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COMMUNITY STRUCTURE IN TIMES PAST: INFLUENCE OF HUMAN FISHING PRESSURE ON ALGAL–URCHIN INTERACTIONS[1]

DON R. LEVITAN[2]
Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Abstract. The sea urchin *Diadema antillarum* increases the relative size of Aristotle's lantern (length of demipyramid) when food limited. This provides a tool for investigating algal abundance and biotic interactions in the past. A field collection of *D. antillarum* provided a baseline relationship between demipyramid length and body size (test diameter). Experimental manipulations of food availability and population density resulted in shifts in relative demipyramid length. The baseline and experimental data provide a range of responses that was compared to museum specimens collected over the past 100 yr from 30 locations in the Caribbean. The relative demipyramid lengths from the museum specimens were also compared over time, and with human population density, human fishing pressure, and geographic region. The results indicate that relative demipyramid size is indirectly influenced by human activity and varies with geographic region. This suggests that human fishing pressure has influenced Caribbean coral reef community structure by affecting predator–herbivore relationships. However, this human impact may be small relative to naturally occurring variation in demipyramid size.

Key words: Aristotle's lantern; Caribbean; demipyramid; Diadema antillarum; *food limitation; herbivory; historical ecology; human impact; phenotypic plasticity; predator–prey relationships.*

INTRODUCTION

Determining community structure in a pristine environment is becoming increasingly difficult as humans continue to disrupt natural communities. This disturbance can distort our understanding of the complex ecological relationships and evolutionary forces between species and the environment. A current controversy is the human role in influencing community structure by the removal of predators (Aronson 1990, Witman and Sebens, *in press*). For example, it has been suggested that our removal of lobsters from the northeast coast of North America (Mann and Breen 1972) and sea otters from the northwest coast of North America (Estes and Palmisano 1974) has led to increased sea urchin abundance and the creation of "urchin barrens," large tracts of bottom devoid of kelp and other fleshy algae. However, the validity of the lobster hypothesis (Miller 1985, Elner and Vadas 1990) and the generality of the sea otter hypothesis (Foster, *in press*) have been challenged and are still controversial.

This study addresses the historical importance of sea urchins in the Caribbean. Research from the 1970s and 1980s on the Caribbean sea urchin *Diadema antillarum* Philippi suggests that this herbivore has a major controlling influence on coral reef community structure. *D. antillarum* influences coral recruitment and survivorship, algal abundance, species diversity, and bioerosion of reef habitats (Ogden et al. 1973, Sammarco et al. 1974, Bak and van Eyes 1975, Sammarco 1980, Scoffin et al. 1980, Carpenter 1981, 1986). Levitan (1989) demonstrated experimentally that in areas of high *D. antillarum* density, algal abundance diminished and urchin growth became food limited. Further evidence of *D. antillarum* food limitation is the pattern of an inverse relationship between body size and population density noted in several locations in the Caribbean (St. Croix: Carpenter 1981; Barbados: Hunte et al. 1986; St. John: Levitan 1988*a*). Thus, when an unknown pathogen destroyed 99% of the *D. antillarum* in the Caribbean (Lessios et al. 1984, Lessios 1988), algal abundance increased dramatically on many reefs (de Ruyter van Steveninck and Bak 1986, Liddell and Ohlhorst 1986, Hughes et al. 1987, Levitan 1988*b*, Carpenter 1990*a*).

However, Hay (1984) suggested that many well-studied parts of the Caribbean were near areas of high human abundance, and *D. antillarum*'s apparent influence may have been an artifact of over-fishing by humans. His evidence came from assessing fish and sea urchin grazing on strips of seagrass placed on reefs designated as "over-fished" or "less-fished." Similarly, Aronson (1990) argued that geographically expanding fishing pressure resulted in increased urchin density and altered nearshore community structure, in the Caribbean, Aleutian Islands, and New England.

The simplest explanation for these suggestions is that removal of *D. antillarum* predators such as triggerfish (Hay 1984) resulted in increased urchin numbers and grazing pressure. The emerging paradigm of Caribbean

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[2] Present address: Department of Zoology, University of California, Davis, California 95616 USA.

coral reef community structure is that *D. antillarum* is the dominant herbivore in areas subject to heavy human fishing pressure, but herbivorous fish dominate in more pristine conditions when urchin populations are kept in check by fish predators. Although a large number of papers address this hypothesis (e.g., Carpenter 1986, 1990*a*, *b*, Lewis 1986, Levitan 1988*b*, Morrison 1988, Aronson 1990), it is still controversial; there has been no direct test to determine if the variance in herbivore pressure is due to human impact or other regional differences.

Addressing hypotheses concerning past events requires more than spatial surveys or experiments, since these techniques only provide information on current conditions in the former case and a range of possibilities in the latter. The ideal evidence comes from the time period in question. A combination of historic, geographic, and experimental approaches provides both the sequence of events and the basis of change in community structure.

