

for food patches, one would expect a greater foraging rate in groups. This was supported by the foraging rates of juveniles (outside territories, Table 2A). Adults did not seem to benefit from groups in this way (Table 2B). Perhaps with increasing age, fish learn to find patches more efficiently when solitary, maybe having learned from the groups when young. It is also possible that the higher foraging rate juveniles experience when in groups is due to factors other than patch search time.

Our general prediction was that juveniles use groups more than adults because while they benefit equally from decreased search time, juveniles gain more from the access to damselfish territories. It seems, however, that the two ontogenetic stages use groups with similar frequency, but for different reasons. The juveniles benefit from an increase in foraging rate outside of damselfish territories while the adults gain better access to protected algae inside the territories.

Our data may have been biased by pool-

ing all fish observed and discerning between the majority, which were foraging, and a few which may have been involved in other activities (e.g. travel and hiding). Further study should include detailed time budget analysis and an investigation of the variation in patch search time across ontogenetic stage, when solitary and in groups.

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POTENTIAL LIMITATIONS TO *DIADEMA ANTILLARUM* DISTRIBUTION IN A JAMAICAN FOREREEF

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ABSTRACT (JLB)

The long-spined sea urchin, *Diadema antillarum* [Philippi] was ubiquitous at depths to 50 feet in the forereef of Discovery Bay. Since the mass mortality event of 1983, the *D. antillarum* population appears to be increasing, yet, only in waters less than 15 feet depth. We hypothesized that food quality and quantity, physiological stresses and/or availability of suitable habitat may limit the distribution of *D. antillarum* to shallow waters. When exposed to macroalgae from 15 and 45ft depths, individuals displayed no significant difference in grazing intensity. However, herbivory of enclosed urchins on the same food resource was 75% lower at 45ft compared to 15 feet. Macroalgae cover in the absence of *D. antillarum* decreased with depth. Although measurements of substrate heterogeneity showed no significant difference between the 15, 30 and 45ft sites, physical characteristics of the substrate may limit the number of suitable refuges. At the present rate of population increase, future competition for resources may force *D. antillarum* into a less preferred environment at depths greater than 15 feet.

Key Words: *Diadema antillarum* [Philippi], mass mortality, Discovery Bay, Jamaica

INTRODUCTION (ANS)

In July of 1983, populations of *Diadema antillarum* in Jamaican coral reefs suffered greater than 95% mortality (Lessios, 1988). A water-borne pathogen, the most likely agent of the epidemic, spread throughout the Caribbean eradicating the long-spined sea urchin population and producing changes in reef fish, algae and coral communities (Lessios, 1988).

Prior to the mass mortality, densities reported in Jamaican shallow reefs (< 15ft) were ≈ 15 individuals/m² (Morrison, 1988) and 6.6 individuals/m² at 45ft (Liddell, 1982). After 1983, densities at all depths were nearly 0 individuals/m². Since that time, the population of *D. antillarum* has increased close the rate of 0.02-0.11 individuals/yr predicted by Karlson and Levitan (1990) in the shallow waters. However, in waters greater than 15ft deep, popula-

tions have remained close to zero (personal observation). Because *D. antillarum* is a broadcast spawner whose larvae are capable of travelling several kilometers (Karlson and Levitan, 1990), a more uniform distribution throughout the reef might have been expected. In deeper waters, it is possible that intraspecific competition may decrease with lower population density, while resources may remain abundant. In addition, as natural predators (large Balistidae [triggerfish], Labridae [wrasses] and Scaridae [parrotfish] individuals) are absent from our site (personal observation), predation cannot adequately explain the absence of individuals from deeper waters. Therefore, although the forereef deeper than 15 feet is a potentially habitable environment, it appears to be less preferred by *D. antillarum*.

In this study we examine the current abundance of *D. antillarum* and possible factors in-

fluencing the distribution of a natural population in a Jamaican forereef environment. More specifically, we assess the viability of the deeper reef environment by testing several hypotheses which may account for the absence of *D. antillarum* in waters greater than 15ft deep.

