competition for resources, *D. antillarum* exhibit density-dependent indeterminate growth, such that growth rates and asymptotic sizes decline with increasing population density. Growth in the model population is therefore described by a density-dependent extension of the von Bertalanffy growth function (VBGF) as described by Lorenzen (1996a) such that the diameter of urchin $D_\infty(B)$ is a linear function of biomass B :

$$D_\infty(B) = (D_{\infty L} - dB) \quad (2)$$

Where $D_{\infty L}$ is the limiting asymptotic diameter in the absence of resource competition and d is the competition coefficient. This growth rate equation is used to produce the growth projection matrix, G by the method described by Shepherd 1987.

Mortality

The annual mortality rate, M in the model population is the sum of size-dependent baseline mortality excluding predation, M_b and additional predation mortality M_p .

$$M = M_b + M_p P_1 P_2 \quad (3)$$

Baseline mortality, M_b is a function that describes the inverse relationship between individual size and mortality (Lorenzen 1996b). Predation mortality, M_p is a vector of values that describes additional size-dependent predation mortality. The values of M_p are estimated from a recent study that used a tethering experiment to show that predation risk was greatest in the smallest size classes and non-existent after a threshold size of 40mm (Clemente et al 2007) (Fig. 1).

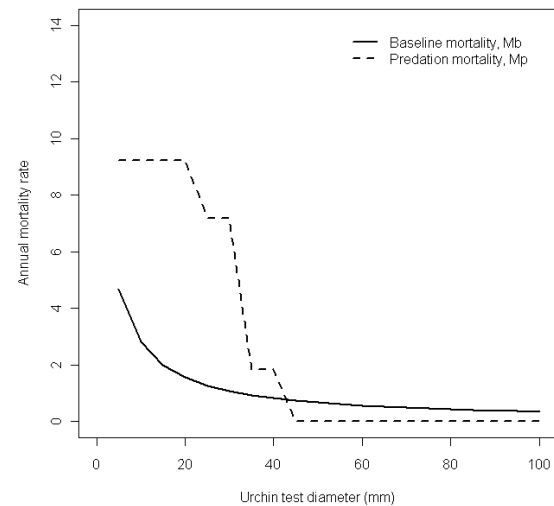


Figure 1: The shape of the relationships used to describe baseline mortality, M_b (Lorenzen curve) and predation mortality, M_p from Clemente et al 2007.

Due to the artificial nature of tethering experiments, the values assigned to M_p are considered to represent maximum levels of predation mortality.

Predation mortality is moderated by two parameters P_1 and P_2 which represent predation refuge effects associated with the hypotheses described previously, the adult spine canopy and the cultivation effect. P_1 is a function of adult surface area and acts such that predation risk, M_p declines as adult surface area and

thus spine canopy increases (Fig. 2a). P_2 is a function of macroalgal biomass and acts such that predation risk, M_p increases as macroalgal biomass increases (Fig. 2b). In this instance, macroalgal biomass is the variable used to represent the link between habitat cultivation and refuge availability.

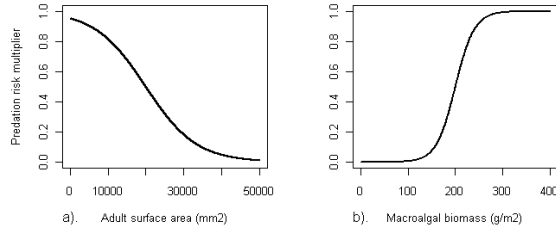


Figure 2: The shape of functions determining the extent to which predation mortality is applied to urchins. a). represents a decline in predation risk with increasing adult surface area due to the spine canopy refuge effect and b). represents the increase in predation risk with increasing macroalgal biomass due to the cultivation effect.

Incorporating an effect of macroalgal biomass required the inclusion of a simple biomass dynamic model for macroalgal growth and urchin grazing such that macroalgal biomass, A at time t is represented by:

$$A_t = A_{t-1} + vA_{t-1}\left(\frac{1 - A_{t-1}}{C}\right) - gU_{t-1}A_{t-1} \quad (4)$$

Where C represents the carrying capacity of macroalgal biomass, v the growth rate of macroalgae, and g , the proportion of algal biomass consumed per unit of urchin biomass, U .

