

Recruitment and population recovery of *Diadema antillarum* (Echinodermata; Echinoidea) in Barbados

W. Hunte, D. Younglao

Bellairs Research Institute of McGill University, St James, Barbados
and
Biology Department, University of the West Indies, Cave Hill, Barbados

ABSTRACT: Population recovery of *Diadema antillarum* following the Caribbean-wide mass mortality of the urchin in 1983 is documented in Barbados. Recruitment (urchins 10 to 15 mm test diameter) occurred 3 to 4 mo after peak spawning. Recruits settled near the front (offshore) of reefs and were aggregated with adults. Populations grew rapidly on all Barbados reefs; the reef with fastest recovery returning to 57.4 % of its pre-mortality density by December 1985. Reefs with the highest density at the start of the study recovered most rapidly. This may suggest that larvae settle preferentially on reefs with higher adult densities, and/or, that juvenile mortality is lower on reefs with higher adult densities. Populations of *D. antillarum* in Dominica and St Lucia decreased during the study. Moreover, recruitment strength to each island was positively correlated with adult density on that island. This may suggest that island populations are discrete breeding units. Alternatively, the correlation of recruitment strength with island population density may reflect settlement preference by regionally dispersed larvae for areas of high adult density.

INTRODUCTION

A massive mortality of the black sea urchin *Diadema antillarum* Philippi occurred in the Caribbean in 1983, starting in Panama and spreading east to Barbados and north to Bermuda. The causative agent was a water-borne pathogen (Bak et al. 1984, Lessios et al. 1984a, b, Hughes et al. 1985). Mortality on the fringing reefs in Barbados was between 87 and 99.9 % (Hunte et al. 1986). Given the biological and geological importance of *D. antillarum* on Caribbean fringing reefs (e.g. Ogden et al. 1973, Sammarco et al. 1974, Bak & van Eys 1975, Sammarco 1980, 1982a, b, Scoffin et al. 1980, Carpenter 1981, Sammarco & Williams 1982), such mortality is of concern, but it may allow fresh insights into recruitment patterns and hence population dynamics of reef organisms with a planktonic larval stage. A quantitative characterisation of population recovery of *D. antillarum* has not yet been reported for any country.

Three recruitment issues are of particular interest for reef organisms with planktonic larvae. One is the effect

of parental stock size and/or local adult density on recruitment strength. Stock-recruitment relationships are poorly understood, even in exploited stocks which vary over a range of parental stock sizes (Gulland 1983), and the effects of local adult density on habitat selection by juvenile echinoderms have only recently been addressed (Highsmith 1982, Bak 1986). A second issue is whether reef organisms are space-limited (i.e. limited by competitive interactions on reefs; Anderson et al. 1981, Shulman et al. 1983, Shulman 1984) or recruitment-limited (i.e. limited by the number of larvae surviving the plankton; Doherty 1981, Victor 1983, 1986). A third issue is the effect of a planktonic larva on dispersal and hence on the discreteness and genetic structure of local populations (Emery 1972, Johannes 1978, Jackson & Strathmann 1981, Leis 1981, McFarland 1982). The objective of the present paper is to document recruitment and population recovery of *Diadema antillarum* in Barbados, St Lucia and Dominica, and thereby to comment on the recruitment issues outlined above.

METHODS

The study was conducted between October 1984 and December 1985 on 7 fringing reefs on the west coast of Barbados, on 1 fringing reef (Rat Island) on the north-west coast of St Lucia and on 1 fringing reef (Scots Head) on the southwest coast of Dominica (Fig. 1).

Spawning and recruitment. The seasonality of spawning was studied in Heron Bay reef, Barbados, by determining the state of gonad maturity of urchins in each month of the year. Fresh smears of gonads were examined microscopically and 3 gonad states were identified. These were unripe (no mature gametes visible; gonads consisting mainly of nutritive tissue), ripe (gonads consisting mainly of mature gametes with little or no nutritive tissue; gametes sometimes shed immediately before or during dissection), and spent (gonads consisting of few mature gametes scattered throughout the nutritive tissue; in the case of females, remaining eggs in various stages of degeneration). Approximately 64 urchins were examined monthly, and the percentage of urchins in each gonad state was calculated (see also Younglao 1987, Hunte & Younglao in press).

Seasonality of recruitment was studied in Paynes Bay, North Bellairs and Heron Bay reefs in Barbados, and on Rat Island and Scots Head reefs in St Lucia and Dominica respectively. On the Barbados reefs, the test diameters of 50 randomly selected urchins from each reef were measured underwater to the nearest 0.1 mm using vernier calipers, and monthly size-frequency his-

tograms were generated. The smallest urchins typically seen on the reef are within the 10 to 15 mm size class (test diameter). These were therefore considered recruits, and their percentage in each monthly sample was used to indicate recruitment seasonality. The possible presence of urchins <10 mm was investigated monthly in Barbados by breaking open rocks and searching in deep crevices on a reef not used for regular sampling (Tropicana reef). Searches were conducted for 4 h consecutively each month, thereby standardising sampling effort between months. Such individuals are subsequently called settlers, and are used as a separate index of recruitment seasonality. Coupling between timing of spawning and recruitment was investigated by use of Spearman's Rank Correlation. The variable used to indicate spawning activity was the percentage of spent urchins in the population each month. The variable used to indicate recruitment was the percentage of the total annual number of recruits found in each month.

Recruitment seasonality on Rat Island (St Lucia) and Scots Head (Dominica) was investigated by monitoring an area 250 m² on the former reef and 200 m² on the latter. On each sampling day, all urchins within the study area were counted and measured. Sampling was carried out in January, March, April, June, July, September and October 1985 in St Lucia, and in January, May, August and December 1985 in Dominica.

Spatial pattern of recruitment. Spatial characteristics of recruitment were investigated on North Bellairs and Heron Bay reefs, Barbados, by comparing the size