Food limitation or high population density in sea urchins results in an increase in the size of Aristotle's lantern (specifically the length of demipyramids) relative to the size of the body (test diameter, Fig. 1) (Ebert 1980, Black et al. 1982, Edwards and Ebert 1991, Levitan 1991). For *D. antillarum*, this is accomplished by a reduction in the growth rate of the test, and when more severely food limited, a reduction in the size of the test (Levitan 1991). Since this involves changes in skeletal elements, museum and fossil records can be investigated for past food limitation events. Relative demipyramid length, rather than simply body size, provides the best index of food limitation, since body size can be influenced by age, and collectors of museum specimens may be biased in the sizes they collect.

In this study, I first present the allometric relationship between test diameter and demipyramid length in *D. antillarum*, and I demonstrate that food limitation, caused by changes in food availability or population density, results in shifts in relative demipyramid length by summarizing previous work (Levitan 1991). Second, I use museum specimens to investigate patterns of food limitation over the past 100 yr in the Caribbean. Third, I compare museum specimens to patterns of human abundance and human fishing pressure. Finally, I examine regional patterns of relative demipyramid length.

The hypothesis to be tested is that increases in human abundance and fishing pressure led to increases in the relative size of sea urchin demipyramids. The logic behind this prediction is as follows. Human fishing pressure removed predators of *Diadema antillarum*. Free from predation pressure, sea urchin population density increased. Increased urchin abundance led to a decrease in algal food availability and resulted in sea urchin food limitation. Food-limited urchins increased the relative size of the demipyramid.

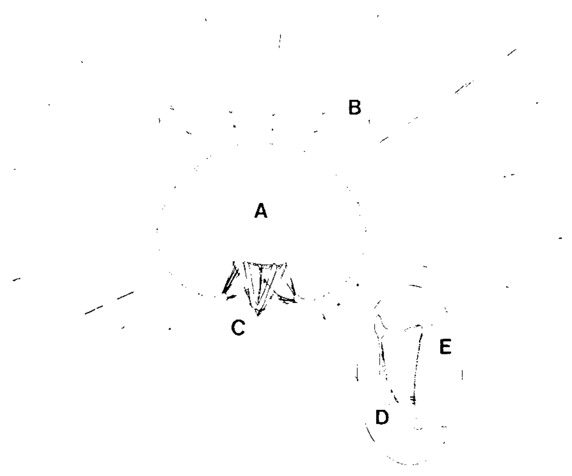

FIG. 1. Illustration of the sea urchin *Diadema antillarum* (A) indicating measure of test diameter (B), and Aristotle's lantern (C). The lantern contains five pyramids. Each pyramid guides a tooth; the pyramids themselves do not scrape and wear. Each pyramid can be divided into two demipyramids. Insert is enlarged to show demipyramid (D) and measure of length (E).

Although fishing pressure would also remove herbivorous fish there are two points to consider. First, the presence of herbivorous fish does not influence the localized and more intense grazing of *D. antillarum* (Hay and Taylor 1985, Carpenter 1986). Second, even if fish did influence *D. antillarum* grazing, it would lead to the opposite prediction; increased fishing pressure would release *D. antillarum* from food competition resulting in reduced relative demipyramid size.

The results of this study provide insight into temporal and spatial variation in food availability and the relative importance of human activity on coral reef community structure.

METHODS

Relationship between demipyramid and test

The allometric relationship between demipyramid length and test diameter was established by collecting *Diadema antillarum* from St. John, U.S. Virgin Islands (regression of ln demipyramid length as a function of ln test diameter (both variables measured in millimetres): ln demipyramid = 1.101 ln test − 1.547, $R^2 = 0.92$, $P < .0001$, $N = 92$, from Levitan 1991). These sea urchins were in a food-abundant environment and growing rapidly (Levitan 1988*a*, 1991). To adjust for allometric growth, all experimental and museum demipyramid/test ratios are standardized as deviations from predicted ratios estimated from test diameter and the regression of these field-collected sea urchins.

Experimental food manipulations

In a previous study (Levitan 1989, 1991), demipyramid lengths and test diameters were measured in a laboratory and field experiment. Here the ratios are calculated from those measurements, and in this study are allometrically adjusted as described above. In the laboratory, *D. antillarum* were provided 1 of 4 levels of food (4, 2, 1, or 0 g wet mass of the green alga *Ulva lactuca* every 4 d). After 6 mo, the adjusted demipyramid/test ratios were 0.002, 0.022, 0.023, and 0.030 for the four treatments, respectively. These ratios increase with the degree of starvation.

In the field, sea urchins from two size classes (27.5 and 37.5 mm test diameter) were placed in cages (0.25 m^2 area) at low and high density (12 and 24 individuals/m^2). This provided average initial sea urchin wet biomasses per cage of 38.08 g (27.5 mm test diameter at 12 individuals/m^2), 76.16 g (27.5 mm at 24 individuals/m^2), 96.27 g (37.5 at 12 individuals/m^2), and 192.53 g (37.5 mm at 24 individuals/m^2). After 8 mo, the adjusted demipyramid/test ratios were 0.029, 0.032, 0.046, and 0.049 for the four treatments, respectively. The ratios increased with population density and sea urchin biomass per unit area. Both experiments were conducted at St. John, U.S. Virgin Islands. These results demonstrate that decreased food availability or increased sea urchin abundance resulted in enlarged relative demipyramid size. These experiments provide a range of values that can be compared to the data collected from museum specimens.