Recruitment

Recruitment in the model population was described in two distinct ways; a stock-recruitment function relating to local adult biomass density and an externally driven density-independent level of recruitment. This distinction is important since speculation remains about the extent of larval dispersal in *D. antillarum* and whether larval supply to a local population is produced by that population or comes from source populations elsewhere (Bak 1985; Lessios 2001; Karlson and Levitan 1990).

The stock recruitment curve used to describe density-dependent recruitment was the product of two elements. The first was a dependant curve representing an increase in fertilization success and larval settlement with increasing spawner biomass density (Fig. 3a). The second was a compensatory curve representing a decrease in larval survival at settlement as spawner biomass density continues to increase (Fig. 3b). Declining larval survival represents conspecific resource competition for suitable

settlement space and acts to limit population growth to a carrying capacity.

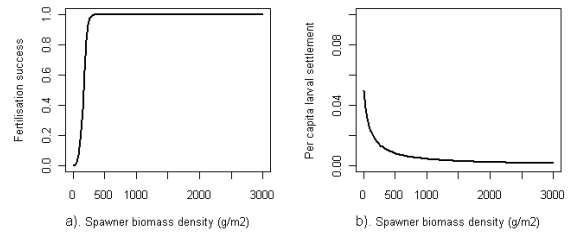


Figure 3: The two functions used to produce the stock-recruit relationship in the model population. A dependant, logistic curve describing fertilization success (a) and a compensatory Beverton-Holt curve describing resource competition (b).

Biomass density was used in this relationship to allow for differences in gamete production between different sized urchins. The parameters of the curve were set such that they reflected maximum fertilization success beyond a threshold density of approximately one urchin per square meter (Levitan 1991; Levitan and Sewell 1992; Levitan and Peterson 1995) and created a maximum level of recruitment which reflects settlement numbers observed in the field prior to the mass mortality event (Bak, 1985). Figure 4 shows the resulting stock-recruitment curve (a) and the number of recruits produced (b).

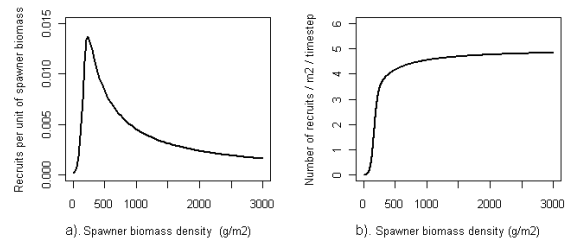


Figure 4: The stock-recruitment curve used to model recruits per unit of spawner biomass density (a) and the resulting level of recruitment per time step with increasing spawner biomass density (b).

Density-independent external larval supply was represented by the addition of a constant number of recruits at each time step.

Results

The *D. antillarum* population can persist in a low and a high abundance state. The low abundance equilibrium is associated with high macroalgal biomass whereas the high abundance equilibrium is associated with low macroalgal biomass. Due to the dependant effects associated with adult spine canopy and macroalgal cover, a high initial abundance of large juvenile or adult *D. antillarum* is required for the system to switch to the high abundance state. (Fig. 5). Note that there can be a

substantial time lag associated with growth to high abundance equilibrium.

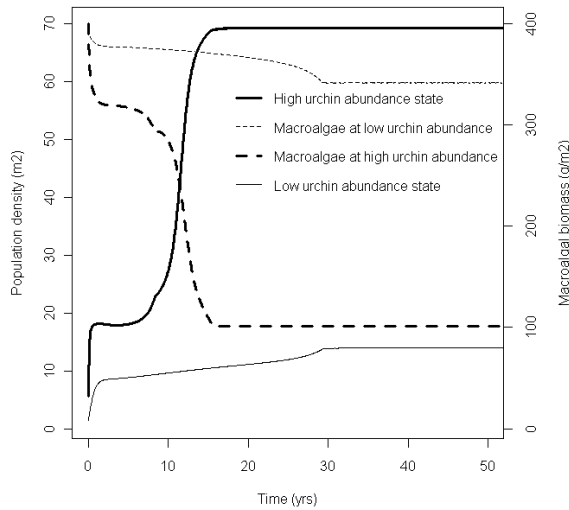


Figure 5: *D. antillarum* abundance and macroalgal biomass trajectories leading to low and high abundance equilibria, following releases of 1.4 and 5.6 medium-sized individuals per square meter. Solid lines represent urchin density, dashed lines represent macroalgal biomass and the thickness of the line denotes high or low abundance state with respect to urchins

We used the model to examine the number of urchins of different sizes required to kick-start rebuilding of a locally extinct population to a viable low or high abundance state, given high or low initial macroalgal biomass (Figure 6). Very high numbers of small urchins are required to establish a viable population, particularly when macroalgae are abundant. Much fewer large urchins would be required and establishment success with large urchins is less sensitive to the abundance of macroalgae.