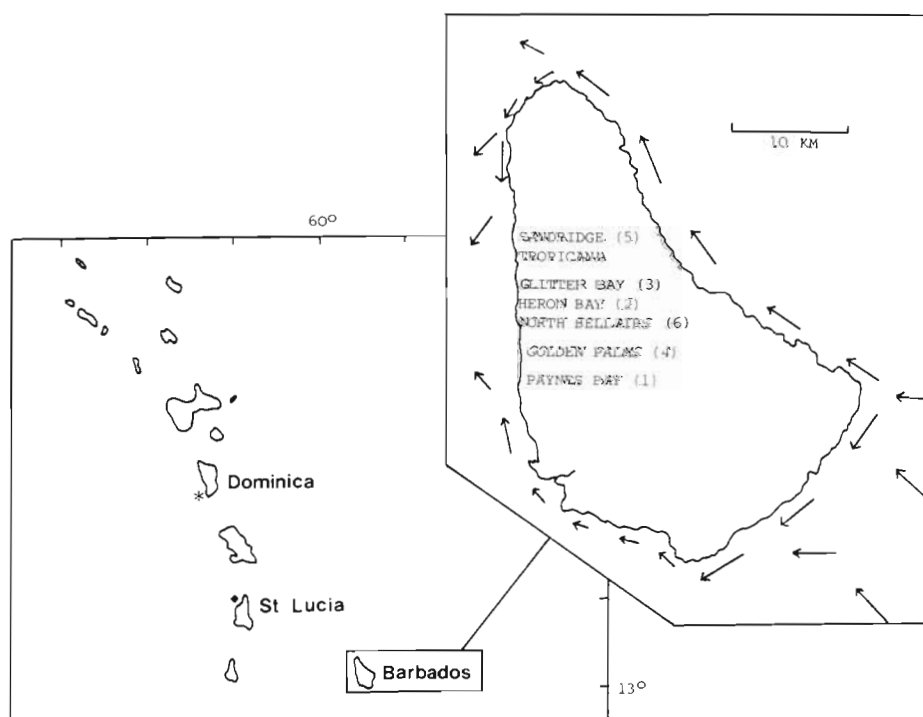


Fig. 1. Barbados, St Lucia and Dominica (general surface circulation around Barbados from Powles 1975 and Coastal Conservation Project 1983) and location of study reefs on Barbados. Bracketed numbers indicate sequence of rate of population recovery of *Diadema antillarum* on the study reefs. (*) Scots Head reef, Dominica; (♦) Rat Island reef, St Lucia

distribution of urchins from the front (offshore) to the back (onshore) of the reef during recruitment months to the distribution in months prior to recruitment. Monthly size distribution was determined by measuring the test diameter of urchins in 10 m intervals along 4 transects (1 m width) from the front to the back of each reef. In addition, the number of recruits that were solitary, aggregated with each other or aggregated with adults was recorded on Paynes Bay, North Bellairs and Heron Bay reefs. An urchin was considered aggregated if its spines were in contact with those of a neighboring urchin (Younglao & Hunte in press).

Population recovery. To monitor population recovery, density profiles were generated from the front to the back of each reef in Barbados each month. Density was determined by counting urchins in 50 quadrats (1 m²), placed at 5 m intervals along 3 transects running perpendicular to the shore (south edge, central, north edge). Population increase was expressed as the increase in density (final density – initial density) as a percentage of initial density, both at monthly intervals and over the entire study period. Population recovery was also investigated in St Lucia and Dominica by counting and measuring, in each

study month, all urchins in a 250 m² area on Rat Island reef, St Lucia, and in a 200 m² area on Scots Head reef, Dominica as above.

RESULTS

Spawning and recruitment

The size structure of the populations on Paynes Bay, North Bellairs and Heron Bay reefs did not differ significantly in any given month (Kolmogorov-Smirnov Test; $p > 0.05$ in all cases). Size-frequency data from the 3 reefs were therefore combined to provide a composite picture for the Barbados population (Fig. 2). Recruits (i.e. urchins 10 to 15 mm) were only observed between July and October, and this is displayed to provide a seasonal picture of recruitment in Fig. 3A.

The method used to determine the presence of settlers (urchins <10 mm) was labor intensive, and the sample size of settlers therefore small. On Tropicana reef, the first settler, measuring 4.0 mm, was discovered in June. Five settlers, measuring from 4.9 to 7.9 mm, were discovered in July, and 4 (size range 6.0 to 9.8 mm) in August.

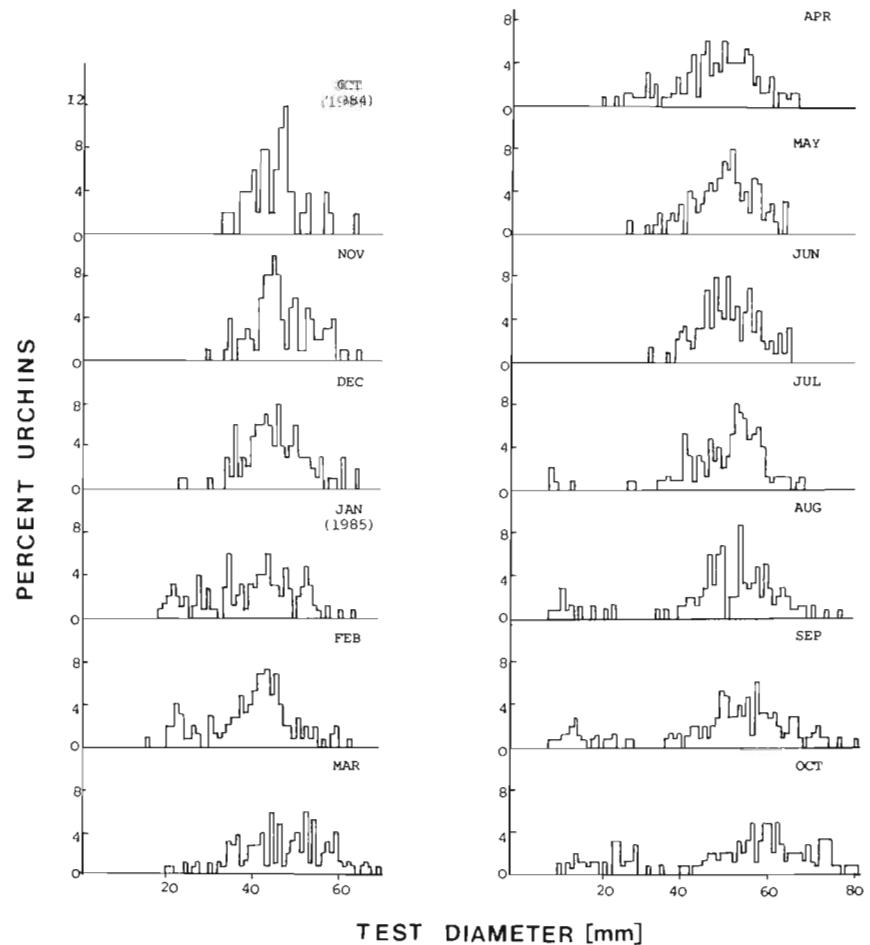


Fig. 2. *Diadema antillarum*. Percentage of urchins in each size class (test diameter in mm) for each month on Paynes Bay, North Bellairs and Heron Bay reefs, Barbados ($N = 150$ for each month)