Previous studies attempting to assess the effect of depth on *D. antillarum* have been unsuccessful (Morrison, 1988), although individuals have been observed to actively avoid deeper environments (Gilmartin and Young, 1991FSP). We hypothesize, therefore, that physical characteristics of depths greater than 15ft (i.e. pressure) may limit the distribution of *D. antillarum*. If so, we predict that individuals in deeper waters should demonstrate decreased grazing, indicative of a less preferable habitat.

The absence of *D. antillarum* at depths greater than 15ft could also be potentially explained by a decrease in either food resource quality or quantity. Although populations were distributed at depths greater than 45ft prior to the mass mortality event, densities of 45ft were $\approx 50\%$ of those at 15ft (Liddell, 1982), indicating that high population pressures (i.e. resource competition) may have potentially focused *D. antillarum* into more marginal, deeper habitats. Because algal species composition changed following the mass mortality (Lessios, 1988), it is possible that present food resources in deeper waters may be less preferred. We test the hypothesis that food quality and relative algae abundance at depths greater than 15ft may limit the distribution of *D. antillarum*.

Because *D. antillarum* found in shallow waters require three-dimensional substrates, ca-

pable of providing refuge from wave action (personal observation), substrate complexity may be a third factor limiting distribution. Although surge may decrease with depth, a spatial refuge may still be required for predator avoidance. We predict a decrease of suitable habitat structure at depths greater than 15ft, implying that deeper waters may be incapable of supporting higher populations of *D. antillarum*.

Historical evidence indicates the possibility of *D. antillarum* inhabiting depths greater than 15ft, yet, to present, there is little evidence of recolonization at these depths. A continued absence from such geographic regions of the coral reef will inevitably affect community structure. The purpose of our study is to address the potential for recolonization of deeper waters by *D. antillarum* in the Jamaican reefs and to assess possible factors limiting its distribution. Our goal is to determine whether environmental constraints prohibit re-colonization in deeper waters, or, if time is the only requirement for *D. antillarum* to re-establish itself to pre-mass-mortality abundances.

METHODS (JLB)

The study was conducted 3-9 March, 1994, on the west forereef of Discovery Bay, Jamaica. To assess the impact of depth on *D. antillarum* viability, three chicken-wire experimental cages (0.3m^2 each) were placed in a sand channel at 45ft depth, north of LTS (shallow) mooring, and three cages in a sand patch at 15ft depth, south of the same mooring.

Rocks with algal cover representative of the 15ft site were placed in all six cages, covering the entire bottom of the cage, and drawings of algal coverage were made for each enclosure. Three *D. antillarum*, taken from coral outcroppings at 15ft, were placed in each cage. The cages were sealed for the 72 hours of the trial. On 6 March, percent algal cover remaining was evaluated and quantified as: m^2 of algae consumed per urchin per enclosure.

To assess food quality between depths, all cages were moved to the 15ft site; three were filled with algae covered rocks from the surrounding area, and three with rocks covered with algae representative of the 45ft. site. Percent algal cover was pictorially recorded for each cage. Cages, again with three *D. antillarum* each, were sealed, and percent algal cover removed per individual was quantified after 72 hours.

Variation of urchin populations and physical characteristics with depth were evaluated with 50m transects at 15, 30, and 45ft depths near the M1 mooring, $\approx 400\text{m}$ east of LTS. Every 5m, a $2 \times 5\text{m}$ plot perpendicular to the transect line was surveyed for abundances of *D. antillarum* and *Tripneustes ventricosus*. The amount of algal cover in each 10m^2 plot was ranked (0-25%, 25-50%, 50-75%, or 75-100%) based on visual appraisal. Topographic complexity was evaluated by conforming a chain to the substrate along the 5m bisect line of each plot, employing the formula:

$$\text{rugosity} = \frac{\text{length of chain conformed to substrate}}{5\text{m}}$$

Differences in herbivory between depths and between algae sources were analysed with t-tests. Comparison of *D. antillarum* density with depth and spatial complexity with depth were evaluated with one-factor ANOVA. The relationship between macroalgae cover in areas uninhabited by *D. antillarum* and depth was tested with a Spearman correlation analysis, and a simple regression was performed on *D. antillarum* density in relation to spatial complexity.

