

## DISTRIBUTION AND SOURCES OF FISH SPECIES RICHNESS IN WEST DISCOVERY BAY

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*Abstract:* Fish communities in coral reef ecosystems exhibit tremendous diversity, perhaps due to effective partitioning of a highly diverse resource base. We conducted day and night fish censuses in turtle grass flats and the back reefs in Discovery Bay, Jamaica, to test the hypothesis that resources in the bay are both spatially and temporally partitioned. We found 88 fish species: 37 species found only in back reef habitat and 13 species found only in turtle grass. Additionally, we found 41 fish species only during the day and 21 found only during the night. Species-area curves for back reef and turtle grass habitats suggested that the back reef displayed higher species richness, as well as higher alpha and beta diversity, indicating that the putative greater structural complexity of the back reef habitat contributes more to the overall fish community diversity than the structurally simpler turtle grass.

*Key Words:* resource partitioning, fish community,  $\alpha$ - and  $\beta$ -diversity

## INTRODUCTION

Fish communities in coral reef ecosystems are highly speciose (Horn 1989), and researchers have proposed many hypotheses to explain this high degree of diversity (Begon et al. 1990). One such hypothesis is resource partitioning, in which resources are divided among species (either temporally or spatially), reducing interspecific competition and allowing greater species coexistence (Gutierrez 1998, Pitts 1991).

We observed fish populations in 2 different habitats—turtle grass flats and the back coral reef—in Discovery Bay, Jamaica. We sampled community species richness during both daytime and night-time hours to test for both spatial and temporal partitioning. By assessing the community composition overlap spatially and temporally, we hypothesized that we would find evidence for resource partitioning within the greater coral reef

fish community. We predicted that observed fish species would vary between day and night sampling in both habitats, indicating temporal partitioning. Additionally, we hypothesized that fish species would vary across habitats, showing evidence of spatial partitioning.

We also investigated the relative contributions of each habitat type to the overall fish community diversity. Determining species richness depends on the scale at which it is assessed. Therefore we attempted to quantify both alpha (mean number of species per plot) and beta (rate at which new species are included with increased samples) diversity for these two Discovery Bay habitats. We predicted that fish species richness, as well as alpha and beta diversity, will be greater in the back reef—possibly due to the increased spatial complexity found there.

## METHODS

On 24 February 2006, eight volunteer pairs observed 16 turtle grass and 16 back reef plots near the Discovery Bay Marine Laboratory for 30 minutes per plot. We observed half of the plots ( $n = 8$  turtle grass,  $n = 8$  back reef) during daytime hours between 10:00 – 12:00, and the remaining plots during night-time hours between 21:00 – 22:00. Each volunteer pair compiled a list of fish species observed at each plot. We then generated Venn diagrams to compare the overlap in species community composition between habitats and times.

We combined night and day observations within each habitat to compare each habitat's relative contribution to overall fish community diversity. We generated a species-area curve for each habitat by pooling each habitat's daytime and night-time samples and calculating the mean number of species observed in all possible combinations of 1 through 16 samples, using PC Ord v.3 software. We estimated habitat species richness by fitting a Michaelis-Menten saturation function to the data from our species-area curves:

$$y = \frac{K * x}{d + x} \quad [Eq. 1]$$

Where  $K$  is an estimate of total species richness for each habitat and  $d$  is the half saturation point of the species-area curve (Raines and Stork 2006). We estimated each habitat's beta diversity using Gleason's (1922) logarithmic model:

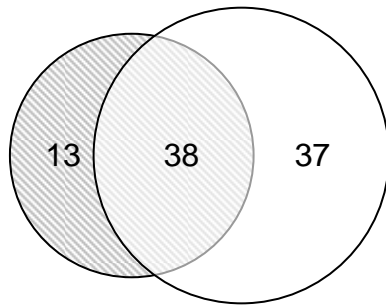
$$\log(E[S_n]) = h\log(n) + k \quad [Eq. 2]$$

where  $k$  is the y-intercept and  $h$  is slope, where greater slope equals increased beta diversity (Raines and Stork 2006).

## RESULTS

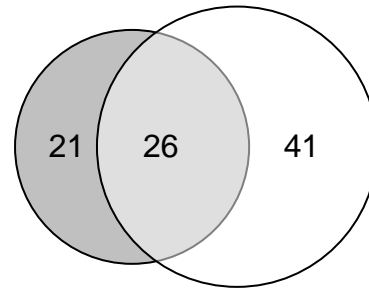
We observed a total of 88 fish species in both habitats (Appendix A). Fish species diversity was highest in the daytime back reef habitat (60 species), followed by night-time reef (38), daytime turtle grass (32) and night-time turtle grass (24). The community composition actually exhibited a high amount of overlap, with many species found in both habitat types and observed during both times of the day (Figure 1). Species overlap was highest when pooled daytime and night-time observations compared turtle grass and back reef habitats: we observed 38 species (or 42% of all species) in both habitats. Daytime and night-time spatial partitioning was approximately equivalent. We observed 37% of all diurnal species and 35% of all nocturnal species in both habitats. Turtle grass habitat displayed the great proportion of temporal partitioning. Of the 51 species observed in turtle grass, we found only 12% in both daytime and night-time sampling.

Turtle grass (left) v. Back reef (right)

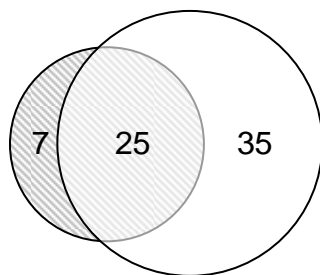


Both day and night

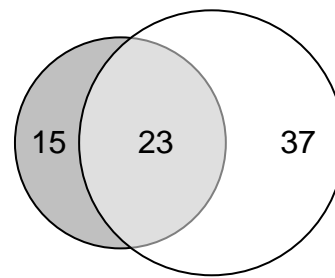
Night (left) v. Day (right)



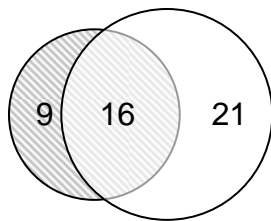
Both Turtle grass and back reef



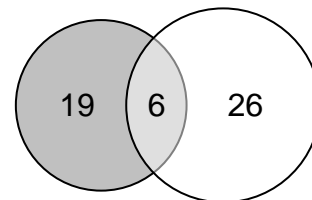
Day



Back reef



Night



Turtle grass

Figure 1. Number of fish species observed during day and night sampling in both turtle grass and back reef habitats in Discovery Bay, Jamaica. Size of circles is proportional to the total number of species observed in each population.

Back reef habitat displayed evidence of higher alpha diversity than turtle grass (mean species per sampled plot  $\pm 1$  SE; back reef =  $15.69 \pm 1.64$ , turtle grass =  $8.38 \pm 0.91$ ;  $t_{1,31} = 2.87$ ,  $P < 0.01$ ). Michaelis-Menton functions fit to our sample data (Figure 2) show that the species-area curve for back reef habitat approaches significantly greater species richness than turtle grass ( $K$  [Eq. 1],

$\pm 1$  SE; back reef =  $100.13 \pm 2.17$ , turtle grass =  $81.32 \pm 1.15$ ,  $t_{1,30} = 43.16$ ,  $P < 0.0001$ ). Beta diversity was actually higher in the turtle grass area than the back reef area (back reef:  $\log(E[S_n]) = 0.534\log(n) + 2.858$ ,  $r^2 = 0.990$ ; turtle grass:  $\log(E[S_n]) = 0.634\log(n) + 2.256$ ,  $r^2 = 0.988$ ;  $t_{1,30} = 4.49$ ,  $p < 0.001$ , Fig. 2).

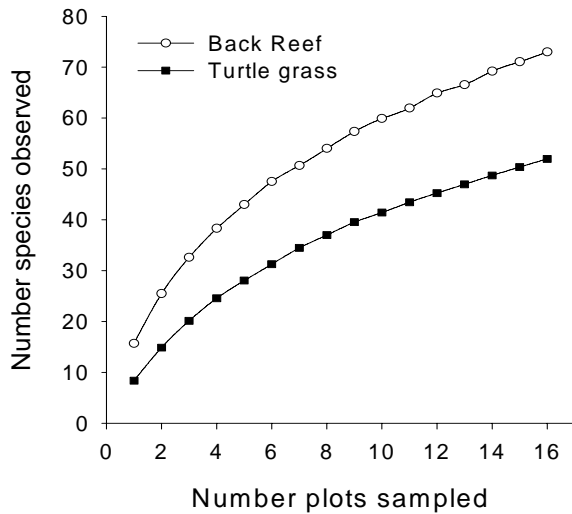


Figure 2. Species-area curves for back reef and turtle grass habitat in Discovery Bay, Jamaica, including both day and night sampling. Points represent the mean number of species found in all permutations of pooled sites, and obscure the standard error bars.

## DISCUSSION

We found evidence for spatial and temporal resource partitioning in the coral reef fish communities of Discovery Bay, yet we found more species overlap between times and habitats than would be expected had there been complete resource partitioning between species. There were generally many more species during the day, potentially among more fish species depend on vision to locate food resources, find mates, and avoid predators. The diel fluctuation in the turtle grass habitat has less species overlap than in the back reef, perhaps because turtle grass primarily represents a food resource and is not a suitable refuge from predators during rest; therefore, the changeover from diurnal to nocturnal communities is more pronounced. It is possible that the observed

temporal and spatial species overlap is an artifact of the sampling design: observers did not distinguish between active and resting fish, which may overestimate overlap in resource use. Moreover, it was more difficult to observe fish in the dark of night and species found in just one habitat may have gone undetected.