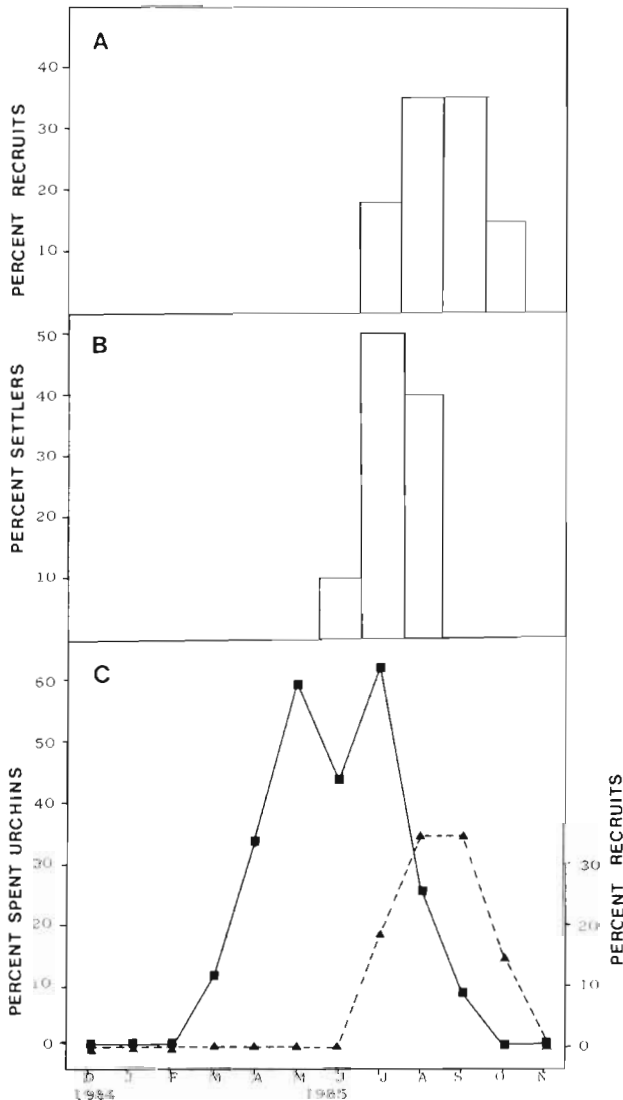


Fig. 3. *Diadema antillarum*. (A) Percentage of recruits (urchins 10 to 15 mm) each month. Data combined for Paynes Bay, North Bellairs and Heron Bay ($N = 59$). (B) Percentage of settlers (urchins <10 mm) each month on Tropicana reef ($N = 10$). (C) Percentage of (■—■) spent urchins and (▲---▲) recruits each month in Barbados

The seasonality of settlement as indicated by this method (i.e. intra-rock; urchins <10 mm) is shown in Fig. 3B. Note that it precedes recruitment onto the visible surface of the reef (Fig. 3A).

A plot of percentage of urchins spent each month is superimposed on a plot of recruits present each month in Fig. 3C. The figure suggests a time lag of about 3½ mo between peak spawning and peak recruitment. Spearman's Rank Correlation indicates significant correlation ($p < 0.05$) between spawning and recruitment with time lags of 2 ($r_s = 0.78$), 3 ($r_s = 0.83$) and 4 ($r_s = 0.93$) mo. Note that recruitment here refers to the appearance of urchins between 10 and 15 mm onto the

visible surface of the reef, not to the initial settlement of smaller urchins (<10 mm). Monthly size frequency histograms for Rat Island (St Lucia) and Scots Head (Dominica) reefs are shown in Fig. 4. Recruits (urchins <15 mm) were observed at Rat Island in June and July 1985; most recruits appearing in the former month. The few recruits to Scots Head were recorded in January 1985.

Spatial pattern of recruitment

Settlers and recruits were always found within the front (offshore) third of the reef, on rugose rather than on smooth substratum. Mean urchin size (test diameter) increased with increasing distance from the reef front on both study reefs (linear regression on data pooled for all months, $R^2 = 0.51$ and 0.36 for North Bellairs and Heron Bay respectively, $p < 0.001$ in both cases). The slope of the relation between mean urchin size and distance from the reef front was significantly greater in recruitment months than in non-recruitment months ($t = 4.62$ and 8.05 for North Bellairs and Heron Bay respectively, $p < 0.001$ in both cases; Fig. 5). This suggests that recruitment occurs towards the front of reefs. Finally, recruits were more likely to be aggregated with adults (59% of recruits were aggregated with adults) than with other recruits (34%), and more likely to be aggregated with other recruits than to be solitary (7%; recruits not evenly distributed between categories, $\chi^2 = 11.65$, $p < 0.01$).

Population recovery

Population growth, expressed as monthly urchin density and percentage increase in urchin density, is shown for 6 Barbados reefs in Fig 6A to F. Density increased over the sampling period on each reef (linear regression of density on months $p < 0.05$ for all reefs). Population growth appeared exponential on some reefs, e.g. Paynes Bay, Heron Bay and Glitter Bay, but in no case was growth better fitted by a curve than by a straight line (polynomial regression, $p > 0.05$ for all second order polynomials). Fluctuations in density between months were due to variability in visibility on sampling days.

Pre-mortality densities were available for North Bellairs, Golden Palms and Sandridge reefs (Hunte et al. 1986). Monthly densities as percentages of pre-mortality densities are shown in Fig. 7. By the end of the study, these reefs had returned to 17.9, 37.7 and 57.4 % of their pre-mortality densities respectively.

Reefs with a higher population density at the start of the study recovered faster, i.e. had a greater percen-

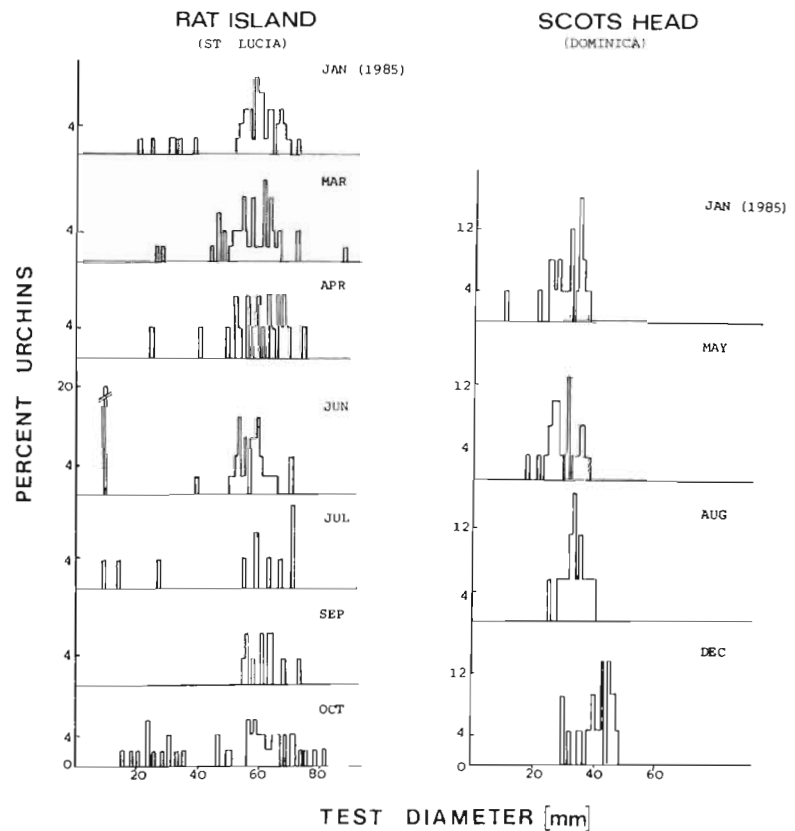


Fig. 4. *Diadema antillarum*. Percentage of urchins in each size class (test diameter in mm) on Rat Island reef, St Lucia, and Scots Head reef, Dominica. Data presented separately by month