RESULTS (JLB)

D. antillarum abundance varied significantly between 15ft and greater than 15ft depths ($F = 3.854$, $df = 4$, $p = 0.032$) with no long-spined sea urchins found at either 30 or 45ft depths. However, the urchin population in shallow waters appears to be increasing from recent years (Table 1).

When urchins were provided the same macroalgae diets from 15ft, grazing intensity in cages at the 15ft site was greater than that at the 45ft site ($t = 5.427$, $df = 4$, $p = 0.0056$; Figure 1). Although two urchins, in separate cages at 15ft, died during the final 24 hours of the trial, grazing calculations were based on six *D. antillarum* per cage. The cause of death was presumed to be exposure, as the urchins were unable to seek protection from the considerable amount of surge and turbulence of 3-6 March.

Macroalgal cover at all depths was dominated by *Dictyota divaricata*, *Sargassum hystrix* var. *buxifolium* and *Lobophora variegata*. *Jania adherens* and *Halimeda optunia* were present in low abundances at 45ft while low densities of

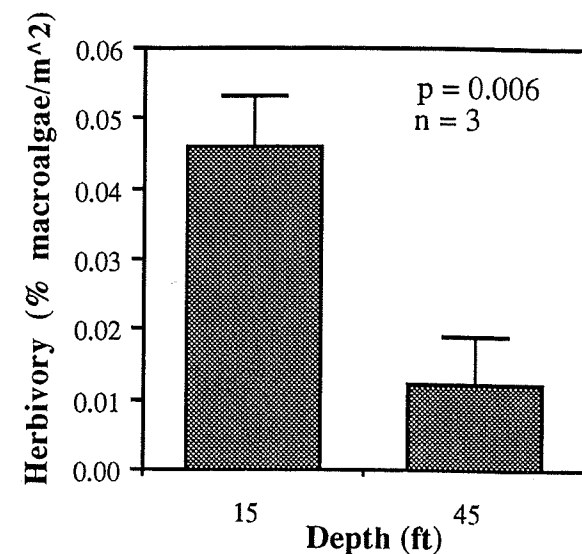


Figure 1. Amount of herbivory by *D. antillarum* at 15 and 45 ft depths, on macroalgae representative of 15 ft depth.

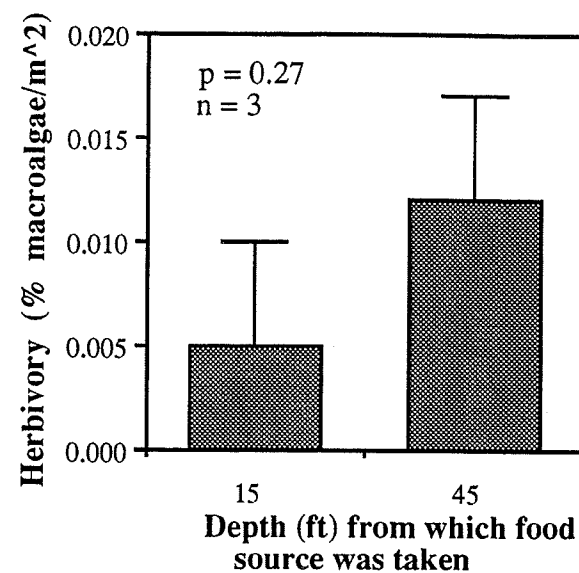


Figure 2. Amount of herbivory by *D. antillarum* at 15 ft, on macroalgae representative of different depths.

Galaxaura subverticillata, *H. optunia* and *Turbinaria turbinata* were found at 15 feet. Ranked macroalgae abundance in areas not inhabited by *D. antillarum* diminished significantly with depth (Spearman's Rho = -0.588, $z = -2.941$, $p = 0.003$).

The effects of *D. antillarum* on algal cover has been documented thoroughly (Carpenter, 1981, Lessios, 1988). However, *D. antillarum* at 15 ft appeared not to distinguish between algae from 15 or 45 ft depths as the amount of grazing was not significantly different between cages ($t = -1.265$, $df = 4$, $p = 0.275$; Figure 2).