Both observed and projected species richness were far greater in the back reef habitat than in turtle grass, perhaps because the back reef is a more topographically complex habitat and provides more diverse food resources in the form of algal growth and invertebrate communities. This abundance and diversity of resources may result in a greater number of available niches for species to fill, and could explain the higher species richness. The overlap we observed in fish species' habitat use for our pooled daytime and night-time observations may be caused by fishes moving to and fro between turtle grass and coral reef habitats, using different habitats for either foraging or refuge.

The higher alpha diversity of the back reef can be explained by (1) more complex topographic structure and more diverse food resources, and (2) a combination of both foraging grounds and refuge habitats over a 24-hour period. The higher beta diversity in the turtle grass can be explained by the larger scale of topographic complexity within this habitat, with different topographies found tens of meters apart as opposed to tens of centimeters apart in the back reef.

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Dartmouth Studies in Tropical Ecology 2006

Appendix A. Fish species observed in two Discovery Bay habitat types on February , 2006.

Species	Back reef		Turtle Grass	
	Day	Night	Day	Night
Angel, French	X	X	X	
Balloonfish	X	X		X
Bass, Harlequin	X			
Basslet, Fairy			X	
Bigeye		X		
Blenny, Dusky			X	
Blenny, Hairy	X			
Blenny, Redlip	X			
Blenny, Rosey	X			
Blenny, Saddled	X			
Blue tang	X		X	
Butterflyfish, Foureye	X		X	
Cardinalfish, Dusky		X		X
Cardinalfish, Mimic		X		
Cardinalfish, Roughlip		X		X
Coney		X		
Damselfish, Beaugregory	X	X	X	
Damselfish, Bicolor	X			
Damselfish, Cocoa	X			
Damselfish, Longfin	X			
Damselfish, Three spot	X	X	X	
Damselfish, Yellowtail	X	X	X	
Damslefish, Dusky	X	X	X	
Doctorfish	X	X	X	X
Eel, Gold Stopped				X
Flamefish		X		X
Flounder, Eyed	X			
Goatfish, Dwarf		X		
Goatfish, spotted	X		X	X
Goby, Bridled			X	
Goby, Cleaning			X	
Goby, Goldspot			X	
Grunt, Bluestriped	X			
Grunt, French	X			X
Hamlet, Barred	X			
Hamlet, Black		X		
Hamlet, Blue	X			
Hamlet, Indigo	X	X		
Herring				X
Hound Fish	X			
Lizardfish, Bluestriped	X		X	
Major, Sargeant	X	X	X	
Moray, Spotted		X		
Murray, Goldentail				X
Needlefish, Keeltail	X			
Ocean surgeonfish	X	X	X	
Parrotfish, Bluelip	X			
Parrotfish, Bucktooth	X		X	
Parrotfish, Greenblotch	X			

## Discovery Bay

Parrotfish, Princess	X		X	
Parrotfish, Queen	X			
Parrotfish, Redband	X	X	X	X
Parrotfish, Redfin	X			
Parrotfish, Stoplight	X	X	X	X
Parrotfish, Striped	X		X	X
Parrotfish, Yellowtail	X			
Pinfish	X			
Pipefish, Harlequin	X		X	
Porcupinefish	X			
Porgy, Sheepshead		X		X
Ray, Lesser Electric				X
Reef croaker		X		X
Rock beauty	X			
Rock hind			X	
Sand Diver	X	X		
Scorpionfish, Spotted	X	X	X	
Sergeant, Night	X	X		
Silversides	X	X	X	X
Slippery dick	X		X	
Snapper, Glasseye		X		
Snapper, Yellow Fin	X			
Snapper, Yellow Tail			X	
Soapfish, Greater		X		
Soldierfish, Blackbar	X	X		
Squirrelfish	X	X		X
Squirrelfish, Dusky		X		X
Squirrelfish, Longjaw	X	X		X
Squirrelfish, Reef	X	X		X
Squirrelfish, Longspine	X	X		X
Stingray, southern	X			
Stingray, Yellow				X
Sweeper, Glassy		X		X
Trumpetfish	X	X	X	
Wrasse, Blackear	X			
Wrasse, Bluehead	X	X	X	
Wrasse, Clown	X		X	
Wrasse, Yellowhead	X		X	

## SEEING RED: EXAMINING THE POSSIBLE FUNCTIONS OF APYLSIA DACTYLOMELA INK

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*Abstract:* Many marine mollusks, including cephalopods and some sea slugs, eject ink when disturbed. There have been many studies investigating the possible function of sea hare (*Aplysia* spp.) ink, such as intraspecific communication and predator deterrence, but the results have been inconclusive. We investigated two possible functions of spotted sea hare (*Aplysia dactylomela*) ink: 1) defense against the giant sea anemone (*Condylactis gigantea*) and 2) communication between sea hare individuals in response to the presence of a predator. We found that, although spotted sea hares released ink in response to coming in contact with an anemone, their ink did not prevent anemones from ingesting pieces of spotted sea hare tissue. We found that spotted sea hares respond to ink only over very short distances. This may be ecologically significant as spotted sea hares were often found aggregated in tight mating groups. Thus, ink may function in intraspecific communication. Finally, we also evaluated whether spotted sea hares preferentially ate certain algal species, and determined that their distribution in the field is not driven by the distribution of their preferred food.

*Key Words:* *Aplysia Dactylomela, communication, defense, ink, mollusca, spotted sea hares*

### INTRODUCTION

Marine animals employ a wide range of defenses to avoid predation. Many mollusks, including cephalopods and some sea slugs, eject ink when disturbed. Spotted sea hares (*Aplysia dactylomela*) are nocturnal gastropods that eject clouds of red ink, which they produce from red algae in their diet. Researchers have hypothesized the ink is for defense (DiMatteo 1982), communication (Fiorito and Gherardi 1990), or elimination of sequestered algal toxins (Chapman and Fox 1969). Previous studies have focused on ink's role as a defense against predators such as anemones and decapods, and results have suggested that ink is effective against some, but not all, predators (Tobach et al. 1989, DiMatteo 1982, Rogers et al. 2000).

Little of the published work on the ink of sea hares has focused on the spotted sea hare, which is common on the west

back reef of Discovery Bay, Jamaica. Previous studies suggest that the ink of spotted sea hares is unpalatable to crabs (DiMatteo 1982) and may be used to communicate with conspecifics (Hang et al. 1997). We tested whether ink deters predation by the giant sea anemone (*Condylactis gigantea*) or acts as an alarm signal to warn conspecifics of potential danger. If ink is a defense against the giant sea anemone, we expected giant sea anemone individuals exposed to ink to reject intact sea hares or pieces of sea hares. If ink functions as an alarm signal, we expected that spotted sea hares will respond to conspecifics' ink over distances by which they are likely to be separated from one another in the field.

If ink functions in defense or communication, the distribution of spotted sea hares in the field may reflect access to the red algae from which they sequester ink-producing compounds. We tested for

algal preferences in the laboratory and observed in the field whether sea hares were found exclusively near these species. Sea hares may preferentially feed on those red algae from which they produce their ink, in which case their distribution in the field may reflect the distribution of preferred algal species.

## METHODS

To test the use of ink as a defense against predators, we offered both live sea hares and pieces of sea hare tissue to giant sea anemones. We collected 23 spotted sea hares from the west back reef of Discovery Bay, Jamaica on 28 February, 2006. We performed the following trials: 3 trials offering live sea hares containing ink, 6 trials offering live sea hares drained of all their ink, 2 trials offering approximately 8 cm<sup>3</sup> pieces of sea hare tissue to the anemone without adding ink, 2 trials adding 1.5 ml of ink into the anemone while it was feeding on a tissue piece, 4 trials adding 50 ml of ink into the anemone while it was feeding on a tissue piece, 4 trials adding 5 ml of ink into the anemone without feeding it, and 2 trials adding 10 ml of ink into the anemone without feeding it.

To determine if ink has a function in intraspecific communication, we conducted experiments with 20 individuals in laboratory tanks. We added a 10 mL solution of either saltwater (control), 1% ink, 10% ink, 50% ink, or pure ink with a syringe. We used individual sea hares more than once, but waited at least 6 hours between trials. We added the treatments in close proximity to each individual and observed their responses. Additionally, we

performed each treatment once with ink collected from sea hares in the field, and once with ink collected from each particular individual. We waited half an hour between extracting ink from a sea hare and exposing ink to the same individual. We evaluated which treatments spotted sea hares responded most often using a chi-square test.

We investigated the distribution of spotted sea hares within the west back reef of Discovery Bay with two 20-minute searches in three habitats: shallow turtle grass near the shoreline, rocky substrate near the shoreline, and reef within 20 m of the reef crest. We recorded the number of sea hares found and whether individuals were solitary or in groups.

We evaluated the food preferences of spotted sea hares in the laboratory to see if there is a relationship between distributions of preferred algal species and spotted sea hares. We performed one cafeteria experiment with algae collected from the back reef and one with algae collected from near the shoreline. In these we placed 20 g (wet mass) each of 15 different algal species into tanks containing three spotted sea hares, and after 24 hours we removed and weighed the algae again to determine mass eaten. We also placed 20 g of each algal species in a control tank without spotted sea hares to determine changes in algal mass not due to sea hare grazing.

## RESULTS

Feeding trials with live spotted sea hares indicated that sea hares were equally capable of escaping giant sea anemones regardless of inking ability. The three

spotted sea hares capable of releasing ink when introduced to giant sea anemones did release ink upon contact, yet even spotted sea hares without ink managed to escape without apparent injury. However, sea hare tissue was a palatable food item for giant sea anemones. In all eight trials in which sea hare tissue was fed to an anemone, the anemone consumed the entire portion. The presence of spotted sea hare ink did not influence giant sea anemone feeding: anemones did not respond to ink in any concentration.