Museum specimens

Specimens of *Diadema antillarum* in the National Museum of Natural History, Smithsonian Institution, collected between 1881 and 1986, were measured to obtain historical data. Museum specimens are maintained as "lots" representing a sample taken at one location and time. For each lot, the sea urchin's test diameter (mean of three measurements per test) and demipyramid length (mean of four demipyramids per sea urchin) were measured and the date and location of the collection were noted. Usually one sea urchin per lot was randomly selected and analyzed. However, when lot size was large (>10), two or more were analyzed. No more sea urchins were analyzed since these collections are a unique and nonrenewable resource. Variation in demipyramid/test ratios between lots was investigated with an analysis of variance (only using lots with >1 sea urchin). The results indicate highly significant differences between lots (df = 20/37, mean squares between lots/mean squares within lots = 0.0048/0.0005, $P < .0001$, $N = 21$ lots). This indicates that the sampled populations of sea urchins differed in respect to demipyramid/test ratio and suggests that food availability varied among populations. The use of only one sea urchin per site/time would tend to obscure any patterns and would underestimate any effects noted.

Human abundance

Museum specimens were compared to patterns of human abundance. Human population density was calculated from the island area (or nation/state size if on the mainland) and the human population size at the time the museum specimen was collected. Generally, human population size was estimated from national census data. However, when more specific information was available, it was used (e.g., population size and area of Monroe County, Florida, USA, for sites in the Florida Keys). Human abundance is not a direct measure of fishing pressure, but should be roughly correlated. Variance in this relationship would tend to obscure patterns and would underestimate any effects noted.

Human fishing pressure

Museum specimens were also compared between sites characterized as either "over-fished" or "less-fished" by Hay (1984). Islands or countries that were classified by Hay (1984) and had museum specimens collected since 1950 were analyzed for differences in demipyramid/test ratios. The sites categorized as less-fished were Panama and the Bahamas and those categorized as over-fished were St. Thomas, Jamaica, and Haiti. Hay (1984) only investigated one or a few reefs at each island (or island group). Ignoring within-island variation in fishing pressure would tend to obscure patterns and underestimate any effects noted.

Geographic region

The museum data were divided into six regions based on island size and proximity to continental land masses. The geographic regions were (1) Florida (including the Keys and Dry Tortugas), (2) Central and South American mainland, (3) Bahamas (including the Turks and Caicos), (4) Greater Antilles, (5) Lesser Antilles, and (6) islands in the mid-Atlantic (the Ascension Islands, Ilha de Trinidade, and Madeira Island). It should be noted that sea urchins from the Ascension Islands have been classified as the subspecies *Diadema antillarum ascensionis.*

RESULTS

Time

The demipyramid length, test diameter, allometrically adjusted ratio, human population density, and sample size are presented in Table 1. There was a significant positive relationship between the adjusted ratios and time ($R^2 = 0.114$, $P < .002$, Fig. 2). Relative demipyramid size increased over this 100-yr period. This corresponded to a fivefold increase in human abundance (Table 1).

Human abundance

There was also a significant positive relationship between adjusted ratios and human abundance ($R^2 = 0.061$, $P < .03$, Fig. 3). Increased human abundance was related to increased relative demipyramid size.

TABLE 1. Properties of *Diadema antillarum* museum specimens from 30 different collections, and human population density at the site at time of collection.