tage increase in density than those with a lower initial density (Fig. 8; Spearman's Rank Correlation Coefficient $r_s = 1.0$; $p < 0.001$). Moreover, for the 3 reefs on which numbers of recruits were recorded, density of recruits increased with increasing initial adult density (adult densities on Paynes Bay, Heron Bay and North Bellairs 4.7, 4.3 and 1.8 m^{-2} respectively; recruit densities 0.13, 0.05 and 0.01 m^{-2} respectively). Pre-mortality densities and population recovery rates for North Bellairs, Sandridge and Golden Palms reefs are shown in Table 1. Reefs with higher pre-mortality density did not recover faster, as indicated either by initial density, final density or percent increase in density.

The initial population densities on Rat Island, St Lucia (0.8 m^{-2}) and Scots Head, Dominica (0.5 m^{-2}) were considerably lower than the mean for Barbados reefs (3.3 m^{-2}). In both St Lucia and Dominica, population densities declined during the study (Fig. 9).

Finally, the total number of recruits m^{-2} of reef for each island and the initial adult density on that island suggest that recruitment strength to an island is a positive function of adult population density on that island (adult densities for Barbados, St Lucia and Dominica 3.3, 0.8 and 0.5 m^{-2} respectively; recruit densities 0.06, 0.04 and 0.005 m^{-2} respectively).

DISCUSSION

Recruitment of *Diadema antillarum* to Barbados reefs in 1985 occurred primarily between July and October, i.e. 3 to 4 mo after peak spawning. This recruitment refers to the emergence of juveniles between 10 and 15 mm (test diameter) onto the visible surface of the reef. It is presumably preceded by settlement/metamorphosis from the plankton and growth within refuges on the reef. In spite of the small sample size, intra-rock investigations indicated a peak in appearance of settlers (<10 mm) which preceded the peak in appearance of recruits. Bak (1986) recorded newly metamorphosed *D. antillarum* in Curaçao at a size of 1 mm and estimated an initial growth rate of 1 mm wk^{-1} . If true for *D. antillarum* in Barbados, the time lag between peak spawning and the appearance of settlers and recruits would suggest a larval period for *D. antillarum* of between 4 and 6 wk. This is consistent with that previously estimated (Mortensen 1937, Hawkins & Lewis 1982). The coupling of recruitment to spawning, with a biologically plausible time lag, tentatively suggests that most recruits on Barbados reefs are products of adult populations in Barbados, i.e. island populations are largely discrete. Alternatively, the coupling may result from simultaneous spawning regionally, and

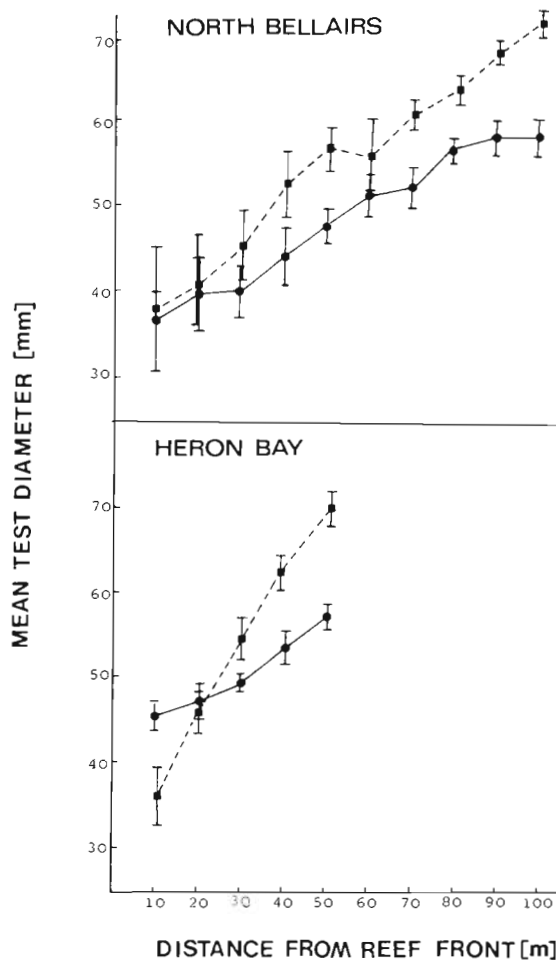


Fig. 5. *Diadema antillarum*. Mean urchin size (test diameter in mm) vs distance from front of reef (m) on North Bellairs and Heron Bay reefs. Data presented separately for (●—●) non-recruitment months (October 1984 to July 1985) and (■---■) recruitment months (August and September 1985)

recruitment from a regional panmictic larval population. Cameron (1986) found a close coupling of recruitment with spawning in *Lytechinus variegatus* in Puerto Rico, but not in *Tripneustes ventricosus*, *Echinometra viridis* nor *E. lucunter*.

Settlement from the plankton apparently occurs near the front (offshore) of reefs. Within about 2 mo of settling, the surviving juveniles migrate onto the visible reef surface, presumably because they have outgrown their initial refuges. Post-settlement migrations of echinoderms have previously been reported for *Echinocardium cordatum* (Moore et al. 1963), *Meoma ventricosa* (Chesher 1969), *Lytechinus variegatus* (Engstrom 1982) and *Strongylocentrotus franciscanus* (Breen et al. 1985).

Most recruits of *Diadema antillarum* were either aggregated with adults, or less commonly, with other recruits. Juveniles of the red sea urchin *Strongylocen-*

trotus franciscanus are also found under the spine canopy of adults (Tegner & Dayton 1977, Breen et al. 1978, 1985), and Breen et al. (1985) have shown that this distribution results from active preference for adult spine canopies by juveniles. They suggest that such behavior provides protection from predators, and the same may be true for juveniles of *D. antillarum* (Younglao & Hunte in press).

Populations on all reefs in Barbados grew rapidly during the study, the density increase ranging from 72 to 144 % of initial density. Considering the reefs for which pre-mortality densities were available (Hunte et al. 1986), densities increased from an average of 19.5 % (range 10.4 to 29.5 %) to 36.9 % (range 17.9 to 57.4 %) of pre-mortality density during the study year. This rapid recovery may suggest that populations of *Diadema antillarum* are not typically 'recruitment-limited' (*sensu* Victor 1983, 1986). Even at densities some 80 % below pre-mortality densities, enough individuals survived the plankton and recruited to reefs to allow rapid population increase. This, and the observation that at pre-mortality densities the growth rate of individuals of *D. antillarum* is density-dependent (Hunte et al. 1986), suggests that *D. antillarum* populations are typically 'space-limited'. Only when adult populations are extremely low will the number of larvae surviving the plankton be inadequate to allow population increase. Densities on Dominica and St Lucia at the start of the study were 15 and 24 % of that in Barbados, and there was no indication of population recovery during the study on either island. In Panama, where post-mortality densities were also considerably lower than in Barbados, populations of *D. antillarum* have not recovered (Lessios pers. comm.).