Spotted sea hares did respond to the presence of ink, and were significantly more likely to respond to ink at 100% and 50% concentrations than 10% and 1% concentrations ( $X^2 = 41.4$ ,  $df = 3$ ,  $P < 0.001$ ; Fig. 1). Responses consisted of withdrawing the head, contracting the body, and closing the parapodia. Individual spotted sea hares responded similarly ( $X^2 = 17.8$ ,  $df = 19$ ,  $P = 0.53$ ) and did not respond differently to their own ink than to the ink of others ( $X^2 = 1.48$ ,  $df = 1$ ,  $P = 0.22$ ).

We found significantly more spotted sea hares near the shoreline than on the back reef ( $X^2 = 19.9$ ,  $df = 2$ ,  $P < 0.001$ ), with 13 spotted sea hares found on rocky substrate near the shoreline, 16 found in habitat dominated by turtle grass near the shoreline, and 0 found on the back reef. Thirteen of the 29 spotted sea hares observed were aggregated, and all but 2 of these were mating.

Lab experiments found that spotted sea hares selectively feed on algae ( $X^2 = 131.1$ ,  $df = 14$ ,  $P < 0.001$ ; Fig. 2), preferring mostly noncalcareous red algae and some noncalcareous green algae. They did not feed on any brown algae. The change in the

mass of the control algae was negligible. Preferred algal species were abundant in all areas sampled.

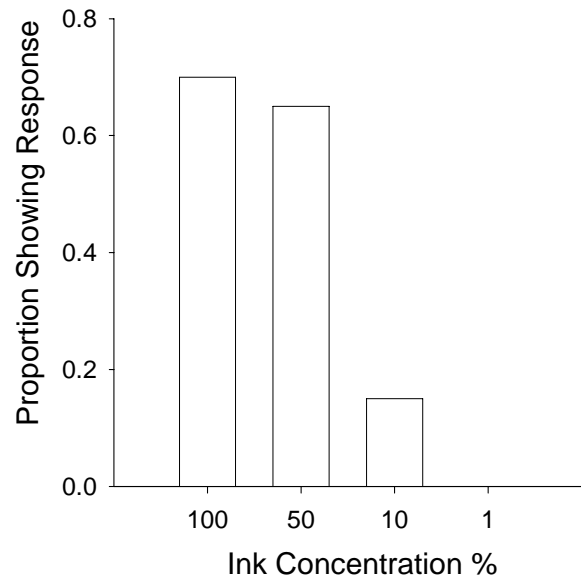


Figure 1. The percentage of *Aplysia dactylomela* that responded to being squirted with ink at different concentrations. A response was defined as a sudden change in behavior that involved withdrawing its head, balling up, or closing its parapodia.

## DISCUSSION

Ink likely functions as a defense, but was ineffective against the giant sea anemone. All individuals with ink ejected it upon contact with a giant sea anemone. However, giant sea anemones did not consume whole adult spotted sea hare regardless of whether they released ink, and ink did not deter them from eating smaller pieces of spotted sea hare tissue. Ink may function as a general predator deterrence method and is released against all perceived threats, regardless of efficacy. If ink serves as an alarm signal to conspecifics, our findings suggest that its role is likely limited. Individuals retracted

their heads and other body parts when exposed to high concentrations of either their own or other individuals' ink, suggesting that ink could be used to induce a defensive posture in nearby conspecifics. Alternatively, posture changes in response to ink may occur in response to the noxious compounds in ink and not reflect anti-predator behavior. Because spotted sea hares did not respond to low concentrations of ink, there seems to be a limited range (centimeters) over which ink may be used to communicate between individuals. Moreover, individuals did not display different responses to their own ink than to the ink of conspecifics, suggesting that the alarm signal is not directed. We found spotted sea hares aggregated in nearly half of our field observations, suggesting that they are often close enough to be able to detect one another's ink. However, the majority of these individuals were mating, which may occur only at certain periods.

We found no evidence that the distribution of spotted sea hares is correlated with the distribution of noncalcareous red algae, their preferred food. We did not find spotted sea hares in the back reef, even though individuals readily ate algae collected from there. This suggests that their absence in this region is more likely the result of other biotic conditions such as predation of young or adults or abiotic conditions such as greater water turbulence.

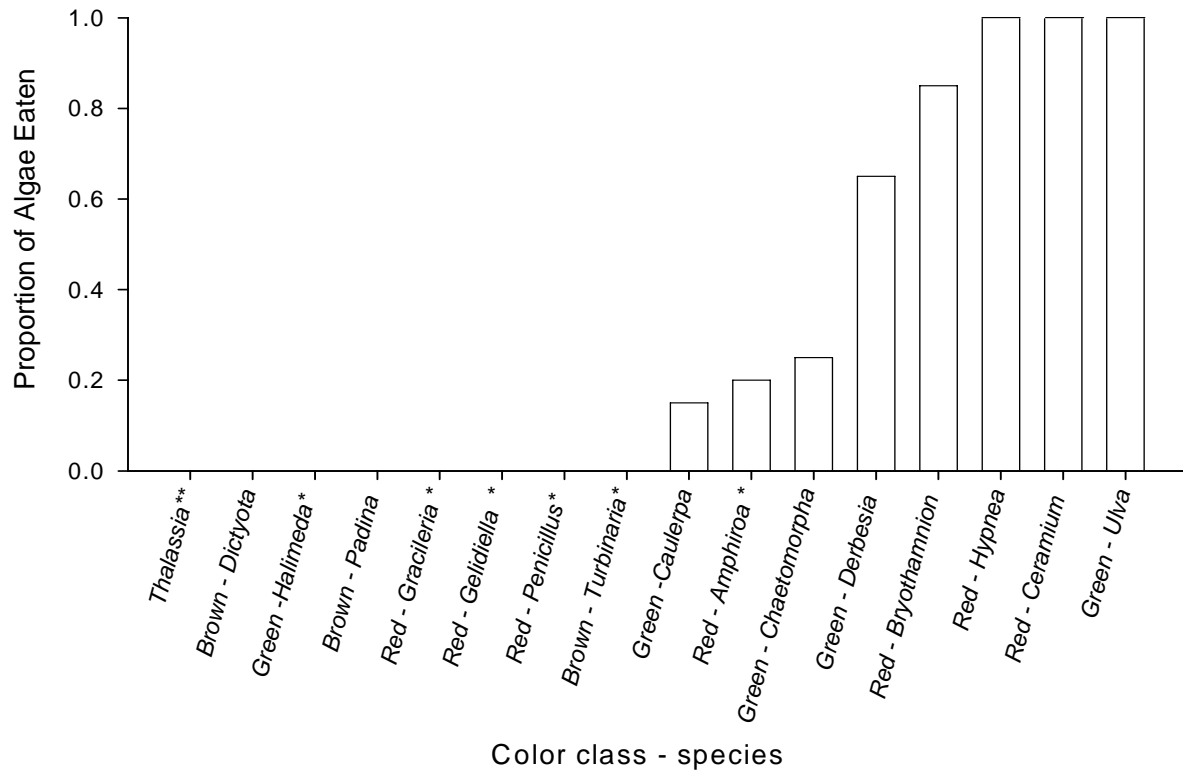


Figure 2. The proportion of algae eaten by *Aplysia dactylomela* after 24 hours in a lab setting exposed to 20 grams of each type of algae. An asterisk denotes calcareous algae, while all others are noncalcareous. \*\**Thalassia* is a true plant rather than an algae.

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# MECHANISMS AFFECTING THE COLONIZATION OF AN ARTIFICIAL SUBSTRATE BY MARINE INVERTEBRATES

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*Abstract:* Understanding the mechanisms regulating the colonization of marine reef organisms aids predictions for how these systems will respond to disturbance. Many marine invertebrates are either completely planktonic, or have complex life cycles which include a planktonic larval stage. The colonization of vacant settling sites and new reef patches by these organisms may be affected by distance from a coral reef source population and by predation. To test for effects of distance from a reef source and predation pressure, we set out artificial colonization sites (bristle brushes) that were exposed to or screened from predators at different distances from a reef. We observed the fish in the vicinity of our study area to assess whether the abundance and diversity of predators changes with distance from reef. We found that both the abundance of marine invertebrate colonizers decreased with distance from reef, and that the abundance and diversity of predators sharply decreased with distance from the reef. We found a significantly higher abundance and diversity of invertebrate colonizers on artificial colonization sites excluded from predators across all distances. Therefore, post-colonization predation pressure may cause high mortality on these colonizing invertebrates, and thus contribute to structuring marine invertebrate communities.

*Key Words:* invertebrate, coral reef, colonization, predation, artificial colonization site

## INTRODUCTION

Understanding the dynamic mechanisms contributing to the vitality of coral reefs is necessary to predict the consequences of habitat destruction and fragmentation on patterns of species diversity (Munday 2004). Reestablishment of coral reef communities is dependent on successful colonization by marine organisms.

Many marine organisms are either entirely planktonic, or have evolved a complex life cycle which includes a planktonic larval stage. These planktonic organisms may exhibit diel vertical migrations during which they seek benthic refuges (settling sites) from predators during the day and move into the water column to feed at night. This may create

invertebrate communities linked by migration and dispersal that differ in their abundance and diversity due to varying local factors. Colonization of vacant settling sites and new reef patches may depend on ocean currents, distance between the settling site and a source population, habitat preference, and invertebrate predators foraging either in the water column (pre-colonization mortality) or on the benthos (post-colonization mortality).