Collection site	Year of collection	Mean test diameter (mm)	Mean demi-pyramid length (mm)	Adj. ratio*	Human density (no./km^2)†	No. urchins analyzed
Dry Tortugas, Florida	1881	84.9	26.2	−0.025	3.8	1
Madeira, Portugal	1881	54.6	19.0	0.029	130.0	1
Indian Key, Florida	1884	73.8	22.7	−0.021	3.8	2
Dry Tortugas, Florida	1884	66.2	18.3	−0.049	3.8	1
Jamaica	1884	24.2	7.3	0.007	52.8	1
St. Thomas	1884	51.1	14.8	−0.027	158.5	2
St. Thomas	1884	84.2	23.2	−0.058	158.5	1
St. Thomas	1884	21.6	6.6	0.014	158.5	1
St. Thomas	1884	49.6	14.7	−0.020	158.5	1
Isla Providencia, Colombia	1884	73.2	21.9	−0.029	2.8	1
Isla Providencia, Colombia	1884	85.8	25.9	−0.032	2.8	1
Isla Providencia, Colombia	1884	71.1	20.2	−0.041	2.8	2
Indian Key, Florida	1885	41.0	11.0	−0.041	3.8	1
Indian Key, Florida	1885	96.8	25.1	−0.079	3.8	1
Yucatan, Mexico	1885	87.3	22.6	−0.076	5.1	1
Big Pine Key, Florida	1886	37.6	10.5	−0.028	3.8	1
Nassau, Bahamas	1886	44.4	13.8	−0.010	4.2	2
Arroyo, Puerto Rico	1899	65.4	18.7	−0.039	106.8	1
Mayaguez, Puerto Rico	1899	74.9	20.4	−0.057	106.8	1
Puerto Rico	1899	27.3	8.1	−0.004	106.8	3
Hawk Channel, Florida	1903	30.5	8.5	−0.021	3.8	1
Loggerhead Key, Florida	1908	78.5	22.5	−0.044	3.8	2
Dimas, Cuba	1914	44.0	17.2	0.079	22.6	1
St. Thomas	1915	44.1	15.6	0.041	122.0	10
Sand Key, Florida	1916	48.2	12.2	−0.062	7.6	2
Antigua	1918	26.2	9.2	0.054	22.7	1
Dry Tortugas, Florida	1924	91.4	26.2	−0.049	7.6	1
Dry Tortugas, Florida	1932	28.0	7.0	−0.047	7.6	1
Port Antonio, Jamaica	1936	31.8	9.1	−0.017	101.0	1
Puerto Rico	1937	60.5	17.2	−0.037	200.1	1
Cuba	1937	22.4	7.2	0.030	39.3	2
Lantana, Florida	1950	22.1	6.0	−0.020	11.3	1
Bimini, Bahamas	1950	60.3	18.4	−0.016	35.7	1
Vera Cruz, Mexico	1954	22.2	5.8	−0.029	15.1	1
Cartagena, Colombia	1958	44.1	17.0	0.073	12.7	1
Boca Raton, Florida	1960	48.2	12.6	−0.053	18.9	1
Dominican Republic	1963	26.1	8.7	0.039	69.4	1
Dominican Republic	1963	24.8	6.8	−0.018	69.4	1
Sawyer Key, Florida	1963	93.1	24.3	−0.075	18.9	1
Molasses Key, Florida	1963	24.8	6.5	−0.033	18.9	1
Dominica	1964	31.9	12.0	0.077	93.2	7
Dominica	1964	35.3	11.8	0.030	93.2	1
Galeta, Panama	1967	49.0	15.5	0.000	17.9	2
Egmont Key, Florida	1967	80.9	20.9	−0.074	18.9	2
Egmont Key, Florida	1967	44.1	11.8	−0.044	18.9	1
St. Thomas	1967	24.0	7.7	0.028	243.9	1
Galeta, Panama	1969	61.7	22.1	0.035	18.4	1
St. Vincent	1969	18.6	5.2	−0.002	257.7	1
St. Kitts	1969	23.3	6.8	0.001	229.9	2
Yucatan, Mexico	1969	28.3	7.9	−0.017	20.43	2
Jamaica	1970	65.2	19.7	−0.022	182.0	1
Jamaica	1970	49.0	17.9	0.050	182.0	2
Jamaica	1970	22.0	6.8	0.017	182.0	1
Jamaica	1970	36.9	14.6	0.088	182.0	2
Jamaica	1970	71.8	22.4	−0.015	182.0	2
Jamaica	1970	21.8	6.1	−0.011	182.0	1
Haiti	1970	36.5	13.5	0.065	175.5	1
Dominican Republic	1970	23.3	7.6	0.033	88.6	1
Turtle Beach, Ascension	1970	18.9	5.6	0.009	9.6	1
Puerto Belo Road, Panama	1970	41.1	15.7	0.072	18.9	1
Rio Piedras, Panama	1971	21.4	6.6	0.019	19.2	1
Limon Bay, Panama	1971	47.7	13.0	−0.041	19.2	3
Galeta, Panama	1971	27.0	7.6	−0.016	19.2	1
Galeta, Panama	1971	22.7	5.6	−0.047	19.2	1
Galeta, Panama	1971	16.8	4.3	−0.025	19.2	1

TABLE 1. Continued.

Collection site	Year of collection	Mean test diameter (mm)	Mean demi-pyramid length (mm)	Adj. ratio*	Human density (no./km^2)†	No. urchins analyzed
Collyer Point, Ascension	1971	26.8	10.0	0.075	9.6	1
Collyer Point, Ascension	1971	32.6	11.6	0.053	9.6	1
Dominican Republic	1971	17.9	5.0	−0.005	85.8	1
Turks and Caicos	1971	17.7	5.0	0.000	14.0	1
San Blas, Panama	1972	64.1	20.1	−0.011	19.7	1
Salvador, Brazil	1972	67.7	19.1	−0.042	12.9	3
Galeta, Panama	1972	23.2	6.2	−0.025	19.7	1
Galeta, Panama	1972	23.6	6.7	−0.010	19.7	1
Maria Chiquita, Panama	1972	49.3	14.8	−0.015	19.7	1
San Blas, Panama	1973	21.0	5.7	−0.020	20.4	1
Ilha de Trinidade	1976	40.9	12.7	0.002	8.3	1
S.W. Bay, Ascension	1981	36.4	12.8	0.047	9.6	1
Florida	1981	17.1	4.4	−0.028	22.7	1
Florida	1982	29.1	8.9	0.008	22.7	2
Florida	1982	31.6	10.4	0.029	22.7	2
Florida	1983	17.2	4.5	−0.022	22.7	1
Looe Key, Florida	1984	40.1	13.6	0.031	22.7	1
Looe Key, Florida	1986	19.5	5.4	−0.013	26.4	1

* The allometrically adjusted ratio is the ratio of demipyramid length to test diameter, minus the ratio predicted by the St. John regression equation for a particular test diameter {Ratio = [demipyramid/test] − [exp(ln test × 1.101 − 1.547)]/test}.

