

Recruitment-limitation in open populations of *Diadema antillarum*: an evaluation

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Summary. Empirical evidence from studies of the sea urchin *Diadema antillarum* suggests that this organism widely disperses its offspring, that both recruitment and mortality rates are independent of local densities, and that local food availability does not regulate local population sizes. These attributes would indicate that local populations are generally open and recruitment-limited. Given that current populations have been devastated by a 1983–1984 mass mortality event which spread throughout the range of this species, we examine current population trends and evaluate the prospects for population recovery under the assumptions of recruitment-limitation and density-independent rates of recruitment and mortality. Specifically, we evaluate the dynamics of five, local populations at Lameshur Bay, St. John, U.S.V.I. in order to 1) determine current rates of recruitment and mortality, 2) predict population densities based on the above assumptions, 3) compare predicted densities against observed 1984–1988 densities, and 4) predict future population densities based on current trends. We estimate current recruitment rates at 0.02–0.11 individuals/m²/yr and per capita mortality rates at 0.27–0.47 deaths/yr. Over the period 1985–1988, predicted densities based on these annual rates did not differ significantly from actual observed densities. Therefore, the assumptions that recruitment and mortality rates are density-independent and that local populations are recruitment-limited are sufficient, at present, to adequately predict current population trends. These trends indicate no recovery towards pre-mass mortality densities. The above description of the dynamics of open, recruitment-limited populations may be appropriate for a wide variety of organisms. We note the prevalence of animals with extensive larval dispersal capabilities. Populations located near the limits of their distribution, in freshwater streams and ponds, mountain tops, or other similarly isolated populations may also be subject to recruitment-limitation. Remote, recruitment-limited populations are likely to be more susceptible to local extinction than less remote populations. Dispersal distances and the scale of the processes controlling recruitment and mortality are important determinants of the degree of openness of local populations.

Key words: Open populations – Recruitment-limitation – Density-independence – *Diadema antillarum*

Among all living species of marine, benthic invertebrates, approximately 70% have pelagic larvae that are dispersed

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over long distances (Thorson 1950). Although such widespread dispersal capabilities may not have arisen as a direct result of natural selection (Strathmann 1985), the evolutionary consequences of this phenomenon include enhanced gene flow, lower rates of genetic divergence among local populations, and greater longevity in the geologic record (e.g., Hansen 1978; Vermeij 1978). The ecological consequences of widespread dispersal include the colonization of new habitats, recolonization and reestablishment of previously devastated populations, and stabilization of animal numbers (Ehrlich and Birch 1967; den Boer 1968; Reddingius and den Boer 1970; but see Vance 1980, 1984).

Roughgarden et al. (1985) recently recognized the general problem of trying to use traditional ecological models to describe the dynamics of populations of marine, benthic invertebrates with widespread dispersal capabilities. Traditional models describe the dynamics of closed populations in which new individuals recruiting into a local population are offspring of females present in that population. Virtually all of these models assume that once a local population goes extinct, it will remain so (May and Oster 1976; Caswell 1978). In contrast, population models for most marine, benthic invertebrates should allow for recruitment of individuals from other populations (or habitats as discussed in Pulliam 1988) and the possibility that local extinction can be followed by recolonization. In other words, these models should describe the dynamics of open rather than closed populations (e.g., Caswell 1978; Frogner 1980).

The most commonly used approach to modeling the dynamics of open populations invokes local resource-limitation on population size. Vance (1980, 1984) developed some general models which incorporated dispersal of juveniles among isolated, local populations in addition to the traditional dynamics of closed populations. Among the assumptions of these models are the following: 1) the size of each local population is resource-limited as a consequence of density-dependent mortality, 2) population birth and recruitment rates are a linear function of the size of each population producing offspring, and 3) dispersal among all possible populations is equally likely. One implication of this last assumption is that the range of larval dispersal is "so great compared to the spatial dimensions of local populations" that the relative location of each population and the transport processes affecting recruitment can be ignored. Vance's evaluation of the consequences of dispersal using these general models was directed at testing

the spreading of risk hypothesis (den Boer 1968; Reddingius and den Boer 1970). His general conclusion was that dispersal does not always result in the stabilization of animal numbers (Vance 1980, 1984).