The same method was used to assess threshold densities under a scenario of density-independent larval supply. The threshold densities for a high abundance state were very similar to those shown in Figure 6, the only significant difference being that there was no extinction threshold and the population would always persist even at low abundance.

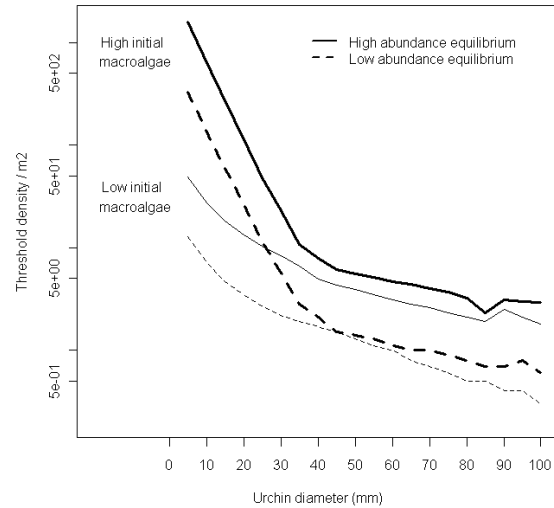


Figure 6: Threshold initial densities of urchins in each size class required to produce a population at low or high population abundance with an Allee effect in fertilization success, a spine canopy refuge and a habitat cultivation effect. Density thresholds are shown on a log scale.

Discussion

This study represents the first attempt to model the population dynamics of *D. antillarum* and gain a quantitative understanding of mechanisms impeding population recovery. The model represents mathematically key ecological processes and allows exploration of their population-level consequences.

The existence of both low and high abundance equilibria associated with high and low macroalgal biomass provides a possible explanation for the observed persistence of population densities much smaller than those seen prior to the mass mortality event of 1983. If, as our study suggests, macroalgal biomass plays a role in *D. antillarum* population dynamics then stable low population abundance may be due to the phase shift in macroalgae observed since the mass mortality event. However, the time lag involved in switching from the low to the high abundance state suggests that some low abundance natural populations may eventually recover

The existence of threshold densities for extinction and the two equilibria provides support for the potential for active rebuilding strategies. If we can aid populations to overcome threshold densities, then positive feedback associated with fertilization success, a spine canopy refuge and habitat cultivation may allow populations to persist and to recover to high abundance states.

As our studies show, even in the presence of sufficient larvae, population growth to high abundance is determined largely by juvenile predation mortality and the availability of predation refuges. The release of hatchery reared larvae alone is

therefore unlikely to prove effective if not coupled with some sort of refuge provision.

Model predictions show that urchin size and macroalgal biomass have significant effects on the thresholds required for population persistence and growth. In all situations, the larger the size of individuals, the lower the threshold densities required. It was also true that threshold densities were always lowest from a starting situation of low macroalgal biomass. These results suggest that adult release or translocation alongside prior macroalgal removal to mimic habitat cultivation may be the best rebuilding strategies. Adult urchins are less susceptible to predation mortality but also act to improve the survival of juveniles through spine canopy refuge and habitat cultivation. However, the large-scale release of urchins of large enough size at high enough density is logistically difficult since few are naturally available for translocation and we are yet to develop aquaculture technology for rearing adult *D. antillarum*. Previous translocation attempts have in fact proved unsuccessful due to low levels of retention and high levels of mortality (Miler et al 2007). A recent study in Curacao however, showed encouraging evidence that the provision of artificial predation refuges could greatly improve translocation success (Dame 2008). This supports the predictions of our model by highlighting the importance of predation mortality and refuge availability. An alternative to artificial refuge provision may be in the artificial removal of macroalgal to mimic the cultivation effect. Removal of macroalgae may free up existing predation refuges whilst simultaneously promoting larval settlement.

We propose that habitat modification in the form of macroalgal removal should be coupled with future attempts at translocation or hatchery release in order to promote survival and recruitment.

It is hoped that this study will promote further investigation into the role of macroalgal cover and habitat structure on larval settlement and juvenile survival in *D. antillarum*. This and future population dynamic models for *D. antillarum* provide an invaluable tool with which to quantify population recovery, direct future empirical work and advise rebuilding strategies.

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