† For sources of human census data see Anonymous 1891, 1923, 1931, 1950–1980, 1965, Wilke 1985.

Human fishing pressure

The demipyramid/test ratios from sites designated as over-fished were significantly greater than ratios from sites designated as less-fished (Fig. 4, ANOVA, df = 1/20, mean squares between sites/mean squares within sites = 0.0053/0.0012, $P < .05$, $N = 22$). This result supports Hay's (1984) hypothesis and suggests that analysis of ratios can distinguish between reefs of markedly different human fishing pressure.

The largest single measure of relative demipyramid size was in Jamaica in 1970 (adjusted ratio = 0.088), the smallest was in the Florida Keys in 1885 (−0.079). Relative demipyramid size increased over time (sites divided into before 1936 and after 1963) on Jamaica (from −0.005 to 0.023) and St. Thomas (from −0.010 to 0.028); both islands have a considerable fishing pressure (Hay 1984). Less change and much lower ratios were noted in the Florida Keys (−0.044 to −0.035) where urchin predators may be more common; fish traps, common in the Caribbean, are illegal in Florida.

Geographic region

I used an analysis of covariance to test the effect of geographic region on demipyramid/test ratio, with the following covariates: human population density, island size (or nation size), and time. The analysis indicated

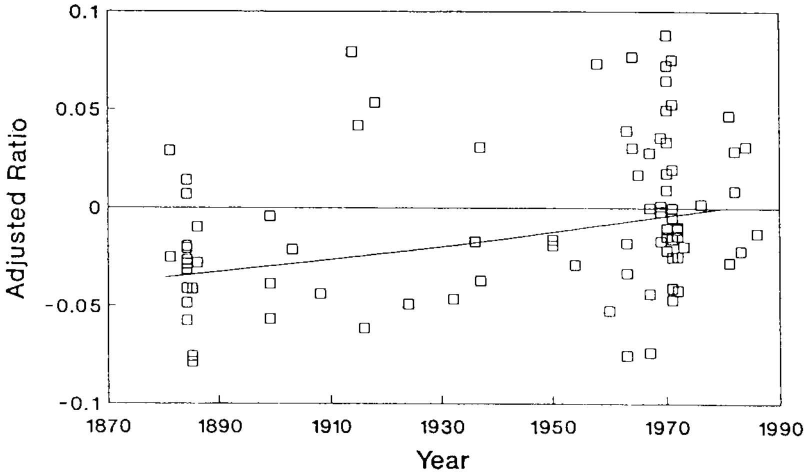

FIG. 2. *Diadema antillarum* demipyramid/test length ratio as a function of time. Ratios are allometrically adjusted (see Table 1). Regression equation: ln adjusted ratio = 0.00435time − 10.923, $R^2 = 0.114$, $P < .002$. (Time is in years and 0.1 is added to the ratio to remove negative numbers and allow for a natural logarithmic transformation.)

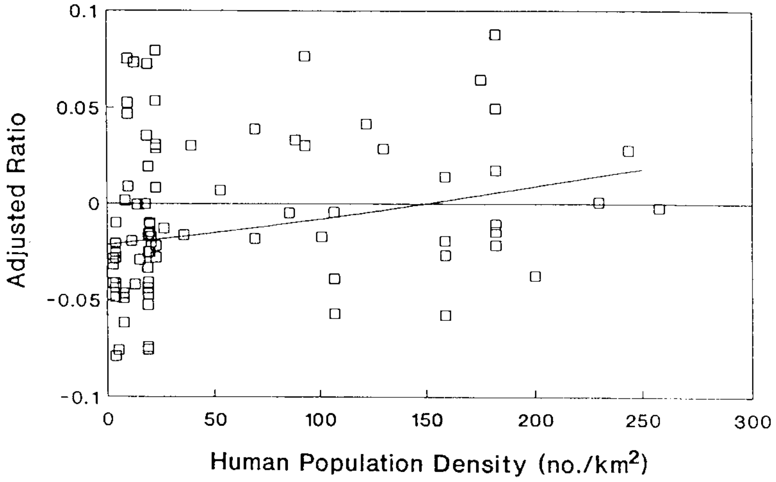

FIG. 3. Relationship between *Diadema antillarum* demipyramid/test length ratio as a function of human population density. Ratios are allometrically adjusted (see Table 1). Regression of the demipyramid/test ratio as a function of population density: ln adjusted ratio = 0.00167density − 2.57, $R^2 = 0.0605$, $P = .025$, $N = 83$. (Time is in years and 0.1 is added to the ratio to remove negative numbers and allow for a natural logarithmic transformation.) Regression with *Diadema antillarum ascensionis* removed has the following statistics: $R^2 = 0.0928$, $P = .006$, $N = 77$.

