LIGHT AVOIDANCE IN *EUAPTA LAPPA*

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Abstract: Euapta lappa sea cucumbers (class: Holothuria) are unique among sea cucumbers at Discovery Bay, Jamaica in that they are highly mobile, entirely nocturnal, and show a strong aversion to light. We investigated why *E. lappa* avoids light, testing how sensitive they are to UV radiation compared to light-tolerant sea cucumbers, and looking at predation on them in daylight and nighttime hours. We also investigated how they avoid light, hypothesizing that they are able to detect shade refuges from a distance and that they generally remain close to these refuges while foraging at night. We found that substantially more UV radiation passes through its cuticle than the cuticle of a day-active sea cucumber, suggesting UV sensitivity is one reason *E. lappa* avoids light. We also found that *E. lappa* preferentially moved towards shade refuges during the day from 30 cm away but not from 60 cm away, and that nearly half of all cucumbers found in the wild at night stayed within 30 cm of a refuge, which suggests they remain close enough to a refuge to find it easily.

Key Words: Euapta lappa, *Sea Cucumber,* Holothuria*, Discovery Bay, UV radiation, palatability*

INTRODUCTION

Euapta lappa is a nocturnal, deposit-feeding holothurian (sea cucumber) which is strongly averse to light. During the day, it stays concealed in coral, under rocks, or in shells. It has pigmented photoreceptors on its tentacles which may aid in sensing and avoiding light (Hendler et al. 1995). Individuals leave their refuges after dusk to forage, and will rapidly contract and seek shelter when light is shone on them.

We investigated both why and how *E. lappa* avoids daylight. We hypothesized that daytime predation and UV radiation are reasons for light-avoidance. Thus, we evaluated the palatability of *E. lappa* and the effectiveness of its cuticle in blocking UV light. Daylight avoidance necessitates that *E. lappa* move between night-time foraging areas and day-time refuges. The ability to navigate between these areas is important because an undirected search for shelter could prevent an individual from finding shelter before sunrise. We hypothesized that, in the field, *E. lappa* will preferentially forage near potential refuge sites, and, in the lab, they will be able to detect shelter from a distance.

METHODS

We collected 20 *E. lappa* on the nights of 23 February and 25 February, 2006 at the Discovery Bay Marine Laboratory in Jamaica. We observed all individuals in the laboratory both at night and during the day to test for avoidance of light. We also released four individuals into their original habitat during daylight and observed their behavior. Additionally, we attempted to determine where individuals find refuge during the day by tethering individuals both with string tied around their bodies and safety pins affixed to their tissue.

We tested *E. lappa's* palatability to predators by offering them three samples each of *E. lappa, Holothuria mexicana*

(Donkey Dung Sea Cucumber), *Isostichopus badionotus* (Three-rowed Sea Cucumber), and a control (frozen, pre-cooked shrimp). We placed the samples in the water at mangrove and shallow back reef habitats for 20 continuous hours to test for palatability to both diurnal and nocturnal predators.

To test for vulnerability to ultraviolet light, we exposed four *E. lappa* individuals each of both dark and light morphotypes to an ultraviolet lamp and observed how much light passed through each sample by placing a piece of paper that fluoresces under UV behind them and categorizing the amount of florescence. We compared this to the amount of florescence produced by shining a UV light through cuticle samples from *H. Mexicana,* a diurnal sea cucumber.

To test for behavior related to strategies for avoiding light, we surveyed the location of *E lappa* at night with respect to distance from shade refuge. To determine the distance at which *E. lappa* can locate shade refuge, we tested 17 individuals in a 1 m tank in natural sunlight with a shade area located at one end. We placed each individual at 30 and 60 cm from the shade refuge at each end of the tank and observed whether they went towards or away from the refuge. We alternated at which side of the tank we placed the shaded area.

RESULTS

In the lab, all *E. lappa* collected were active at night, but sought shade refuge when a light was turned on. Additionally, all individuals sought shade refuge during daylight in the lab. Of the four individuals released during daylight at the site where they were collected at night, two were not immediately able to grip the substrate due to strong water currents. However, the two that did gain a purchase sought refuge immediately. Both methods of tethering (safety pin and tying) failed, as the cucumber escaped both tethers. Other researchers also experienced this difficulty (Southam 1987 and Hammond 1983).

Our results for palatability were inconclusive. We did not observe any feeding on pieces of *H. mexicana*, *I. badionotus*, *E. lappa* or the control shrimp in the floating buffet. More ultraviolet light passed through the entire body of *E. lappa* than through one layer of the cuticle of *H. mexicana*. We found high UV penetration for dark morphotypes of *E. lappa* and very high penetration for light morphotypes.