The abundance and diversity of organisms colonizing available substrate will depend on the relative strength of the factors involved (Fig. 1). If the effect of predation is greatest on planktonic individuals that travel the farthest from the reef (thus spending the longest period of time exposed to predators) the abundance and/or diversity of invertebrate colonizers

will decrease with distance from the source (Fig. 1A). An equally likely possibility may be that colonizers are dispersal limited. If the reef is the source, and if dispersal away from the reef is limited, the pattern of colonizer abundance would appear the same as one with dominant pre-colonization predation (Fig. 1A).

If planktivorous fish predators restrict foraging to source areas (Belmaker et al. 2005), predation pressure will be highest closest to the source, and diversity and/or abundance of invertebrate communities will increase with increasing distance from the source (Fig. 1B). However, if pre-colonization and post-colonization predation pressure synchronously, colonizer abundance and diversity would peak at an intermediate distance from the source (Fig. 1C). If planktonic invertebrates have high dispersal abilities, a mixing of planktonic invertebrates from distant sources could result in a dampening of the effect of a single source on colonization rates. Therefore, diversity and abundance of colonizers would not change with distance from any one source.

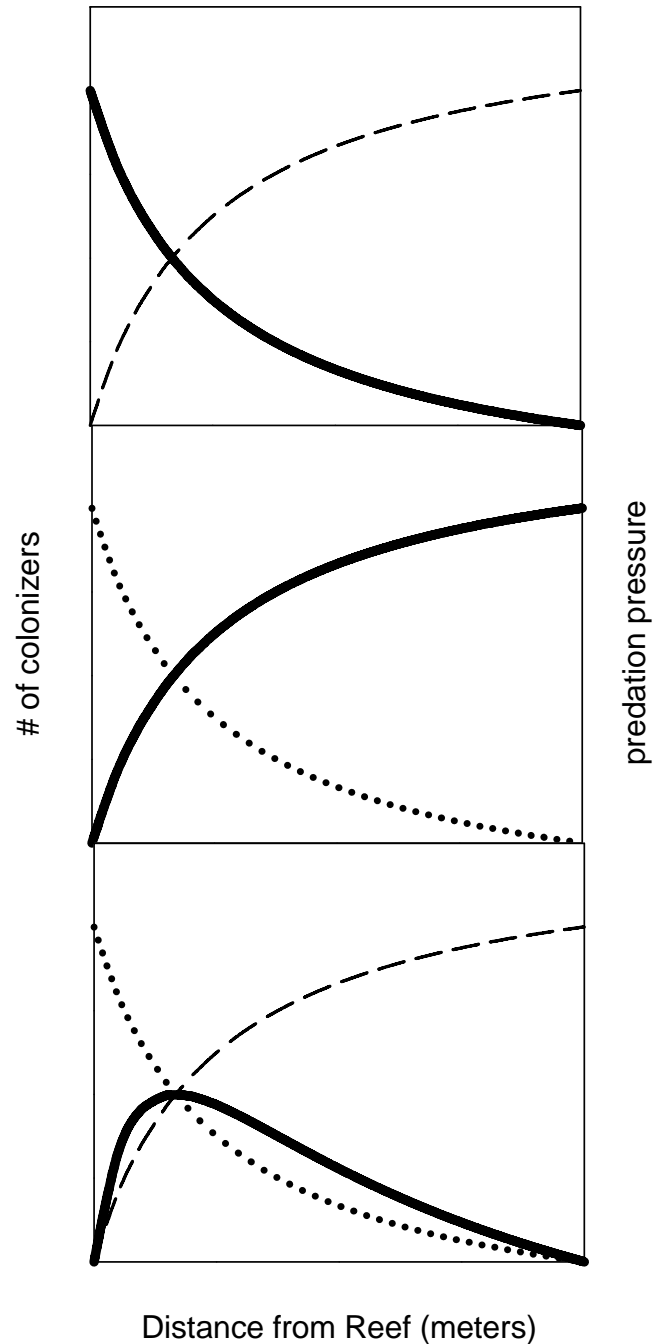


Figure 1. Potential relationship between total invertebrate colonizer abundance (solid line) and A) dominant pre-colonization predation pressure (dashed line) (Note: pattern of colonizer abundance also consistent with dispersal limitation from source), B) dominant post-colonization predation pressure (dotted line), and C) the combination of both pre- and post-colonization pressure, with increasing distance from a coral reef.

We investigated invertebrate colonization of artificial colonization sites and distribution of vertebrate predators at varying distances from a reef source to: 1) determine whether the abundance and diversity of marine invertebrate colonizers on artificial settling sites is affected by distance from a large reef, 2) establish whether the abundance and diversity of potential predators on these invertebrate colonizers changes with distance from the main reef, and 3) determine whether post-settlement predation may affect the abundance and diversity of colonizers and 4) whether post-settlement predation varies with distance from the main reef.

## METHODS

### *Construction of artificial colonization sites (ACS)*

We used twenty-four 10 x 3.5 cm cylindrical bristle brushes as artificial colonization sites (henceforth ACS) (Fig. 2). Using 1.25 cm chicken wire, we created cylinders of 10 cm diameter around half of the brushes to serve as predator exclusion cages. These cages were closed at both ends, and the brushes were suspended in the middle using wire. We attached four bolts to the bottom of each bristle brush to anchor the ACS to the benthos. We also used a small foam float attached to the top of each exclusion cage or non-exclusion brush with 25-30 cm of twine to hold the ACS upright under water.

### *Placement and retrieval of ACS*

On 3 March 2006, we used SCUBA to place 24 ACS units in large sandy channels within coral fore reef of Discovery Bay,

Jamaica. We placed two ACS units, one caged and one uncaged, 2 m apart, at each of 0, 5, 10 and 20 m from the reef along three transects running perpendicular to the reef edge in approximately 20 m of deep water. Transect 1 was located at Dancing Lady and the other transects were at Mooring 1. We visually inspected the

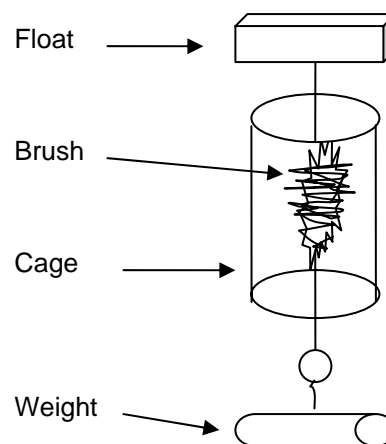


Figure 2. ACS device

transect to ensure that no other coral reef wall or patch was within 20 m.

We retrieved all ACS after 72 hours. Assistants helped cut buoys and bolts and placed each ACS into two Ziploc bags to prevent loss of fauna. In the wet laboratory, we filtered the water in the bags through a 153  $\mu\text{m}$  mesh. We then rinsed each brush with two seawater washes followed by two freshwater washes, and ran these washes through the mesh. We preserved the invertebrates and detritus retained on the mesh filter in 10% formalin. We then we sorted invertebrates by taxon and size class using dissecting microscopes.

### *Spatial distribution of fish predators*

While the ACS units were deployed we observed the abundance and species of

fish present for 10 minutes in 10 m<sup>2</sup> areas located at 0 to 5 m, 5 to 10 m, and 15 to 20 m intervals along each transect. We determined potential fish predators on invertebrates based on feeding guilds described by Randall (1967).

### Analysis

To determine if invertebrate colonization were non-random with respect to distance from reef or predator exclusion, we investigated how distance from reef, ACS type (caged and uncaged), and the interaction between distance and ACS type affected colonizer abundance, taxa richness, taxa diversity, and taxa size by running a two-way ANOVA for each. To calculate taxa diversity of the colonizer community, we used the Gini diversity index:

$$D = 1 - \sum_{i=1}^n p_i^2 \quad [Eq. 1]$$

Where n = taxa  $p_i$  = fraction of individuals in the sample that represents taxon i.

To determine the directionality of invertebrate colonization patterns for abundance, we ran an *a priori* linear contrast predicting a linear trend with decreasing abundance of colonizers with distance from reef (JMP 5.0.1).

## RESULTS

We counted 848 total invertebrates distributed across 10 taxa: copepod, amphipod, isopod, decapod, mysid, polychaete, medusae, gastropod, nematode, echinoderm.

The abundance of invertebrate colonizers decreased with distance from reef edge (ANOVA;  $F_{3,16} = 3.25$ ,  $P = 0.05$ : *a priori* linear contrast;  $F_{1,16} = 6.92$ ,  $P = 0.02$ ), and was significantly greater in predator exclosures ( $F_{3,16} = 8.63$ ,  $P = 0.01$ ; Fig. 3). However, the interaction of distance and

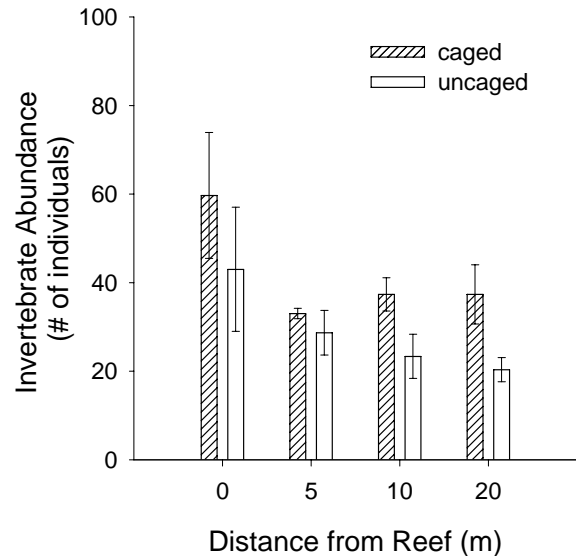


Figure 3. Mean invertebrate abundance ( $\pm 1$  SE) after 72 hours on caged and uncaged artificial colonization sites placed at 0, 5, 10 and 20 m from large coral reefs in Discover Bay, Jamaica. Abundance decreased significantly with distance from reef ( $F_{3,16} = 3.25$   $P = 0.05$ ) and was significantly higher in sites excluded from predators ( $F_{3,16} = 8.63$   $P = 0.01$ ).