Population recovery in Barbados was faster on reefs with higher initial densities. There are several possible explanations for this. First, each reef population may be discrete, i.e. recruits to a given reef are produced by spawning on that reef. Hence, more breeding adults on a reef would produce more larvae/recruits to that reef. However, given the proximity of reefs (the distance between the 2 farthest reefs was only 11.5 km), the length of the larval stage (4 to 6 wk), and the observation that nearshore water movement on the west coast of Barbados always has a north or south component (Emery 1972, Coastal Conservation Project 1983, Hunte & Younglao in press, Bevan unpubl.), mixing of larvae between reefs seems inevitable.

A second possibility is that onshore currents returning larvae to reefs may impinge more directly on certain reefs than on others (Johannes 1978, Bailey 1981, Jackson & Strathmann 1981, McFarland et al. 1985). Hence, some reefs will continuously have higher recruitment rates, which would explain their higher initial density and their higher population recovery.

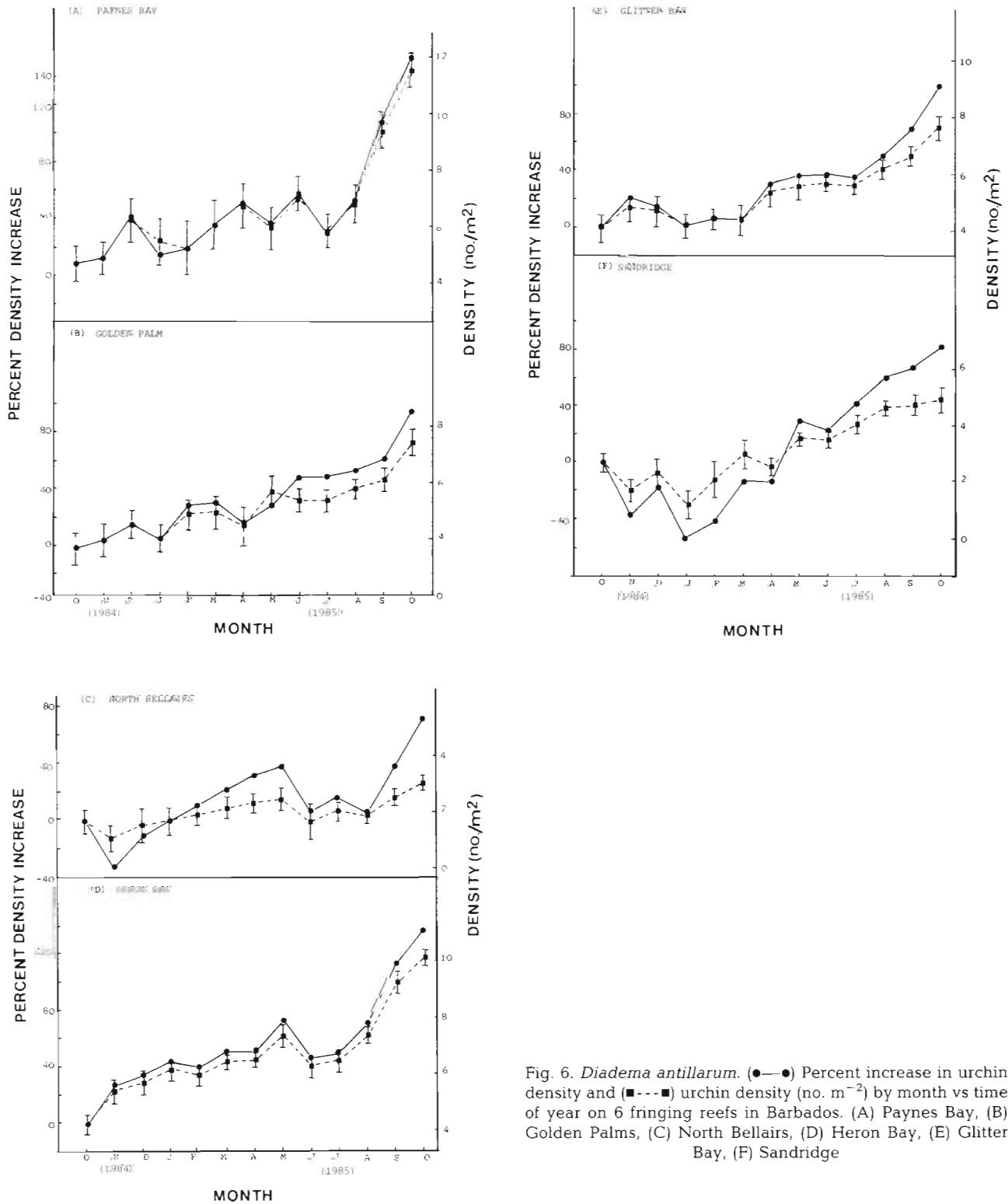


Fig. 6. *Diadema antillarum*. (●—●) Percent increase in urchin density and (■---■) urchin density (no. m⁻²) by month vs time of year on 6 fringing reefs in Barbados. (A) Paynes Bay, (B) Golden Palms, (C) North Bellairs, (D) Heron Bay, (E) Glitter Bay, (F) Sandridge

Current differences may be responsible for between-site differences in recruitment in the seastar *Asterias rubens* in Britain (Barker & Nicholls 1983) and the bluehead wrasse *Thalassoma bifasciatum* in Panama (Victor 1986). However, recovery rates of reefs showed

no north/south spatial pattern (Fig. 1), and it seems unlikely that onshore current patterns would differ sharply and continuously on neighboring reefs in such close proximity.