Roughgarden and his colleagues have examined the dynamics of open populations of sessile, space-limited invertebrates (Roughgarden et al. 1985; Roughgarden and Iwasa 1986; Iwasa and Roughgarden 1986). Space-limitation in these populations sets an upper limit to local population size. Below this limit, local population size is determined by factors affecting the numbers of recruits. These factors include larval transport processes (Jackson and Strathmann 1981; Olson 1985; Shanks and Wright 1987), larval mortality (van der Veer 1985; Pennington et al. 1986; Gaines and Roughgarden 1985; Olson and McPherson 1987), settlement success (Gaines and Roughgarden 1985; Gaines et al. 1985), and post-settlement mortality (Caffey 1985; Connell 1985). Such populations are said to be recruitment-limited when recruitment rates are insufficient to fill all the available space (e.g., Sutherland 1987).

Here we evaluate recruitment-limitation in open populations of the sea urchin *Diadema antillarum*. Local population sizes in this echinoid do not appear to be resource-limited. Generally, population birth rates are determined by extrinsic factors affecting recruitment. This organism is a broadcast spawner, its larvae require 50–90 days to complete development (R. Carpenter personal communication), and dispersal distances from source populations to sites of settlement and recruitment are thought to be on the order of hundreds of km (Lessios 1988a; but see Hunte and Younglao 1988). Furthermore, recruitment appears to be independent of local density (Lessios 1988a, b). Mortality rates also appear to be density-independent. Instead of mortality rates increasing in response to increased density or reduced food availability, these echinoids respond by reducing their body size (Levitan 1988a, 1989).

If both recruitment and mortality rates are independent of local density and resources, there can be no resource-dependent regulation of local population sizes (i.e., no carrying capacity in terms of numbers of individuals). Instead, these populations will fluctuate with changes in these rates in a density-independent manner. If these rates were to remain constant, a local equilibrium population size equalling the ratio between the rates of recruitment and mortality (Hughes in press; Warner and Hughes in press) will be approached and the number of individuals recruiting into these populations will be balanced by the number dying (Hughes 1984; Roughgarden et al. 1985).

During 1983–1984, populations of *Diadema antillarum* experienced a mass mortality event which spread throughout its range in the western Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (Lessios 1988a; Lessios et al. 1983, 1984). At established study sites in Lameshur Bay, St. John, U.S.V.I., more than 99% of the *Diadema* died as a result of this event and the algae, upon which this herbivore feeds, has undergone dramatic increases in abundance (Levitan 1988b). As we demonstrate below, abundant local resources have not resulted in increased *Diadema* recruitment or densities. Using estimates of density-independent recruitment and mortality rates for five, local populations, we predict 1985–1988 densities. Given that these predictions closely match observed densities over this period, we extend this approach to consider how these populations may behave in the future.

Methods and results

Prior to the mass mortality event in 1983, the mean density of *Diadema antillarum* in Lameshur Bay, St. John, was 14.380/m² (Levitan 1988b). By the summer of 1984, it had declined over two orders of magnitude to 0.078/m² (Levitan 1988b and Table 1). In summer censuses from 1985–1988 at five sites in Lameshur Bay, the overall mean density was 0.276/m² (Table 1), there were no significant density differences among years, but there were significant differences in densities among sites (Table 2). Below we use size frequency data collected during five summer and two winter censuses (Levitan 1988b and unpublished data) to independently estimate recruitment and mortality rates for *Diadema* populations at these sites. We then compare observed densities with those predicted using densities from the previous year and the estimated rates of recruitment and mortality.

We estimated annual per capita mortality rates (μ) using the standard method described by Ebert (1975). This method includes the use of the following equation:

$$\mu = \frac{K(S_{\infty} - \bar{S})}{(\bar{S} - S_t)} \quad (1)$$

Table 1. Annual recruitment rates (R_t in observed numbers of individuals less than 50 mm/m²/yr), annual mortality rates (μ in estimated number of deaths/individual/yr), mean body sizes (\bar{S} in observed mm test diameter), actual densities (N_t in observed #/m² and predicted densities (\hat{N} in #/m²) for five populations of *Diadema antillarum* in Lameshur Bay, St. John, U.S.V.I. Details regarding sampling methods and site descriptions appear in Levitan (1988b)