ACS type ( $F_{1,16} = 0.41$ ,  $P = 0.74$ ) did not affect colonizer abundance.

Neither distance ( $F_{3,16} = 0.65$ ,  $P = 0.59$ ), ACS type ( $F_{1,16} = 2.23$ ,  $P = 0.16$ ) nor the interaction ( $F_{3,16} = 0.77$   $P = 0.53$ ) between distance and ACS type affected invertebrate taxa richness. Colonizer diversity was greater in caged than uncaged ACS ( $F_{1,16} = 12.38$ ,  $P = 0.003$ ), but distance from reef edge ( $F_{3,16} = 0.32$ ,  $P = 0.81$ ), and the interaction between distance and ACS type ( $F_{3,16} = 1.05$ ,  $P = 0.40$ ) did not affect diversity of the colonizing community. These trends were consistent across all size classes for

the most abundant taxa (copepod, amphipod, and polychaete) (all  $P < 0.04$ ).

We observed 406 total fish visitors among 34 species at our transects, with 354 individuals identified as potential invertebrate predators. Predation pressure was concentrated at the reef, with a sharp decrease in abundance and diversity of predators with increasing distance from the reef (Table 1).

## DISCUSSION

Our results indicate that the abundance of marine invertebrate colonizers on ACS decreases with distance from the coral reef, which may serve as the source population for dispersing planktonic organisms. This trend follows the one predicted by colonizer abundance if pre-colonization predation pressure increases with distance from a source reef (Fig. 1A). However, it is the same trend predicted if invertebrate colonizers are dispersal limited (Fig. 1A). Thus, our results cannot distinguish between these two mechanisms.

Our two methods of examining predation pressure provided contrasting results. The sharp decline in observed

potential predators with distance from the reef suggests that predatory fish have a preference for three dimensional structure provided by a coral reef, and that distance from a reef may be a major factor affecting marine reef fish distribution. This may lead to predation pressure decreasing with increasing distance from edge. Yet, colonizer abundance also decreased with distance from the reef, and we found a similarly higher abundance and diversity of invertebrate colonizers on predator-excluded ACS across all distances. Therefore, though it appears that post-colonization predation pressure (as measured with predator-exclusion cages) strongly influences invertebrate populations after colonization, we found no variation in post-colonization predation with distance from the reef. This result is in contrast with our observations on spatial distribution of predators. However, it is possible that our exclusion cages may have led to artifacts (effects due not only to predator exclusion but other factors), for example cages may create a more hospitable microclimate for colonization (Sale 1991). Our study does not distinguish effects of predation versus caging artifacts.

TABLE 1. Observations of potential predators on invertebrate colonizers (fish predators were observed during 10 minute intervals) with increasing distance from the reef source at three transects in two sites (Dancing Lady, Mooring 1) in Discovery Bay, Jamaica.

Site	Transect	Distance from reef	# of fish observed	# of fish species observed
Dancing Lady	1	0	61	15
Dancing Lady	1	5	7	2
Dancing Lady	1	15	0	0
Mooring 1	2	0	158	21
Mooring 1	2	5	0	0
Mooring 1	2	15	5	1
Mooring 1	3	0	123	23
Mooring 1	3	5	0	0
Mooring 1	3	15	0	0

The results of our study suggest that both distance from a source reef and predation, both pre- and post-colonization, may serve as important underlying regulatory mechanisms affecting the colonization and survival of populations of marine invertebrates. Based on our conclusion that abundance of invertebrate colonizers is affected by distance from the coral reef or source, it may be useful to pursue the application of island biogeography theory (Belmaker et al. 2005) to understand the effect of distance on the recruitment of marine invertebrates to potential settling sites. It will be important to consider the effects of these mechanisms on successful re-establishment of coral reef communities after disturbance.

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## FACTORS DRIVING FISH COMMUNITY COMPOSITION ON PATCH REEF ISLANDS

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*Abstract:* Large, continuous coral reefs support diverse fish communities, yet the fish community composition of nearby patch reef islands can differ noticeably from the main reef. Island biogeography theory predicts that species richness, abundance, and diversity will increase with increasing patch reef size and distance to a reef-crest source. Alternatively, patch reef species richness, abundance, and diversity may increase with patch size and distance from the reef crest due to decreased predator abundance and diversity away from the reef crest. We tested these somewhat competing hypotheses by investigating patch reef-fish communities in Discovery Bay, Jamaica, and tried to determine which characteristics of patch reefs (distance from reef crest, area, or topographical complexity) are most important in driving fish community composition. We did not find complete support for either hypothesis. The patch reef network in Discovery Bay does not appear to be a simple island system as assumed by both hypotheses, perhaps because overfishing has altered the larger fish community and patch reefs do not function strictly as islands. Patch reef area was the strongest factor driving fish community composition, with species richness and total abundance increasing with area. Species richness and abundance also increased with the interaction between area and complexity. As coral reef communities continue to decline from a combination of natural and anthropogenic pressures, an understanding of the mechanisms driving fish community composition may be crucial for effective management of coral reef fish populations.

*Key Words:* coral patch reefs, island biogeography, fish community composition

## INTRODUCTION

Coral reefs support abundant and diverse fish communities. In the back reef of Discovery Bay, Jamaica, fish communities occur on the coral reef crest mainland and on different-sized patch reef islands, separated from the reef crest by an expanse of turtle grass, where barracuda and other piscivorous fish hunt. Preliminary observations suggested that fish community composition differed both among patch reefs and between the patch reefs and the continuous reef crest. We investigated the relative importance of three putative mechanisms driving the diversity and abundance of fish communities on patch reefs: patch reef area,

topographical complexity, and distance from the reef crest.

The equilibrium theory of island biogeography (IBG: MacArthur & Wilson 1967) may explain how fish community composition varies among patch reef islands associated with the coral reef mainland. The theory predicts that island species richness will decrease with increasing distance from a mainland source because more remote islands receive fewer immigrants. An addition to the theory known as the target effect suggests that species richness will increase with island size because large islands are larger targets for immigrants from the mainland (Whitehead & Jones 1969).

We hypothesized that fish species richness on patch reefs will increase with increasing patch reef area and proximity to the continuous coral reef crest. We also hypothesized that fish abundance and diversity would follow similar trends and increase with island size and proximity to the reef crest.

Alternatively, fish species richness, abundance and diversity may increase on patch reefs located farther from the reef crest. In contrast to IBG theory, Belmaker et al. (2005) found that species richness on isolated patch reefs increased with distance from a natural, continuous fore reef, because predators may be more abundant and diverse on continuous reefs where fish populations are larger and can support more predators. Isolated patch reefs farther from the continuous reef crest may provide a refuge from predation and thus harbor higher species richness, abundance, and diversity than proximate patch reefs of equal size. Because predator abundance and diversity may also increase with increasing patch reef area, large patch reefs may have decreased species richness, abundance and diversity.

Small reef fish may have more success avoiding predators in patch reefs with greater structural complexity, if greater complexity offers fish more refuge sites. Complex patch reefs may also support a larger food base due to a higher recruitment of algae and marine invertebrates (Almany 2004; Bizzarro 1992). Therefore, we hypothesized that species richness, abundance and diversity will increase with increasing topographical complexity of patch reefs.

## METHODS

On 3-5 March 2006, we identified patch reefs by following four 20 x 50 m transects perpendicular to and 10 m from the reef crest, and selecting patch reefs along each transect that were isolated from one another by at least 2 m. To avoid confounding the reef crest source of fish with any potential shore source, we only observed patches in the section of reef separated from the shore by a large, deep section of open water.

We measured the length, width, complexity, and distance from the reef crest of each patch reef. The shape of the patch reefs generally resembled an ellipse, so we approximated patch reef area with the formula  $\pi \times \text{length} \times \text{width}$ . We determined patch reef complexity by tracing the topographical surface of each patch reef with a metal chain along the same lines at which we measured length and width. We then generated a complexity index (rugosity) for each patch reef using the equation  $\text{rugosity} = \text{complexity} / [(2 \times \text{height}) + (\text{length or width})]$  and averaging the rugosity of length and width measurements.

We monitored each patch reef for 5 minutes, recording all observed fish and determined the total fish abundance and species richness of each patch reef. We used these data to calculate the Gini diversity index,

$$I = 1 - \sum_{i=1}^n p_i^2$$

[Eq. 1]

for each patch reef, where  $I$  is the probability that two randomly selected individuals from a community are of different species, and  $p$  is the proportion of individuals on a patch reef belonging to one species.

We analyzed the effect that patch reef area, complexity, and distance from the reef crest had on patch reef species richness, abundance, and diversity by using a simple linear model in JMP 5.0.1. We checked for covariation of predictors and transformed data where necessary to meet the condition of normality.

## RESULTS

We observed 40 patch reefs with areas varying from 0.10 m<sup>2</sup> to 16.6 m<sup>2</sup> at distances of 11.5 m to 66 m from the reef crest. We found patch reefs supporting 0 to 86 fish and up to 12 species of the 26 total fish species we observed.

Patch reef area was the strongest factor explaining fish community composition: increasing patch reef area predicted increasing species richness ( $F_{1,39} = 7.63$ ,  $P = 0.01$ ) and greater abundance ( $F_{1,39} = 12.40$ ,  $P < 0.01$ ). Species richness and abundance also increased with the interaction between increasing patch reef complexity and area (richness:  $F_{1,39} = 4.29$ ,  $P = 0.05$ , abundance:  $F_{1,39} = 6.65$ ,  $P = 0.01$ ), but not with complexity alone ( $P > 0.45$ ). Distance from reef alone was not a predictor of richness, abundance, or diversity (all  $P > 0.15$ ).