D. antillarum density was positively correlated with increased substrate complexity ($r^2 = 0.314$, $p = 0.0239$; Figure 3). Substrata at all depths surveyed were not found to vary in structural heterogeneity based on our determination of rugosity ($F = 1.584$, $df = 4$, $p = 0.22$; ANOVA). *T. ventricosus* was found at densities of $0.056 \pm .06$ at 15 ft, $0.022 \pm .01$ at 30 ft and 0.0 at 45 feet. Those densities were compared with previous population studies (Table 2).

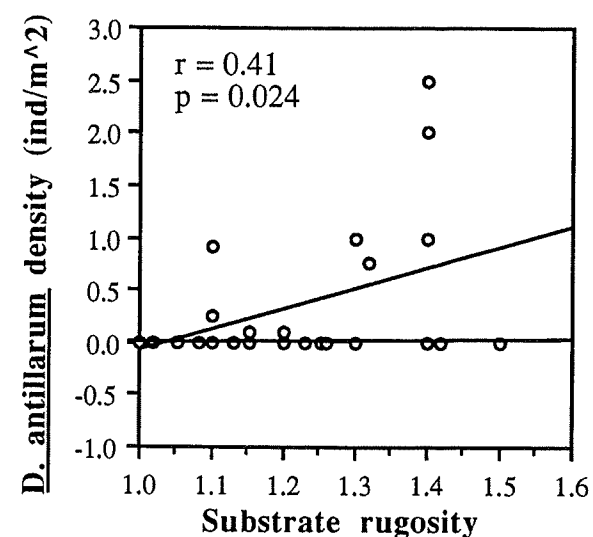


Figure 3. *D. antillarum* density in relation to substrate complexity

Table 1: Changes in *D. antillarum* density over twelve years, Discovery Bay, Jamaica (bar indicates mass-mortality event).

Year	10 ft	15 ft	20 ft	25 ft	30 ft	45 ft
1982 ¹	----	----	----	8.8±0.9	----	4.0±0.8
2	----	13.9±2.8	----	----	11.5±1.6	6.6±1.9
1983 ¹	----	----	----	10.5±1.6	----	4.7±0.5
2	----	0.2±0.4	----	----	0.0	0.0
1	----	----	----	0.1±0.1	----	0.0
1984 ¹	----	----	----	0.1±0.1	----	0.0
2	----	0.0	----	----	----	0.0
1989 ³	0.18	----	0.16	----	0.02	----
1994 ⁴	----	0.525±0.2	----	----	0.0	0.0

¹Hughes et al., 1985

²Liddell and Ohlhorst, 1986

³Dols and Walter, 1989

⁴Swanson and Bykowski, FSP 1994

DISCUSSION (ANS)

Since the mass mortality event of *D. antillarum* in 1983, the population has increased at a rate of ~ 0.05 ind/yr/m² in less than 15 ft in the Discovery Bay forereef. This falls within the range predicted by Karlson and Levitan (1990) of 0.02 - 0.10 ind/yr/m². However, at greater than 15 ft depth, the population of *D. antillarum* has remained close to zero.

In 1991, Gilmartin and Young observed an increase in the abundance of *Tripneustes ventricosus* in the West Fore Reef for the first time. It was likely the increase in *T. ventricosus* was a result of *D. antillarum* mortality, a probable competitor for resources. Data from

1994 indicates a > 85% reduction in *T. ventricosus* abundance at 15 and 30 ft depth. As Gilmartin and Young (1991) suggested, it seems likely that the re-establishment of the *D. antillarum* population is resulting in a decrease in the population of *T. ventricosus*. Although both species occur sympatrically (personal observation), it appears that *D. antillarum* is out-competing *T. ventricosus* for the shallow water niche. It is possible that a continued increase in the abundance of *D. antillarum* will force the abundance of *T. ventricosus* to return to pre-mass mortality levels. However, niche partitioning may provide for co-existence, especially if *T. ventricosus* continues a migration to deeper waters.

Table 2: *Tripneustes ventricosus* density, Discovery Bay, Jamaica.