Year	Parameter	Site designations					Mean
		SQST	WELL	NELL	DOBI	TECL	
1984	R_t	0.069	0.161	0.045	0.048	0.066	0.078
	N_t	0.071	0.161	0.045	0.049	0.066	0.078
1985	R_t	0.154	0.534	0.130	0.074	0.174	0.213
	N_t	0.160	0.710	0.145	0.117	0.236	0.274
	\hat{N}	0.208	0.650	0.161	0.110	0.216	0.269
1986	R_t	0.029	0.105	0.047	0.052	0.107	0.068
	N_t	0.146	0.569	0.103	0.173	0.284	0.255
	\hat{N}	0.151	0.616	0.146	0.137	0.256	0.261
1987	R_t	0.030	0.112	0.077	0.031	0.093	0.069
	N_t	0.185	0.670	0.186	0.189	0.329	0.312
	\hat{N}	0.141	0.522	0.147	0.157	0.272	0.248
1988	R_t	0.027	0.017	0.022	0.028	0.076	0.034
	N_t	0.128	0.448	0.224	0.193	0.330	0.265
	\hat{N}	0.168	0.499	0.148	0.166	0.283	0.253
	\bar{S}	71.58	68.20	65.00	68.70	61.27	66.95
	μ	0.27	0.33	0.39	0.32	0.47	0.36

Table 2. Two-way analysis of variance (without replication) of 1985–1988 densities at five sites in Lameshur Bay

Source of variation	df	SS	MS	F
Years	3	0.009	0.003	0.72
Sites	4	0.575	0.144	33.57***
Error	12	0.051	0.004	
Total	19			

*** $P < 0.001$

This equation represents a simple modification of the Beverton-Holt model in which K is the negative natural logarithm of the slope of a Walford plot of body sizes (test diameters in mm) in successive years, S_r is the body size at which recruits were first seen in the censuses, \bar{S} is the mean body size, and S_∞ is the asymptotic body size based on the Walford plot.

Using 1984–1988 size frequency data, we identified a total of 52 distinct size classes which were clearly present in successive censuses. From these data we calculated an annual growth rate and the average body size of each size cohort in successive years (S_t , S_{t+1}). From the Walford plot of data pooled across sites (Fig. 1), we determined the linear regression equation,

$$S_{t+1} = 0.49 S_t + 48.59 \quad (R^2 = 0.62, n = 52) \quad (2)$$

and the estimates $K = 0.71/\text{yr}$ and $S_\infty = 95.09$ mm. $S_r = 10$ mm in our censuses. We assumed that there was no significant variation in the values for these three parameters due to differences among sites.

However, mean body sizes (\bar{S}) were calculated for each site because of site-dependent variation in density (Table 2) and the presumption that mortality rates were likely to vary due to differences among sites in habitat quality and predator densities (Levitan unpublished data). Furthermore, given that we had no basis for assuming significant variation in mortality rates due to differences among years, we chose to estimate a single mortality rate for each site. We used mean body sizes (\bar{S}) from the 1988 censuses to make these calculations. Using Eq. (1), we estimated a range in per capita mortality rates over the five sites of 0.27–0.47/yr (Table 1). Given that the mean body sizes of *Diadema antillarum* have been increasing since 1984 (Levitan 1988b), these populations have not quite reached a stable size distribution and our estimates of mortality rates are likely to be somewhat biased overestimates. For example, if mean body size at equilibrium = 73 or 78 mm, then $\mu = 0.25$ or 0.18/yr, respectively.

We also used the size frequency distributions at each site in each of the five summer censuses to estimate recruitment rates. Because newly settled urchins can grow to an average size of 48.59 mm (test diameter) in one year (Fig. 1