Although abundance increased with patch reef area, the relative abundance of fish (# fish / m<sup>2</sup>) decreased with increasing patch reef area ( $F_{1,37} = 5.20$ ,  $P = 0.03$ ; Fig. 1).

Similarly, relative species richness decreased with increasing patch reef area ( $F_{1,37} = 17.3$ ,  $P < 0.001$ ; Fig. 2).

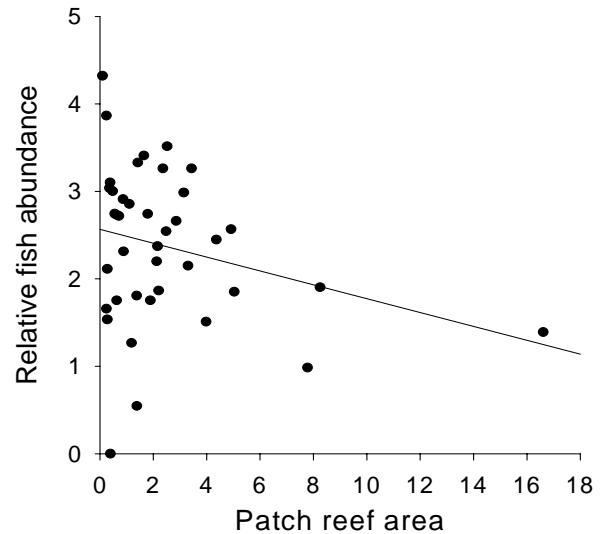


Figure 1. Relative fish abundance,  $\ln [(fish\ abundance / patch\ reef\ area) + 1]$ , as a function of reef patch area in the back reef off of Discovery Bay Marine Laboratory, Jamaica. Relative fish abundance decreases with increasing patch reef area ( $r^2 = 0.12$ ,  $df = 37$ ,  $P = 0.03$ ).



Figure 2. Relative fish species richness,  $\ln [(fish\ species\ richness / patch\ reef\ area) + 1]$ , as a function of reef patch area in the back reef off of Discovery Bay Marine Laboratory, Jamaica. Relative fish species richness decreases with increasing patch reef area ( $r^2 = 0.32$ ,  $df = 37$ ,  $P < 0.001$ ).

Table 1. Effect of various patch reef characteristics (patch reef area, topographical complexity, and distance from reef crest) on (A) fish species richness, (B) total fish abundance [ $\ln(\text{fish abundance} + 1)$ ], and (C) Gini diversity index [ $\ln(\text{Gini diversity index} + 1)$ ], for reef patches extending in from the back reef at Discovery Bay Marine Laboratory, Jamaica. Statistics were generated using a general linear model of patch reef characteristics and interactions between the characteristics. Boldface type indicates significant effect.

A. Effect on fish species richness			
Effect	Sum of squares	F <sub>1,39</sub>	P
<b>Area</b>	<b>42.7</b>	<b>7.63</b>	<b>0.01</b>
Complexity	2.91	0.52	0.48
Distance	12.2	2.18	0.15
<b>Area*Complexity</b>	<b>24.0</b>	<b>4.29</b>	<b>0.05</b>
Area*Distance	1.34	0.24	0.63
Distance*Complexity	2.89	0.52	0.48
Distance*Area*Complexity	0.75	0.13	0.72

B. Effect on normalized total fish abundance			
Effect	Sum of squares	F <sub>1,39</sub>	P
<b>Area</b>	<b>8.69</b>	<b>12.4</b>	<b>0.001</b>
Complexity	0.27	0.38	0.54
Distance	0.92	1.32	0.26
<b>Area*Complexity</b>	<b>4.65</b>	<b>6.65</b>	<b>0.01</b>
Area*Distance	2.36	3.38	0.08
Distance*Complexity	0.08	0.12	0.74
Distance*Area*Complexity	0.46	0.66	0.42

C. Effect on normalized Gini diversity index			
Effect	Sum of squares	F <sub>1,38</sub>	P
Area	0.06	1.72	0.20
Complexity	0.03	0.80	0.38
Distance	0.003	0.10	0.76
Area*Complexity	0.02	0.49	0.49
Area*Distance	0.04	1.18	0.29
Distance*Complexity	0.001	0.04	0.84
Distance*Area*Complexity	0.03	0.90	0.35

## DISCUSSION

We did not find complete support for either of the competing hypotheses potentially explaining how patch reef area and distance from the reef crest should influence fish community composition. Patch reef species richness and abundance increased with patch reef area, consistent with IBG theory. However, large patches hosted fewer species per unit area than small patches. Therefore, we could not distinguish between the hypothesis that

large islands support more abundant, speciose fish communities and the possibility that abundance and species richness simply increased with increasing sample area, a result that would have been expected regardless of whether patch reefs functioned as islands.

The lack of direction in the effect of distance from reef crest on community composition supports neither IBG theory nor the predator risk hypothesis of Belmaker et al. (2005). We suggest that the severe overfishing in Discovery Bay has

removed many top predators from the ecosystem, altering the effects of patch characteristics on fish community composition. For instance, in contrast to Belmaker et al. (2005), predator density at Discovery Bay may be equally low throughout the back reef. Therefore, more distant islands may not provide increased isolation from predators, and there is no trend of corresponding increased fish species richness. Predator scarcity also allows for an increased flow of fish both between patch reefs and between the reef crest and the patch reefs; thus these patch reefs may not act as isolated islands. If there is high species flow between these patch reefs, IBG theory alone cannot explain fish community composition.

The significant interaction effect of area and complexity suggests that larger, more complex patch reefs can support higher fish abundance and species richness than smaller, less complex reefs. Large, complex reefs can potentially provide a greater number of habitats and therefore can support a higher number of individuals and species.

Quantifying the relative importance of factors driving communities of fish on patch reefs will provide an understanding of how patch reefs can support and sustain fish populations. As coral reef communities continue to decline from a combination of natural and anthropogenic pressures, an understanding of the mechanisms driving fish community composition may be crucial for effective management of coral reef fish populations.

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*DIADEMA ANTILLARUM'S* IMPACT ON CORAL COVER AND JUVENILE CORALS  
ALONG THE WEST FORE REEF, DISCOVERY BAY, JAMAICA: PAST AND PRESENT

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Research advisors: Faculty and graduate students. Faculty editor: John J. Gilbert

*Abstract:* The sea urchin *Diadema antillarum* grazes benthic algae, thereby playing a large role in moderating the competitive interaction between corals and algae at Discovery Bay, Jamaica. A massive die-off of *D. antillarum* in 1983 reduced algal herbivory dramatically, leading to an overgrowth of algae on the reef. As *D. antillarum* began to recover in 1996, its feeding created barren zones on the reef where it grazed macroalgae, allowing coral recruits to establish themselves again. We measured the abundance of *D. antillarum* and the abundance, percent cover, and size-class distribution of corals in both the barren and algal zones to determine whether *D. antillarum* abundances are still benefiting the coral population, or whether they have become so high that they are damaging the coral population. We then compared current patterns to those recorded in past years to determine the trends of each population on a larger scale. We discovered greater *D. antillarum* and coral abundances in the barren zone, which suggests that *D. antillarum* is benefiting coral populations. In fact, when compared with past data, our data are consistent with the coral population's general positive growth trend since *D. antillarum* recovery began. However, differences in the size distributions of corals between the two zones suggest that *D. antillarum* may be approaching an abundance at which it begins to harm small corals by grazing them.

*Key Words:* *Diadema antillarum*, coral, size class, Discovery Bay, Jamaica, macroalgae, grazing

## INTRODUCTION

Corals and macroalgae compete intensively for space in shallow tropical waters. In the absence of herbivores, macroalgae densities will increase dramatically—producing deleterious effects on coral colonies (Lirman 2001). At Discovery Bay, Jamaica, overfishing has caused a dramatic reduction in the abundance of herbivorous fish, and the reef has become highly dependent on other herbivores—such as sea urchins—to keep algal growth in check. One such urchin, *Diadema antillarum*, plays an important role in moderating competition between corals and algae because of its high abundance, especially after disturbances when slow-growing corals are at a disadvantage. In 1980, Hurricane Allen destroyed most of

the branching corals at Discovery Bay. Three years later, a large die-off of *D. antillarum* dramatically reduced algal herbivory, dealing a second blow to reef coral by making it more difficult for corals to compete with algae for space. The *D. antillarum* population did not begin to recover until 1996.

Because its distribution is determined by depth and substrate complexity (Copeland, C. 1980; Podolak and Burke 2002), *D. antillarum* only inhabits and grazes macroalgae along certain areas of the shallow fore reef. This creates two distinct zones: (1) a barren zone in which *D. antillarum* abundance is high and macroalga abundance is low, and (2) an algal zone in which *D. antillarum* abundance is low and macroalga abundance is high. The barren zone has more substrate area free of algae

that young corals may colonize, so as *D. antillarum* recovered in the late 1990's and early 2000's, corals also began to recover (Edmunds 2001).

Although both the *D. antillarum* and coral populations in Discovery Bay have been monitored since the 1950's, there have been no surveys in the past several years. Therefore, it is unclear if and how *D. antillarum* abundances continue to influence coral abundance. We investigated the current demographics of *D. antillarum* and coral populations in both the barren zone and the algal zone. We predicted that if *D. antillarum* is still benefiting the corals, live coral abundances would be greater in the barren zone than in the algal zone. We also expected a greater number of medium and large corals in the barren zone than in the algal zone, indicating a history of more coral recruits with higher survival rates. To assess the relationship between *D. antillarum* and corals over time, we also compared our data with data from past studies beginning in 1977. Because there have not been any recent major disturbances, we predicted that the abundance of both *D. antillarum* and all sizes of corals in the barren zone would continue to increase as *D. antillarum* returns to pre-die-off numbers, while algal zone abundances would be largely unchanged.