A third possibility is that reefs vary in quality, in

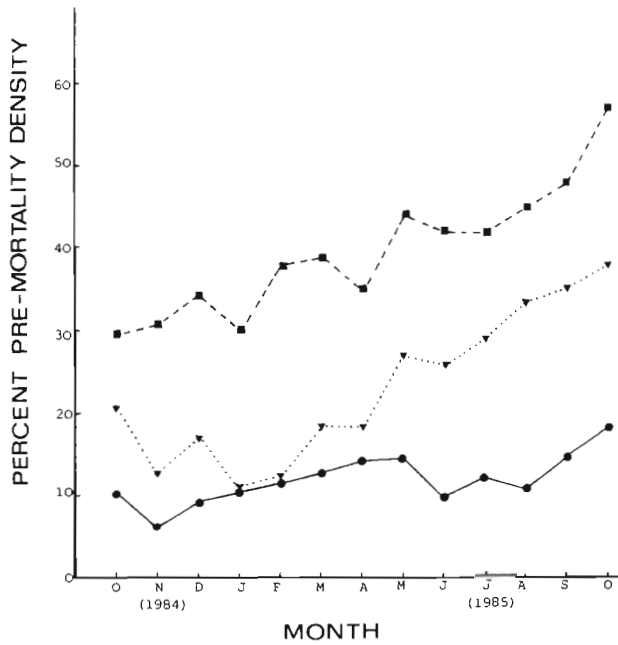


Fig. 7 *Diadema antillarum*. Urchin density (no. m⁻²) as a percentage of pre-mortality density (from Hunte et al. 1986) on 3 fringing reefs in Barbados. (■---■) Golden Palms; (▼.....▼) Sandridge; (●—●) North Bellairs

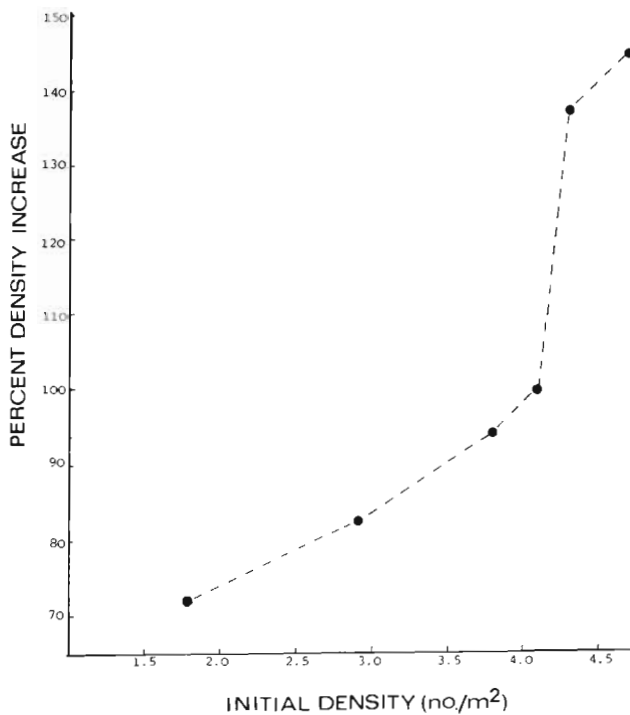


Fig. 8. *Diadema antillarum*. Percent density increase vs initial density (no. m⁻²) on 6 fringing reefs in Barbados

terms of availability of resources per unit area, and that this enhances recovery through lower post-settlement mortality. If so, reefs with higher pre-mortality densi-

Table 1. *Diadema antillarum*. Initial population densities, final densities, percentage increase in density, and pre-mortality densities (from Hunte et al. 1986) on 3 fringing reefs in Barbados. All densities in no. m⁻²

Reef	Pre-mortality density	Initial density	Final density	% Increase in density
North Bellairs	17.3	1.8	3.1	72.2
Sandridge	14.1	2.9	5.3	82.8
Golden Palms	12.9	3.8	7.4	94.7

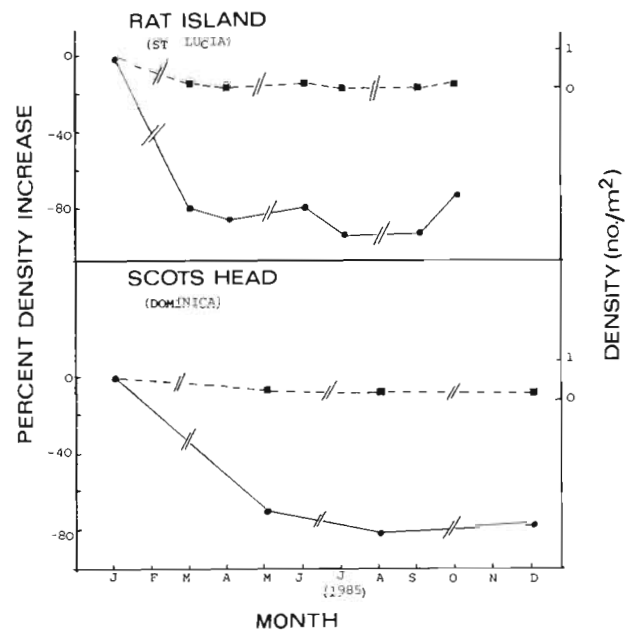


Fig. 9. *Diadema antillarum*. (■---■) Percent increase in urchin density (no. m⁻²) and (●—●) urchin density (no. m⁻²) by month vs time of year on Rat Island (St Lucia) and Scots Head (Dominica) reefs

ties should have higher recovery rates. However, population recovery was not higher on reefs with higher pre-mortality density.

A fourth possibility is that planktonic larvae actively choose reefs (Leis 1982, Leis & Goldman 1984), and that larvae of *Diadema antillarum* prefer to settle on reefs with higher adult density. Highsmith (1982) has shown preference by larvae of the sand dollar *Dendraster excentricus* for adult-associated sand, adults releasing a chemical attractive to larvae. A positive correlation between adult and recruit densities has recently been observed for *D. antillarum* in Curaçao (Bak 1986), and larvae were experimentally shown to choose clean over fouled substrata. Bak (1986) suggested that the more intensive grazing on reefs with higher adult densities would generate the clean substrata preferred by larvae. Hence, preference by larvae for reefs with a higher

adult density is a plausible explanation for the correlation between initial density and recovery rates observed in the present study. Such preference will be adaptive if fertilisation probability is low on low density reefs, and/or if the presence of adults increases recruit survivorship. Indeed, lower recruit mortality on reefs with higher adult density is the final (fifth) possibility for the observed correlation between initial density and recovery rate on reefs. It would occur if predation is lower on recruits that associate with adults; a hypothesis supported by the observation in the present study that most recruits are aggregated with adults, rather than occurring solitarily or in aggregation with other recruits (see also Breen et al. 1985 for *Strongylocentrotus fransiscanus*). Fish that prey on *D. antillarum* include triggerfishes (Balistidae), jacks (Carangidae), wrasses (Labridae), grunts (Pomadasyidae) (Randall et al. 1964), and toadfishes (Batrachoididae) (Hoffmann & Robertson 1983); and Keller (1982) found that predation on *D. antillarum* recruits is greater than on other echinoderms in seagrass *Thalassia testudinum* beds in Jamaica. Possibilities 4 and 5, the 2 most plausible explanations for the observed recovery pattern, are not mutually exclusive. Indeed, lower juvenile mortality at higher adult density could lead to the evolution of preference behavior by larvae for reefs with higher adult densities. However, preference for reefs with higher adult densities may become less advantageous as reefs approach carrying capacity, given the possibility of density-dependent inhibition of growth rates (Hunte et al. 1986). Investigating settlement preference by larvae when reefs are closer to carrying capacity would therefore be of interest.