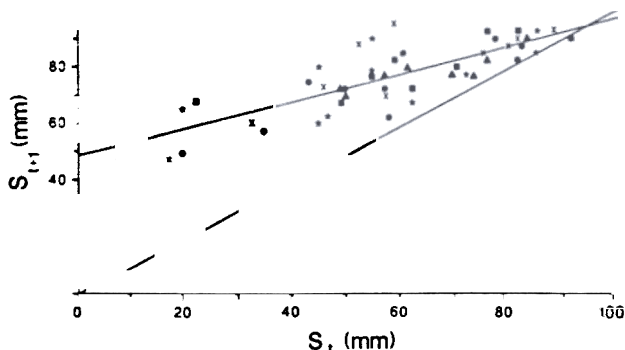


Fig. 1. Walford plot for five populations of *Diadema antillarum* from Lameshur Bay, St. John, surveyed in 1984–1988. Mean body sizes (S_t , S_{t+1}) in successive years are plotted for 52 size cohorts. Also plotted are the linear regression line and the line indicating no growth. Site designations as in Levitan (1988b) are as follows: SQST = triangles, WELL = stars, NELL = circles, DOBI = squares, TECL = crosses

Table 3. Two-way analysis of variance (without replication) 1984–1988 recruitment rates at five sites in Lameshur Bay

Source of variation	df	SS	MS	F
Years	4	0.097	0.024	4.17*
Sites	4	0.063	0.016	2.73
Error	16	0.093	0.006	
Total	24	0.253		

and Eq. 2), we used the total number of individuals less than this size in each census as an estimate of annual recruitment rate (R_t). From 1984–1988, these rates ranged between 0.017 and 0.534 individuals/m²/yr (Table 1). Two-way analysis of variance of these rates indicates that there was significant variation among years, but not among sites (Table 3). Unplanned comparisons among years indicate a single significant difference between the high 1985 rate and the lowest rate in 1988 (T -method, minimum significant range = 0.148 at $P = 0.05$). 1986–1988 rates were not significantly different.

Using the estimated values for recruitment and mortality rates (Table 1), we predicted the 1985–1988 densities for each of the five populations using the following equation:

$$\hat{N} = N_{t-1} e^{-\mu} + R_t \quad (3)$$

This equation is based on the assumption that per capita mortality rates and the total number of recruits entering these local populations are density-independent. These predicted densities were not significantly different from actual observed densities ($\bar{D} = 0.019$ individuals/m², paired two-tailed t -test, $t = 1.643$, $P > 0.10$). Therefore, the 1985–1988 population data are consistent with the above assumptions of density-independence and the notions that local *Diadema* populations are open and local population sizes are not regulated by local resources.

The differences between predicted and observed densities are plotted as a function of the absolute change in density observed over each year interval in Fig. 2. Linear regression analysis of these data indicates that the slope of the regression line (0.012) was not significantly different from zero (MSE = 0.003, $F = 0.014$, $P > 0.75$). Therefore, the errors in predicted densities were independent of the magnitude of the density change. For 12 of the 20 predictions, equation (3) correctly indicated the direction of density change (Fig. 2). In 7 of the 8 cases in which the direction of change was not correctly indicated, the actual density change was very small (i.e., 0.001–0.045 individuals/m², Fig. 2).

If we assume that current recruitment and mortality rates persist without significant change, how will local populations behave in the future? Predictions for 1989 based on equation (3), 1988 densities, and 1988 estimated rates of recruitment and mortality (Table 1) include 0.03–0.13 deaths/m² among the five populations and densities approximately 17% lower than in 1988. At the mean 1988 rates of recruitment and mortality, predicted densities would continue to decline until they reached 0.112 individuals/m². Using the higher estimates for 1987 recruitment, predicted 1989 densities are approximately 4% lower than

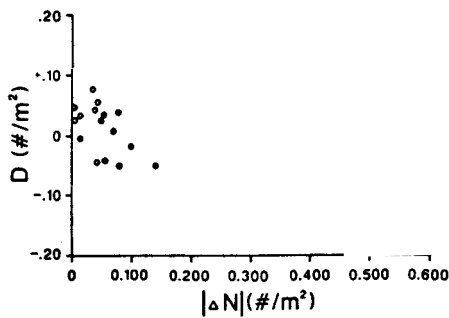


Fig. 2. Difference between observed and predicted population densities ($D = N_t - \hat{N}$, Table 1) plotted against the absolute value of the observed density change in five populations of *Diadema antillarum*. Closed circles indicate correct predictions of the direction of density change. Open circles indicate incorrect predictions.

in 1988. Therefore, 1986–1988 recruitment rates are, on the average, insufficient to maintain even the current low densities and there is no basis for predicting a full recovery to the 1983, pre-mass mortality density of 14.380 individuals/m².