*D. antillarum* abundances may also become so high that they harm coral populations. If resources become limiting for *D. antillarum*, it could begin to graze on small corals along with algae (Sammarco 1980). Small corals are more vulnerable to grazing than large corals, so the probability of surviving intense grazing is positively related to size (Mobley, C.T. 1984). If *D.*

*antillarum* populations have become so large that they harm juvenile coral recruitment, we would expect higher proportions of medium and large corals and lower proportions of juveniles in the barren zone compared to the algal zone.

## METHODS

We collected data on 2-6 March 2006 on the west fore reef at Discovery Bay near two separate dive sites: Dancing Lady and M1. At each site, we haphazardly chose 5 x 4 m transects in two distinct zones: the barren zone (< 20% algal cover; n = 8) and the algal zone (> 70% algal cover; n = 7). All transects were between 3 and 7 m deep. We counted the total number of *D. antillarum* and corals in each transect, and divided corals into eight taxonomic categories: *Diploria* spp., *Siderastrea* spp., *Agaricia* spp., *Porites porites*, *Porites astreoides*, *Acropora palmata*, *Erythropodium caribaeorum*, and other less common corals. We further divided corals into size classes: small corals (< 3 cm diameter), medium corals (3-6 cm), and large corals (> 6 cm). We also estimated total percent coral cover in each zone by haphazardly measuring corals in each size class and then multiplying the mean surface area of each size class by the number of colonies of that size class in a given transect.

To look at current *D. antillarum* and coral abundances in the context of historical trends, we compiled data presented in past studies starting in 1977 on *D. antillarum* abundance, coral cover, and juvenile coral density at depths between 3 and 7 meters on the west fore reef. We added current abundances to the historical data to

determine long-term patterns in *D. antillarum* and coral populations. We present the studies used in Table 1.

We examined differences in *D. antillarum* and coral densities between barren and algal zones using ANOVA. We examined differences in size class

frequencies between zones for all corals and for each coral species individually with G-tests. We looked at the relationship between *D. antillarum* density and juvenile coral density within zones using linear regression. We used JMP 5.0.1 for all analysis.

Table 1: Source, year, and method for obtaining historical data on *D. antillarum* abundance, percent coral cover, and juvenile coral density between 3 and 7 meters depth on the west fore reef, Discovery Bay, Jamaica.

*D. antillarum*

Source	Years	Method for getting data
Carpenter 1981	1977	Estimated from figure
Hughes et al. 1985	1982-84	Value given in paper
Liddel and Ohlhorst 1986	1982	Value given in paper
Hughes 1994	1985-96	Estimated from figure
Hughes et al. 1987	1986	Value given in paper
Balser and Soucy 1992	1993	Value given in paper
Aronson and Precht 2000	1993-96, 98-99	Estimated from figure
Edmunds and Carpenter 2001	2000	Estimated from figure
Erickson et al. 2001	2001	Value given in paper
Podolak and Burke 2002	2002	Value given in paper
Chamberlin and Wickre 2003	2003	Value given in paper
Current study	2006	See methods

Coral cover

Source	Years	Method for getting data
Huston 1985	1977	Estimated from figure
Hughes 1994	1977, 81-93	Estimated from figure
Liddel and Ohlhorst 1986	1982-84	Value given in paper
Hughes et al. 1987	1986	Value given in paper
Aronson and Precht 2000	1993-96, 98-99	Estimated from figure
Edmunds and Carpenter 2001	2000	Estimated from figure
Chamberlin and Wickre 2003	2003	Value given in paper
Current study	2006	See methods

Juvenile corals

Source	Years	Method for getting data
Edmunds and Carpenter 2001	1994, 96, 2000	Estimated from figure
Edmunds and Bruno 1996	1995	Estimated from figure
Erickson et al. 2001	2001	Estimated from figure
Current study	2006	See methods

RESULTS

We found more *D. antillarum* in the barren zone (mean  $\pm$  SE;  $4.4 \pm 5.28$  individuals/m<sup>2</sup>) than in the algal zone ( $0.1 \pm 5.64$  individuals/m<sup>2</sup>;  $F_{1,13} = 122.55$   $p < 0.0001$ ). We found 2144 coral colonies across all barren zone transects, covering a

mean of 18% of total area, and 938 coral colonies in the algal zone, covering a mean of 6% of total area. Coral colony density was significantly greater in the barren zone ( $1340 \pm 166$  individuals/100 m<sup>2</sup>) than the algal zone ( $670 \pm 177$  individuals / 100 m<sup>2</sup>;  $F_{1,13} = 7.61$ ,  $p < 0.02$ ; Fig. 1). This relationship was driven largely by

differences in densities of *Agaricia* spp. and *Porites asteroides* (Fig. 2).

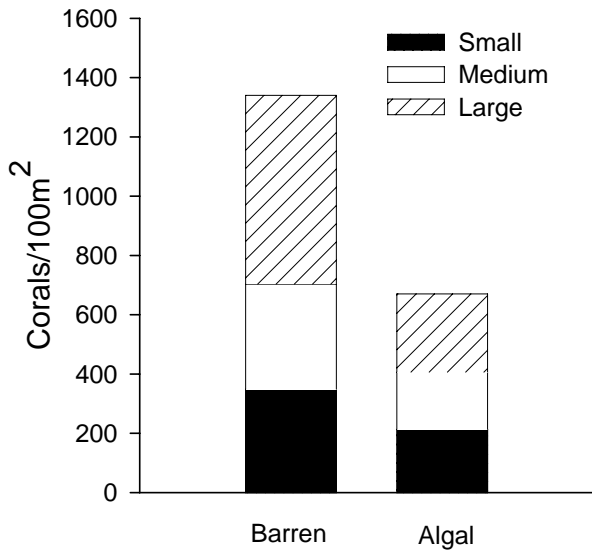


Figure 1: Coral densities and percent composition of total corals by size class pooled across transects at two dives sites in barren (n=4 at M1, n=4 at Dancing Lady) and algal (n=4 at M1, n=3 at Dancing Lady) zones along the west fore reef, Discovery Bay, Jamaica. There was significant difference in density and percent composition between zones ( $p < 0.05$ ).

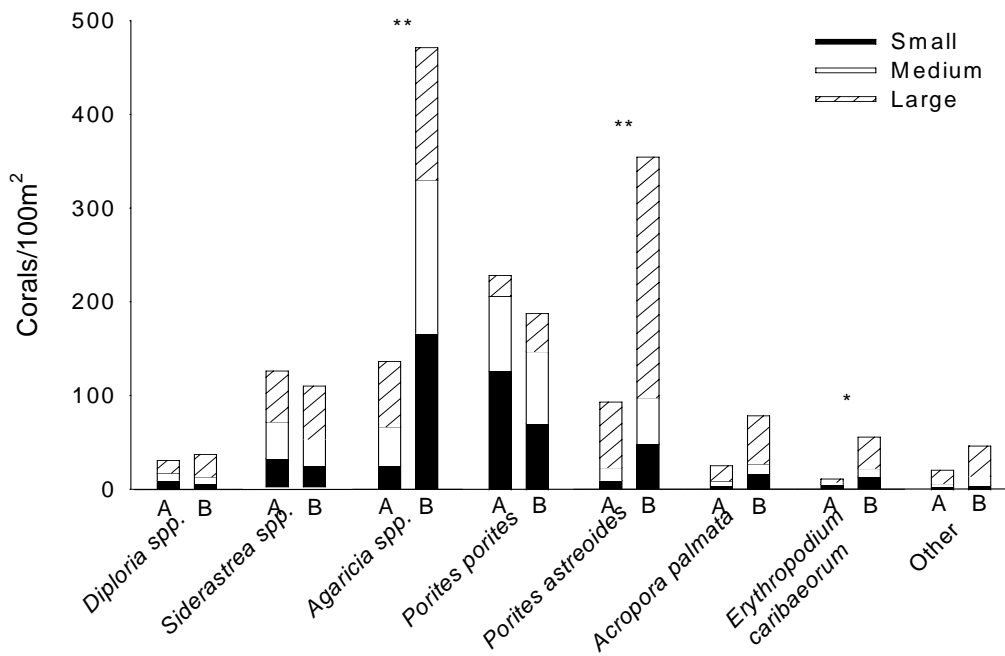


Figure 2: Density of different coral species by size class pooled across transects at two dive sites in algal (A) (n=4 at M1, n=3 at dancing Lady) and barren (B) (n=4 at M1, n=3 at Dancing Lady) zones along the west fore reef, Discovery Bay, Jamaica. \* denotes significant difference in total counts of a coral species between zones ( $p < 0.05$ ), \*\* denotes significant difference ( $P < 0.01$ ). Refer to table 2 for differences in size class composition for each coral species between zones.

Table 2. Differences in abundances of three size classes of seven corals between algal and barren zones in the west fore reef, Discovery Bay, Jamaica. Data are pooled across transects at two sites (Dancing Lady: n=4 in barren, n=3 in algae; M1: n=4 in barren, n=4 in algae).