highly significant effects of geographic region, time, and human population density. There was no significant effect of island (nation) size (Table 2). Regional differences in ratios account for most of the explained variation in the ANCOVA (accounting for 23% of the sums of squares). The demipyramid/test ratios from the mainland regions (Florida and Central/South America) are smaller than island regions. There is no difference in the demipyramid/test ratio between the much larger islands of the Greater Antilles as compared to the Lesser Antilles. The island areas with the largest ratios are the islands farthest from land masses in the mid-Atlantic: the Ascension Islands, Ilha de Trinidade, and Madeira Island (Fig. 5, multiple-comparison test: 95% CI). These offshore areas with the highest ratios also had the lowest human abundance.

DISCUSSION

These results suggest that human abundance led to increased demipyramid size induced by food limitation. The amount of variation in demipyramid/test ratio explained by human abundance is only 6% (9% with the Ascension subspecies removed). However, considering the myriad factors not accounted for in this analysis, a significant finding predicted by an a priori hypothesis is noteworthy. The unexplained variation could be due to within-population variation, variation in fishing pressure not associated with human abundance (such as increased fishing technology over time), or the multitude of biotic and abiotic factors not associated with human impact. In fact, some of the largest ratios are found at the lowest levels of human

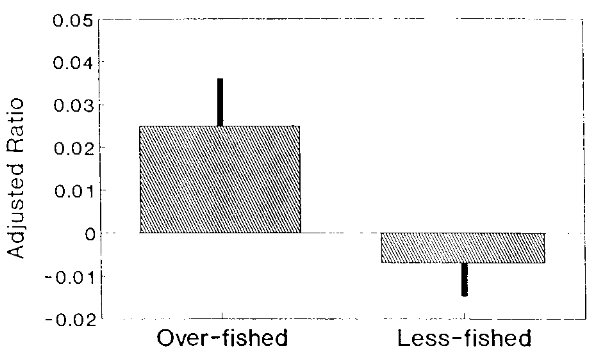

FIG. 4. Relationship between demipyramid/test ratios (allometrically adjusted) and human fishing pressure. The sites designated as less-fished are Panama and the Bahamas, and sites designated as over-fished are St. Thomas, Jamaica, and Haiti (from Hay 1984). Data are the mean ratio and 1 SE.

TABLE 2. Analysis of covariance testing of effects of geographic region (see Fig. 1) with the covariates being: human population density, time, and island size (or mainland region size).

Source of variation	df	SS	MS	*F*	*P*
Covariates					
Density	1	1.053	1.053	7.071	.0096
Time	1	1.997	1.997	13.410	.0005
Area	1	0.058	0.058	0.389	.5413
Main effect					
Region	5	4.277	0.855	5.744	.0002
Residual	74	11.021	0.149		
Total	82	18.414			

* Data are allometrically adjusted demipyramid/test length ratios (see Table 1), 0.1 is added to ratio to remove negative numbers and allow for a natural logarithmic transformation.

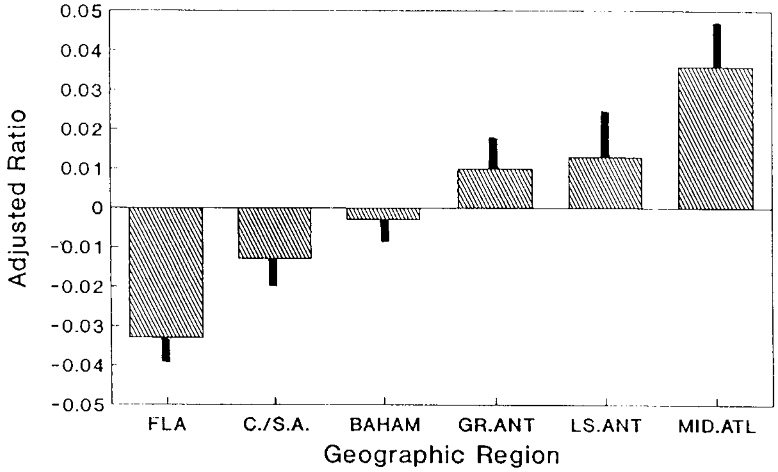

FIG. 5. Relationship between demipyramid/test ratios (allometrically adjusted) and geographic regions. The regions are Florida (FLA), Central and South America (C./S.A.), Bahamas (BAHAM), Greater Antilles (GR.ANT), Lesser Antilles (LS.ANT), and islands in the mid-Atlantic (MID.ATL). Data are the mean ratio and 1 SE.

abundance. This suggests the importance of other factors influencing algal abundance and urchin population dynamics.