Recruitment of *Diadema antillarum* in St Lucia and Barbados occurred in summer, but the recruitment peak in St Lucia (downcurrent) preceded that in Barbados (upcurrent). This suggests that Barbados is not a primary source of recruits for St Lucia. Recruitment in Dominica was negligible, the few recruits observed being present in January. These data suggest that recruitment to Caribbean reefs does not occur from a regional panmictic larval population. Moreover, the observation that recruitment strength on an island is a function of adult density on that island, and that recruitment in Barbados follows spawning by a biologically plausible time lag, may also suggest that island populations are largely discrete breeding units. Note, however, that the correlation of recruitment strength with island population density could also result from settlement preference by larvae for areas of high adult density.

Several authors have reported larvae recruiting to their natal areas although being temporarily part of the oceanic zooplankton; a phenomenon attributed to patterns of water movement which retain larvae near

natal reefs (Leis & Miller 1976, Johannes et al. 1981, Cameron & Rumrill 1982, Richards 1982). Mesoscale (10's to 100's of kilometers) eddies or gyres are regarded as the most probable mechanism of retention of pelagic larvae (Weibe et al. 1976). Indeed, some species apparently time their spawning to coincide with the formation of eddies near the reefs on which they reside (Boden 1952, Lobel & Robinson 1983). A higher than expected abundance of larval nearshore fishes has been reported off the west coast of Barbados, and an eddy system in the wake of Barbados, causing retention of larvae near the island, has therefore been proposed (Emery 1972, Powles 1975). Such a system could trap *Diadema antillarum* larvae, preventing their dispersal to neighboring islands, and is consistent with the observation that recruitment strength to an island increases with adult population density on the island.

Acknowledgements. We thank J. Marsden and 2 anonymous reviewers for comments on the manuscript, and J. Horrocks for assistance with manuscript preparation. This work was supported by Natural Science and Engineering Research Grant A0264 to W. Hunte.

LITERATURE CITED

- Anderson, G. R. V., Ehrlich, A. H., Ehrlich, P. R., Roughgarden, J. D., Russell, B. C., Talbot, F. H. (1981). The community structure of coral reef fishes. *Am. Nat.* 117: 476-495
- Bailey, K. M. (1981). Larval transport and recruitment of Pacific hake *Merluccius productus*. *Mar. Ecol. Prog. Ser.* 6: 1-9
- Bak, R. P. M. (1986). Recruitment patterns and mass mortalities in the sea urchin *Diadema antillarum*. In: *Proc. 5th Int. Coral Reef Symp., Tahiti, Vol. 5: 267-272*
- Bak, R. P. M., Carpay, M. J. E., de Ruyter van Steveninck, E. D. (1984). Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao. *Mar. Ecol. Prog. Ser.* 17: 105-108
- Bak, R. P. M., van Eys, G. (1975). Predation of the sea urchin *Diadema antillarum* Philippi on living coral. *Oecologia (Berl.)* 20: 111-115
- Barker, M. F., Nicholls, D. (1983). Reproduction, recruitment and juvenile ecology of the starfish *Asterias rubens* and *Narthasterias glacialis*. *J. mar. biol. Ass. U.K.* 63: 745-765
- Boden, P. B. (1952). Natural conservation of insular plankton. *Nature, Lond.* 169: 697-699
- Breen, P. A., Adkins, B. E., Miller, D. C. (1978). Recovery rate in three exploited sea urchin populations from 1972 to 1977. *Fish. mar. Serv. MS Rep. (Can.)* 1446: 1-27
- Breen, P. A., Carolsfield, W., Yamanaka, L. (1985). Social behavior of juvenile red sea urchins, *Strongylocentrotus fransiscanus* (Agassiz). *J. exp. mar. Biol. Ecol.* 92: 45-61
- Cameron, R. A. (1986). Reproduction, larval occurrence and recruitment in Caribbean sea urchins. *Bull. mar. Sci.* 39: 332-346
- Cameron, R. A., Rumrill, S. S. (1982). Larval abundance and recruitment of the sand dollar *Dendraster excentricus* in Monterey Bay, California, USA. *Mar. Biol.* 71: 197-202
- Carpenter, R. C. (1981). Grazing by *Diadema antillarum* (Philippi) and its effect on the benthic algal community. *J. mar. Res.* 39: 749-765