Coral taxa	Zone	No. small	No. medium	No. large	G	P
<i>Diploria</i> spp.	barren	9	12	38	4.71	0.09
	algal	13	11	19		
<i>Siderastrea</i> spp.	barren	36	45	91	2.81	0.25
	algal	42	55	76		
<i>Agaricia</i> spp.	barren	266	262	226	34.81	< 0.0001
	algal	35	58	98		
<i>Porites porites</i>	barren	114	123	65	26.38	< 0.0001
	algal	178	112	31		
<i>Porites asteroides</i>	barren	77	79	411	1.27	0.53
	algal	13	19	98		
<i>Acropora palmata</i>	barren	26	17	82	1.34	0.51
	algal	5	7	23		
<i>Erythropodium caribaeorum</i>	barren	21	14	54	4.24	0.12
	algal	7	3	5		
Total	barren	557	568	1019	18.64	< 0.0001
	algal	298	270	370		

Distribution of corals across size classes was significantly different between barren and algal zones ( $G = 18.64$ ,  $p < 0.001$ ; Table 2; Fig. 1). Density of large and medium corals, but not small corals was significantly greater in the barren zone than the algal zone (Table 3; Fig. 1). Size class differences were driven primarily by distribution of *Agaricia* spp. and *Porites porites* (Table 2). However, we found no relationship between *D. antillarum* densities and juvenile coral densities within each zone (linear regression, barren zone:  $r^2 < 0.11$ ,  $p > 0.42$ ; algal zone:  $r^2 < 0.0003$ ,  $p > 0.97$ ).

*D. antillarum* has generally increased in the barren zone and stayed relatively constant in the algal zone since 1996 (Fig. 3a). Coral cover has been increasing in both

zones, but was higher in the algal zone until our study in 2006, where it increased substantially in the barren zone (Fig. 3b). Juvenile corals increased between 1994 and 2000, with greater increases in the barren zone, but have decreased since then in both zones (Fig. 3c).

## DISCUSSION

Because coral abundances are greater in the barren zone where *D. antillarum* abundances are highest, and lower in the algal zone where there are few *D. antillarum*, it seems that the *D. antillarum*

Table 3: Differences in small, medium, and large coral density (mean number  $\pm$  SE/ 100m<sup>2</sup>) between barren and algal zones along the west fore reef, Discovery Bay, Jamaica.

Size class	Barren zone	Algal zone	ANOVA $F_{1,13}$	P
Small	348 $\pm$ 54.0	213 $\pm$ 50.5	3.35	0.09
Medium	355 $\pm$ 48.3	193 $\pm$ 51.6	5.27	0.04
Large	637 $\pm$ 80.3	264 $\pm$ 85.8	10.05	0.007

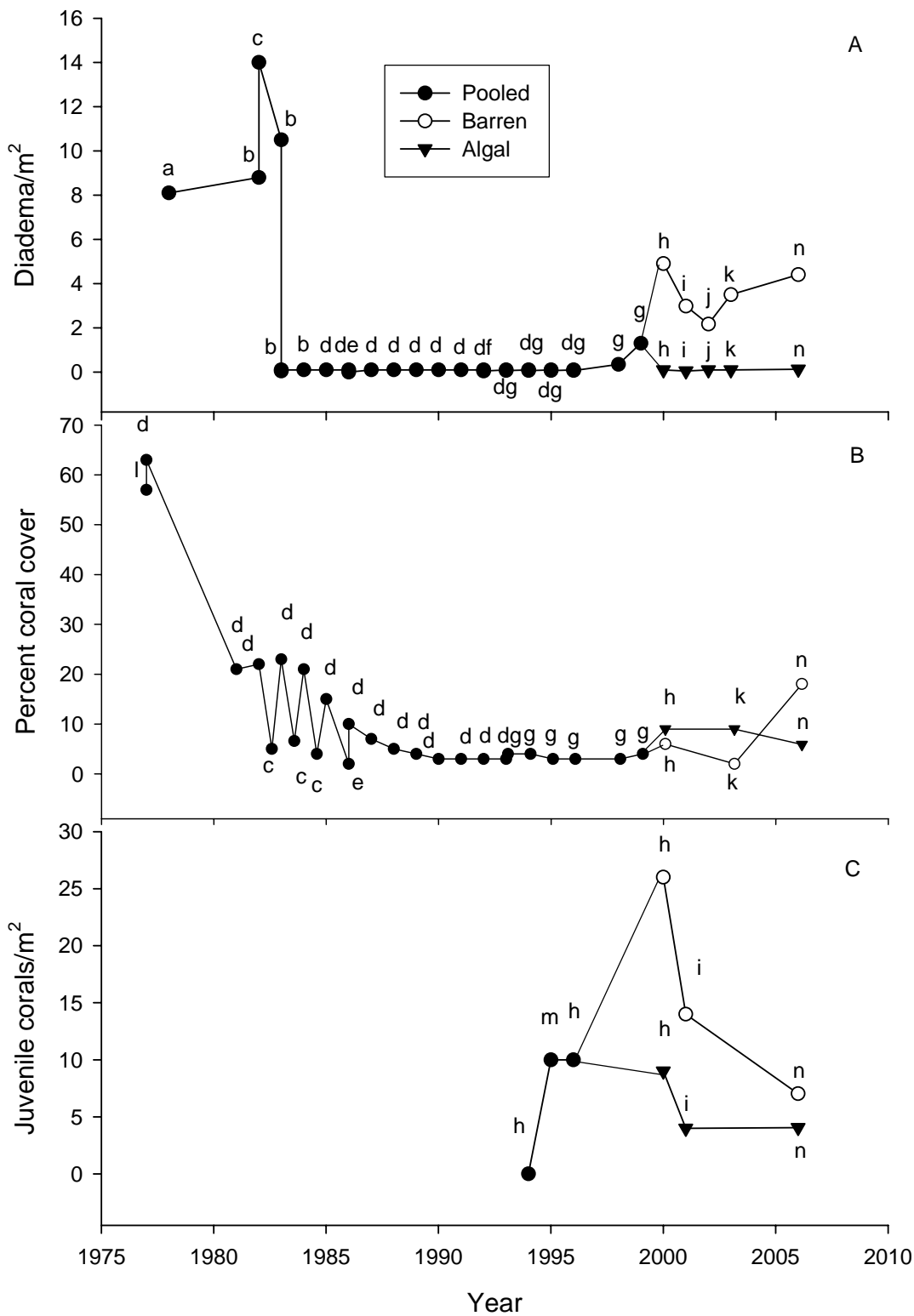


Figure 3: Changes in *D. antillarum* densities (A), percent coral cover (B) and juvenile coral density (C) between 3 and 7 meters depth on the west fore reef, Discovery Bay, Jamaica. Letter above each data point corresponds with its source: (a) Carpenter 1981, (b) Hughes et al. 1985, (c) Liddell and Ohlhorst 1986, (d) Hughes 1994, (e) Hughes et al. 1987, (f) Balsler and Soucy 1992, (g) Aronson and Precht 2000, (h) Edmunds and Carpenter 2001, (i) Erickson et al 2001, (j) Podolak and Burke 2002, (k) Chamberlin and Wickre 2003, (l) Huston 1985, (m) Edmunds and Bruno 1996, (n) current study.

population still benefits the coral population. The past several years' general trend of increasing coral cover in the barren zone and relatively constant coral cover in the algal zone also supports this conclusion. Furthermore, the presence of more large corals in the barren zone reflects the greater number of coral recruits to the zone in the late 90's/early 2000's (Fig. 3) and suggests higher coral recruitment and survivorship coincided with *D. antillarum* recovery.

However, we found evidence that *D. antillarum* may not continue benefiting corals in the barren zone. Small coral abundance in the barren zone has decreased over the past 6 years. We found a greater proportion of large and medium corals to small corals in the barren zone compared to the algal zone (Table 2; Table 3), suggesting that the barren zone's small corals are diminishing. This may indicate that the *D. antillarum* population is reaching a critical size at which it becomes detrimental to the coral population by grazing juvenile corals. Although we found no relationship between *D. antillarum* density and juvenile coral density within zones, it is possible that the high mobility of *D. antillarum* obscured evidence for this relationship at the scale we chose for our sampling. It is also possible that the fluctuations in juvenile coral density indicate a convergence towards a stable age distribution.

The interaction between *D. antillarum* and coral differs depending on coral species: not all coral species were more abundant in the barren zone or showed the same patterns in size class distribution across zones. The difference in abundance (more corals in the barren zone)

was driven largely by *Agaricia* spp. and *Porites astreoides*, while differences in size distribution (more large corals in the barren zone) were driven largely by *Agaricia* spp. and *Porites porites*. Because these species survive equally well across a large depth range (Liddell and Ohlhorst 1987), and because we limited our study to a fairly small depth range, these distribution differences are not likely a result of depth. This suggests that these coral species may be less competitive against algae than other coral species and thus benefit more from the presence of *D. antillarum* (Sammarco 1980).

*D. antillarum* densities have increased steadily since 1996, and there is little reason to think they might stop soon as they continue to recover. If urchins have indeed reached a density at which they start to graze young corals, coral cover could be further diminished as a result. When we compare present *D. antillarum* density-coral population dynamics to those recorded before the hurricane and *D. antillarum* die-off (by Copeland 1980), we see that a negative effect of urchins on coral juveniles is occurring at much lower urchin densities.

It is possible that large-scale environmental conditions (substrate, water temperature, nutrient input, etc.) are making small corals more susceptible to grazing, and lowering the density at which *D. antillarum* becomes detrimental to corals. In fact, it seems that one of these conditions, the substrate topography, is having more local effects in the barren zone. Copeland (1980) found many pieces of loose substrate under which numerous juvenile corals grew, sheltered from *D. antillarum* grazing.

We found no loose substrate. Without this refuge from grazing for juvenile corals, the density at which *D. antillarum* becomes detrimental may be lower. Thus, although *D. antillarum* densities seem to be the primary factor driving coral success on the reef, we must also consider how environmental factors are contributing to coral recovery.

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