Comparison of museum specimens to field data

The field-collected sea urchins from St. John were collected 2 yr after the mass mortality of *D. antillarum*, when density was very low and algal abundance high (Levitan 1988*b*). All museum specimens (except one Looe Key, Florida specimen) were collected previous to the mass mortality. This resulted in a low demipyramid/test ratio for St. John compared to the region (Lesser Antilles, Fig. 5). In comparison, the ratios from the St. John field experiment (0.029 to 0.049) conducted at realistic pre-mass mortality population densities (12–24 individuals/m^2) are similar to post-1963 ratios for St. Thomas (0.028) and Jamaica (0.023). Jamaica, the island with the highest single demipyramid/test ratio (0.088), also has the highest published *D. antillarum* population density estimate (71 individuals/m^2, Sammarco 1980). This suggests that before the mass mortality, algal abundance was low and urchins were food limited in the Antilles, supporting earlier research from that region (Ogden et al. 1973, Sammarco et al. 1974, Bak and van Eyes 1975, Sammarco 1980, Scoffin et al. 1980, Carpenter 1981, Levitan 1988*a, b,* 1989).

The starved sea urchins from the laboratory experiment had demipyramid/test ratios similar to the sea urchins from the mid-Atlantic islands. This indicates a highly food-limited condition for these relatively pristine populations (islands occupied by ≈1000 naval personnel; British Consulate, *personal communication*), suggesting nonhuman factors can produce the same ratios characteristic of "barren" habitats found in Jamaica.

The mainland regions had demipyramid/test ratios lower than the St. John field population. The pattern of increased ratio (suggesting food limitation) with distance from the mainland may be associated with differences in per capita fishing pressure (percent diet, amount exported, technology or preference), continental run-off affecting nutrient availability, or differences in recruitment and survivorship of sea urchins and fish. Interestingly, most sites classified as less-fished come from these mainland regions (Hay 1984 [but see Salt River, St. Croix], Lewis 1986). Perhaps there are other factors besides (or in addition to) fishing pressure determining differences in sites classified as "over-" or "less-" fished.

CONCLUSIONS

The results suggest that humans have indirectly influenced *D. antillarum* morphology. An explanation for this relationship is that removal of predatory fish by human beings led to increased sea urchin abundance and grazing pressure. Alternate explanations, such as the influence of competitive release of urchins from the removal of herbivorous fish or increasing nutrients due to human waste products, lead to opposite predictions, such as a decrease in demipyramid/test ratio with increasing human activity. For these reasons, the predation hypothesis is the most parsimonious explanation. The finding of ratios being related to estimated fishing pressure in the 1960s through 1980s adds support to this notion. However, the amount of change due to this disturbance was within the natural variation seen today and over 100 yr ago when human abundance was markedly lower. Natural variation in *D. antillarum* recruitment (Bak 1985, Hunte and Younglao 1988, Lessios 1988, Levitan 1988*b*, Carpenter 1990*a*, Karlson and Levitan 1990), predation pressure (Randall 1967, Carpenter 1984, Levitan and Genovese 1989), competition (Hay 1984, Hay and Taylor 1985, Carpenter 1986, 1990*b*, Lewis 1986), algal productivity (Carpenter 1988), and catastrophic mortality (i.e., disease: Lessios et al. 1984; hurricanes: D. R. Levitan, *unpublished data*) should not be ignored as important ecological factors determining urchin abundance and grazing impact. It appears that there have occasionally been times and places where algal abundance has been limiting and echinoid densities high, independent of human activity.

The combination of controlled experiments and large-scale temporal and geographic surveys provides a means to examine the mechanisms and dynamics of coral reef community structure. This allows us to test the importance of various factors influencing historical change, and aids in distinguishing between possible and probable past events.

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LITERATURE CITED

Anonymous. 1891. Report on the census of the Bahama Islands taken on the fifth April 1891, 1891. Nassau Guardian, Nassau, The Bahamas.

———. 1923. Population census of Portugal, December 1920, 1923. Imprensa Nacional, Lisboa, Portugal.

———. 1931. Fifteenth census of the U.S., 1931.Volume 1. United States Government Printing Office, Washington, D.C., USA.

———. 1950–1980. Demographic yearbook. Department of International Economy, Society and Affairs, Statistical Office, United Nations, New York, New York, USA.

———. 1965. Annual abstract of statistics, 1965. Department of Statistics, Jamaica.

Aronson, R. B. 1990. Onshore-offshore patterns of human fishing activity. Palaois **5**:88–93.

Bak, R. P. M. 1985. Recruitment patterns and mass mortalities in the sea urchin *Diadema antillarum*. Proceedings of the Fifth Coral Reef Congress **5**:267–272.

Bak, R. P. M., and G. van Eyes. 1975. Predation of the sea urchin *Diadema antillarum* Philippi on living coral. Oecologia (Berlin) **20**:111–115.

Black, R., M. S. Johnson, and J. T. Trendall. 1982. Relative size of Aristotle's lantern in *Echinometra mathaei* occurring at different densities. Marine Biology **71**:101–106.

Carpenter, R. C. 1981. Grazing by *Diadema antillarum* (Philippi) and its effect on the benthic algal community. Journal of Marine Research **39**:749–765.