In order to achieve full recovery, these populations need to experience lower mortality rates and/or higher recruitment rates. If we assume that 1988 recruitment rates remain constant (0.034 individuals/m²/yr, Table 1), a mortality rate of 0.002 deaths/individual/yr is required for full recovery. Based on the study of numerous echinoid species (Ebert 1982), we believe it is unreasonable to expect such a low mortality rate for *Diadema antillarum*. If we assume that 1988 mortality rates (0.36 deaths/individual/yr, Table 1) do not change, a recruitment rate of 4.347 individuals/m²/yr is required to balance the number of individuals dying and to maintain the 1983 density. This is two orders of magnitude greater than the mean 1988 recruitment rate (Table 1). In the only empirical study of recruitment rates in this species conducted before and after the mass mortality, Bak (1985) reported a post-mass mortality decline in recruitment rates of this same magnitude for a population in Curaçao.

Discussion

We have used *Diadema antillarum* to illustrate the dynamics of open, recruitment-limited populations and to predict some of the consequences of the recent, Caribbean-wide mass mortality. This mortality event radically reduced local densities throughout the region and, consequently, has greatly reduced current recruitment rates (Bak 1985; Hughes et al. 1987; Lessios 1988a, b; Levitan 1988b). If the mass mortality had been restricted to just a few local populations, recruitment rates would have continued at pre-1983 levels and population densities would have returned rapidly to their pre-mass mortality levels. At current rates of recruitment and mortality, a return to pre-1983 densities is unlikely.

If *Diadema* densities are to return to pre-1983 levels, these populations are most likely to require increases in recruitment rates. Potential scenarios for such increases might involve self-seeding of local populations (Hunte and Younglao 1988), density-dependent larval production (Pennington 1985; Levitan 1988c), or nonequilibrium pulses of recruitment which may drive population densities upward. Currently, there is evidence for high recruitment rates

in populations of *Diadema antillarum* in Barbados (Hunte and Younglao 1988; Lessios 1988a, b). These high rates may be the result of some degree of self-seeding or of trans-oceanic larval transport bringing recruits from eastern Atlantic populations (R. Carpenter personal communication). Since Barbados is the easternmost of the Caribbean islands, the elevation of local population sizes there may then have a cascading, downstream effect on other populations by enhancing numbers of potential recruits in the region.

Diadema antillarum may be one of a large number of animals whose populations are open and recruitment-limited [e.g., barnacles – (Roughgarden et al. 1985; Sutherland 1987), bryozoans – (Hughes in press), fish – (Doherty 1983; Victor 1986; Shulman and Ogden 1987, Warner and Hughes in press), salamanders – (Gill 1978)]. Population fluctuations (or even apparent stability) in such organisms can result primarily from density-independent processes (den Boer 1981, 1986). Because these organisms widely disperse their offspring, they do not rely on locally produced recruits for population growth. Other potential recruitment-limited candidates include fringe populations living near the edge of their distribution. Such populations may commonly experience local reproductive failure or unusually high mortality rates and be totally dependent on recruitment from other populations; they may be net sinks for dispersed individuals as described by Pulliam (1988). Populations living in freshwater streams or in other unidirectional flow regimes may be dependent on up-current populations for recruits. The degree of isolation is a critical feature of local populations with widely dispersed offspring. This is true whether these populations characterize oceanic islands, freshwater ponds, or mountain tops. Remote populations are more likely to have lower recruitment rates and lower densities than less remote populations and these populations should be more susceptible to local extinction.

The linking of several populations into a large metapopulation (Gill 1978) introduces the question of scale in defining open or closed populations (Caswell 1978). Almost all local populations are open to some extent. Dispersal of adults even in vertebrate and insect populations can have an important influence on recolonization, local extinction, and the stability of local populations (e.g., den Boer 1968, 1986; Pulliam 1988). The geographic scale of recruitment processes and mortality events can also influence the degree of openness of local populations. In the case of *Diadema antillarum*, the mass mortality was so widespread that it had global effects on recruitment rates, population sizes, and population growth rates. For this reason, the question of whether a population is open or closed should be a question of degree, dependent on the dispersal distances and on the scale of the processes regulating recruitment and mortality.

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