- Chesher, R. H. (1969). Contributions to the biology of *Meoma ventricosa* (Echinoidea: Spatangoida). *Bull. mar. Sci.* 19: 72–110
- Coastal Conservation Project Report (1983). Nearshore water circulation. In: Interim Draft and Diagnostic Survey, Technical Background Report, Vol. 3, Government of Barbados, Ministry of Housing and Lands and Inter-American Development Bank. Prepared by Hunter and Associates, Toronto
- Doherty, P. J. (1981). Coral reef fishes: recruitment-limited assemblages. In: Gomez, E. D., Birkeland, C. E., Buddemeier, R. W., Johannes, R. E., Marsh Jr, J. A., Tsuda, R. T. (eds.) *Proc. 4th Int. Coral Reef Symp.*, Manila, Philippines, Vol. 2: 465–470
- Emery, A. R. (1972). Eddy formation from an oceanic island: ecological effects. *Caribb. J. Sci.* 12: 121–128
- Engstrom, N. A. (1982). Immigration as a factor in maintaining populations of the sea urchin *Lytechinus variegatus* (Echinodermata: Echinoidea) in seagrass beds on the southwest coast of Puerto Rico. *Stud. Neotrop. Fauna Env.* 17: 51–60
- Gulland, J. A. (1983). Fish stock assessment: a manual of basic methods. *FAO/WILEY Series On Food and Agriculture*, Vol. 1. Wiley, New York
- Hawkins, C. M., Lewis, J. B. (1982). Ecological energetics of the tropical sea urchin *Diadema antillarum* Philippi in Barbados, West Indies. *Estuar. coast. Shelf Sci.* 15: 645–669
- Highsmith, R. C. (1982). Induced settlement and metamorphosis of the sand dollar (*Dendraster excentricus*) larvae in predator-free sites: adult sand dollar beds. *Ecology* 63: 329–337
- Hoffmann, S. G., Robertson, D. R. (1983). Foraging and reproduction of two Caribbean reef toadfishes (Batrachoididae). *Bull. mar. Sci.* 33: 919–927
- Hughes, T. P., Keller, B. D., Jackson, J. B. C., Boyle, M. J. (1985). Mass mortality of the echinoid *Diadema antillarum* Philippi in Jamaica. *Bull. mar. Sci.* 36: 377–384
- Hunte, W., Côté, I., Tomascik, T. (1986). On the dynamics of the mass mortality of *Diadema antillarum* in Barbados. *Coral Reefs* 4: 135–139
- Hunte, W., Younglao, D. (in press). Spawning patterns in the black sea urchin *Diadema antillarum* (Philippi) in Barbados. *J. exp. mar. Biol. Ecol.*
- Jackson, G. A., Strathmann, R. R. (1981). Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *Am. Nat.* 118: 16–26
- Johannes, R. E. (1978). Reproductive strategies of coastal marine fishes in the tropics. *Environ. Biol. Fish.* 3: 65–84
- Johannes, R. E., Helfman, G. S., Leis, J. M. (1981). Stock boundaries of reef and lagoon food fishes (Abstract). In: Gomez, E. D., Birkeland, C. E., Buddemeier, R. W., Johannes, R. E., Marsh Jr, J. A., Tsuda, R. T. (eds.) *Proc. 4th Int. Coral Reef Symp.*, Manila, Philippines, Vol. 1: 112
- Keller, B. D. (1982). Fish predation and recruitment of echinoderms in a seagrass meadow. In: Lawrence, J. M. (ed.) *Echinoderms: Proceedings of the International Conference*, Tampa Bay. A. A. Balkema, Rotterdam, p. 275
- Leis, J. M. (1981). Distribution of fish larvae around Lizard Island, Great Barrier Reef. In: Gomez, E. D., Birkeland, C. E., Buddemeier, R. W., Johannes, R. E., Marsh Jr, J. A., Tsuda, R. T. (eds.) *Proc. 4th Int. Coral Reef Symp.*, Manila, Philippines, Vol. 2: 471–478
- Leis, J. M. (1982). Nearshore distributional gradients of larval fish (15 taxa) and planktonic Crustacea (6 taxa) in Hawaii. *Mar. Biol.* 72: 89–97
- Leis, J. M., Goldman, B. (1984). A preliminary distributional study of fish larvae near a ribbon coral reef in the Great Barrier Reef. *Coral Reefs* 2: 197–203
- Leis, J. M., Miller, J. M. (1976). Offshore distributional patterns of Hawaiian fish larvae. *Mar. Biol.* 36: 359–367
- Lessios, H. A., Cubit, J. D., Robertson, D. R., Shulman, M. J., Parker, M. R., Garrity, S. D., Levings, S. C. (1984a). Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. *Coral Reefs* 3: 173–182
- Lessios, H. A., Robertson, D. R., Cubit, J. D. (1984b). Spread of *Diadema* mass mortality throughout the Caribbean. *Science* 226: 335–337
- Lobel, P. S., Robinson, A. R. (1983). Reef fishes at sea: ocean currents and the advection of larvae. In: *The ecology of deep and shallow reefs*. Symp. Series for Undersea Res., NOAA Undersea Res. Prog. 1: 29–38
- McFarland, W. N. (1982). Recruitment patterns in tropical reef fishes. In: Huntsman, G. R., Nicholson, W. R., Fox Jr, W. W. (eds.) *The Biological Basis for Reef Fishery Management*, NOAA Tech. Memo. NMFS-SEFC-80: 83–91
- McFarland, W. N., Brothers, E. B., Ogden, J. C., Shulman, M. J., Birmingham, E. L., Kothian-Prentiss, N. M. (1985). Recruitment patterns in young French grunts *Haemulon flavolineatum* (Family Haemulidae) at St. Croix, Virgin Islands. *Fish. Bull. U. S.* 83: 413–426
- Moore, H. B., Jutare, T., Bauer, J. C., Jones, J. A. (1963). The biology of *Lytechinus variegatus*. *Bull. mar. Sci. Gulf Caribb.* 13: 23–53
- Mortensen, T. (1937). Contributions to the study of the development and larval forms of echinoderms III. *D. Kgl. Danske Vidensk. Selsk. Skr. Naturv. Math.* 7: 3–12
- Ogden, J. C., Brown, R., Salesky, N. (1973). Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science* 182: 171–175
- Powles, H. W. (1975). Abundance, seasonality, distribution and aspects of the ecology of some larval fishes off Barbados. Ph.D. thesis, McGill University, Montreal
- Randall, J. E., Schroeter, R. E., Starck, W. A. (1964). Notes on the biology of the echinoid *Diadema antillarum*. *Caribb. J. Sci.* 4: 421–433
- Richards, W. J. (1982). Recruitment of fishes/stock dilution. In: Huntsman, G. R., Nicholson, W. R., Fox Jr, W. W. (eds.) *The Biological Basis for Reef Fishery Management*, NOAA Tech. Memo. NMFS-SEFC-80: 101–102
- Sammarco, P. W. (1980). *Diadema* and its relationship to coral spat mortality: grazing, competition and biological disturbance. *J. exp. mar. Biol. Ecol.* 45: 245–272
- Sammarco, P. W. (1982a). Echinoid grazing as a structuring force in coral communities: whole reef manipulations. *J. exp. mar. Biol. Ecol.* 61: 31–35
- Sammarco, P. W. (1982b). Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. *J. exp. mar. Biol. Ecol.* 65: 83–105
- Sammarco, P. W., Levinton, J. S., Ogden, J. C. (1974). Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. *J. mar. Res.* 32: 47–53
- Sammarco, P. W., Williams, A. H. (1982). Damsel fish territoriality: influence on *Diadema* distribution and implications for coral community structure. *Mar. Ecol. Prog. Ser.* 8: 53–59
- Scoffin, T. P., Stearn, C. W., Boucher, D., Hawkins, C. M., Hunter, I. G., MacGeachy, J. K. (1980). Calcium carbonate budget of a fringing reef on the west coast of Barbados. *Bull. mar. Sci.* 30: 475–508
- Shulman, M. J. (1984). Resource limitation and recruitment patterns in a coral reef fish assemblage. *J. exp. mar. Biol. Ecol.* 74: 85–109

- Shulman, M. J., Ogden, J. C., Ebersole, J. P., McFarland, W. N., Miller, S. L., Wolf, N. G. (1983). Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* 64: 1508–1513
- Tegner, M. J., Dayton, P. K. (1977). Sea urchin recruitment patterns and implications of commercial fishing. *Science* 196: 324–326
- Victor, B. (1983). Recruitment and population dynamics of a coral reef fish. *Science* 219: 419–420
- Victor, B. (1986). Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol. Monogr.* 56: 145–160
- Weibe, P. H., Hulbert, E. M., Carpenter, E. J., John, A. E., Knapp, G. P., Boyd, S. H., Ortner, P. B., Cox, J. L. (1976). Gulf Stream cold core rings: large scale interaction sites for open ocean plankton communities. *Deep Sea Res.* 23: 695–710
- Younglao, D. (1987). Spawning, aggregation and recruitment in the black sea urchin *Diadema antillarum*. M.Sc. thesis, McGill University, Montreal
- Younglao, D., Hunte, W. (in press). Aggregation in the black sea urchin *Diadema antillarum*: reproduction or protection? *Mar. Biol.*

This article was submitted to the editor; it was accepted for printing on March 29, 1988