———. 1984. Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. Marine Biology **82**:101–108.

———. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs **56**:345–363.

———. 1988. Mass-mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. Proceedings of the National Academy of Science (USA) **85**:511–514.

———. 1990*a*. Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. Marine Biology **104**:67–77.

———. 1990*b*. Mass mortality of *Diadema antillarum*. II. Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. Marine Biology **104**:79–86.

de Ruyter van Steveninck, E. D., and R. P. M. Bak. 1986. Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. Marine Ecology Progress Series **34**:87–94.

Ebert, T. A. 1980. Relative growth of sea urchin jaws: an example of plastic resource allocation. Bulletin of Marine Science **30**:467–474.

Edwards, P. B., and T. A. Ebert. 1991. Plastic response to limited food availability and spine damage in the sea urchin *Strongylocentrotus purpuratus* (Stimpson). Journal of Experimental Marine Biology and Ecology **145**:205–220.

Elner, R. W., and R. L. Vadas, Sr. 1990. Inference in ecology: the sea urchin phenomenon in the northwestern Atlantic. American Naturalist **136**:108–125.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science **185**:1058–1060.

Foster, M. S. *In press*. Organization of macroalgal assemblages in the northeast Pacific: the assumption of homogeneity and the illusion of generality. Hydrobiologia.

Hay, M. E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology **65**:446–454.

Hay, M. E., and P. R. Taylor. 1985. Competition between herbivorous fishes and urchins on Caribbean reefs. Oecologia (Berlin) **65**:591–598.

Hughes, T. P., D. C. Reed, and M. J. Boyle. 1987. Herbivory on coral reefs: community structure following mass-mortalities of sea urchins. Journal of Experimental Marine Biology and Ecology **133**:39–59.

Hunte, W., I. Cote, and T. Tomascik. 1986. On the dynamics of the mass mortality of *Diadema antillarum* in Barbados. Coral Reefs **4**:135–139.

Hunte, W., and D. Younglao. 1988. Recruitment and population recovery in the black sea urchin *Diadema antillarum* in Barbados. Marine Ecology Progress Series **45**:109–119.

Karlson, R. H., and D. R. Levitan. 1990. Recruitment-limitation in open populations of *Diadema antillarum*: an evaluation. Oecologia (Berlin) **82**:40–44.

Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? Annual Review of Ecology and Systematics **19**:371–393.

Lessios, H. A., D. R. Robertson, and J. D. Cubit. 1984. Spread of *Diadema* mass mortalities through the Caribbean. Science **226**:335–337.

Levitan, D. R. 1988*a*. Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi. Oecologia (Berlin) **76**:627–629.

———. 1988*b*. Algal-urchin biomass responses following the mass mortality of *Diadema antillarum* Philippi at Saint John, U.S. Virgin Islands. Journal of Experimental Marine Biology and Ecology **119**:167–178.

———. 1989. Density-dependent size regulation in *Diadema antillarum*: effects on fecundity and survivorship. Ecology **70**:1414–1424.

———. 1991. Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. Marine Biology **111**:431–435.

Levitan, D. R., and S. J. Genovese. 1989. Substratum-dependent predator–prey dynamics: patch reefs as refuges from gastropod predation. Journal of Experimental Marine Biology and Ecology **130**:111–118.

Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecological Monographs **56**:183–200.

Liddell, W. D., and S. L. Ohlhorst. 1986. Changes in benthic community composition following the mass mortality of *Diadema antillarum*. Journal of Experimental Marine Biology and Ecology **95**:271–278.

Mann, K. H., and P. A. Breen. 1972. The relationship between lobster abundance, sea urchins, and kelp beds. Journal of the Fisheries Research Board of Canada **29**:603–609.

Miller, R. J. 1985. Seaweeds, sea urchins, and lobsters: a reappraisal. Canada Journal of Fisheries and Aquatic Science **42**:2061–2072.

Morrison, D. 1988. Comparing fish and urchins grazing in shallow and deeper coral reef algal communities. Ecology **69**:1367–1382.

Ogden, J. C., R. A. Brown, and N. Salesky. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. Science **182**:715–717.

Randall, J. E. 1967. Food habits of reef fish of the West Indies. Studies of Tropical Oceanography **5**:665–847.

Sammarco, P. W. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. Journal of Experimental Marine Biology and Ecology **45**:245–272.

Sammarco, P. W., J. C. Levington, and J. C. Ogden. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata:Echinoidea): a preliminary study. Journal of Marine Research **32**:47–53.

Scoffin, T. P., C. W. Stern, D. Boucher, P. Frydl, C. M. Hawkins, I. G. Hunter, and J. K. MacGeachy. 1980. Calcium carbonate budget of a fringing reef on the west coast of Barbados. II. Erosion, sediments and internal structure. Bulletin of Marine Science **30**:475–508.

Wilke, J. W. 1985. Statistical abstract of Latin America. Volume 26. University of California at Los Angeles, Latin America Central Publications, University of California, Los Angeles, California, USA.

Witman, J. D., and K. P. Sebens. *In press.* Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine. Oecologia (Berlin).