Year	10ft	15ft	20ft	25ft	30ft	45ft
1991 ¹	0.01±0.02	0.52±0.44	0.82±0.82	0.19±0.31	0.16±0.10	----
1994 ²	----	0.056±0.06	----	----	0.022±0.01	0.0

¹Gilmartin and Young, FSP 1991

²Swanson and Bykowski, FSP 1994

Our results suggest several possible factors limiting *D. antillarum* to depths less than 15 feet. Grazing activity on the same resource from 15ft decreased 75% at 45ft compared to 15 feet. Thus, it appears that deeper waters may inhibit *D. antillarum* feeding, suggesting that waters greater than 15ft depth may be a more marginal environment. Previous authors have observed the tendency for *D. antillarum* to return to shallow waters when placed at depth (Gilmartin and Young, 1991 FSP; Morrison, 1988). This avoidance of deeper waters suggests a physiological stress on *D. antillarum*. We do not know the nature of this stress or the mechanism behind the reduction in grazing. Also, genotypic and phenotypic variation between animals occurring at different depths needs to be examined. Although our study was limited by a short time period, a small sample size, and im-precise techniques of quantifying percent algae consumed, our results and observations suggest the need for future work to address the effect of deeper environments on grazing rates.

At 15ft depth, *D. antillarum* showed a strong tendency to aggregate in areas in which substrate complexity was high. The positive correlation between density and substrate heterogeneity suggests *D. antillarum* requires a substrate capable of providing refuge from either turbulence or predators. This is supported by the observed mortality of two of nine individuals without refuge in cage enclosures during a period of high wave action. However, no difference in measurements of heterogeneity between sites suggest this does not limit *D. antillarum*

distribution in deeper substrates. One possible explanation for observing no difference in substrate complexity may be the result of our technique. At 45ft., the substrate was composed mostly of *Acropora* rubble. Although heterogeneous, cracks and crevices (potential *D. antillarum* refuges) may be much smaller than those found in more shallow water (personal observation).

When exposed to macroalgae from 15ft. and 45ft., *D. antillarum* showed no difference in grazing rates. In addition, algal species composition between the two depths showed little variance, implying that food quality likely does not limit *D. antillarum* from deeper waters. However, we observed a higher frequency of plots with less macroalgae cover in deeper waters suggesting that food quantity is lower at greater depths. In the absence of *D. antillarum*, macro-algae cover was greater in shallow waters, perhaps as a result of increased sunlight or decreased grazing pressures from herbivorous fish. Because algae cover was abundant at all sites, it is unlikely that food quantity limits *D. antillarum* distribution. This conclusion agrees with Karlson and Levitan (1990), who reported food availability does not regulate *D. antillarum* population size, but instead it is likely that slow recruitment rates prohibit rapid recolonization.

Several other possible explanations exist that may explain the absence of *D. antillarum* from depths which they historically occupied. Carpenter (1984) suggested that when densities of *D. antillarum* are low (< 5 individuals/m²), homing behavior (the tendency to forage at night and then return to the same refuge during

the day) increases significantly. As a result, as long as densities of *D. antillarum* remain below a critical level, migration of individuals to deeper waters may be impaired by homing behavior. It is possible, however, that the absence of predators may offset this increase in homing behavior (Carpenter 1984). If population densities increase, therefore, we might expect a distribution of individuals in waters greater than 15ft. once a critical density is reached and resource competition (i.e. suitable substrate, food) forces populations into a potentially less preferred habitat. In addition, Wittenberg and Hunt (1992) reported that *D. antillarum* larvae prefer clean coral substrates to settle upon. Because algae abundance decreases in patches of high *D. antillarum* density (unpublished data), larvae settlement may be favored in areas which have been already colonized and denuded by adults. As a result, colonization may be a positive feedback loop which may hinder expansion to deeper waters.

It is apparent that *D. antillarum*, ten years after the mass-mortality event, remain virtually absent from waters greater than 15ft. depth. The question thus arises, is *D. antillarum* only at the beginning of a slow colonization process or do biotic and abiotic characteristics of a previously colonized habitat limit individuals to shallow waters? Based upon our results and observations, it appears that *D. antillarum* are absent from an environment which is less preferred. However, it is likely, given the slow process of re-establishment, *D. antillarum* in future years may re-colonize depths where it was once found.

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