E. lappa individuals generally moved towards and into the shade refuge when placed 30 cm away (24 towards, 11 away; $\chi^2 = 4.83$, $p = 0.02$) but did not show this trend from 60 cm away (16 towards, 18 away; $\chi^2 = 0.118$, $p = 0.73$). From our night observations we found that nearly half the individuals foraged within 30 cm of a shade refuge and over 95% were within one meter of a shade refuge (Fig. 1).

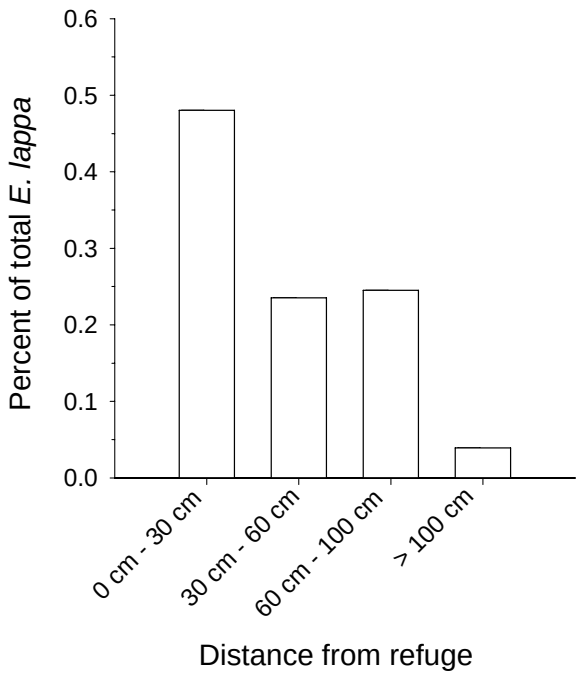

Figure 1: Distribution of *E. lappa* with respect to distance from a shade refuge, based on 102 individuals observed at night at Discovery Bay, Jamaica.

DISCUSSION

E. lappa shows a strong, predictable light avoidance. In both the lab and the field, individuals retracted and sought shelter when exposed to light. UV light easily penetrates its body, suggesting that its aversion to light may have evolved to prevent the harmful effects of this radiation.

The alternate hypothesis that predation drives *E. lappa*'s aversion to light seems less likely, although we cannot exclude it as none of the sea cucumbers or control food we tested were eaten. There could be several explanations for this result. Firstly, the shrimp control was rotten and may have been unpalatable. Secondly, the food was placed in the water column, and this may not have been readily detected by fish or invertebrates who feed at the bottom. Placing the food on the substrate may have been more realistic. Thirdly, predators in the heavily fished area may have been scarce. However, a past study did show *E. lappa* to be unpalatable; Southam (1987) performed a similar buffet experiment in which the control (urchin) was readily eaten, but *E. lappa* was not.

Higher water currents during the day might also contribute to *E. lappa* avoiding light. Flow speed at Discovery Bay is on average 61% greater during the day than at night (Genovese and Witman 2004), and individuals released during the day had difficulty adhering to the substrate because of water movement.

E. lappa likely finds refuge from light both because it can detect a refuge from a distance and because it forages near refuges at night. It can sense the direction of a refuge from at least 30 cm away, and half the individuals observed at night were within 30 cm of refuge. However, past studies have found that *E. lappa* finds refuge before sunrise (Hammond 1982). This means they may use cues other than light, such as chemical trails, to find cover. Alternatively, *E. lappa* may have an internal clock which triggers refuge-seeking without being prompted by light. Further studies could evaluate the relative importance of visual versus other cues for finding refuge.

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WEAR SUNSCREEN: DIFFERENCES IN COVERING BEHAVIOR AND COVERING MATERIAL PREFERENCE IN *LYTECHINUS VARIEGATUS* AND *TRIPNEUSTES VENTRICOSUS*

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Abstract: Two sea urchin species, *Tripneustes ventricosus* and *Lytechinus variegatus*, dominate the turtle grass (*Thalassia testudinum)* beds and coral rubble areas of the west back reef at Discovery Bay, Jamaica. Both species of sea urchin cover their aboral surface with materials from their habitat (such as turtle grass and coral rubble), and must invest energy to collect and hold this covering material. Based on preliminary field observations, we hypothesized that *L. variegatus* would cover more of its aboral surface and with heavier materials than *T. ventricosus*, and that immediate habitat type would also affect covering material preference. To test this, we observed differences in covering behavior of individual sea urchins in the field in each of three habitats: turtle grass beds, coral reef, and mixed. We also presented individuals with an equal proportion of turtle grass and coral rubble in experimental tanks. We recorded the percent of aboral surface an individual covered and what proportion of the covered surface consisted of turtle grass versus coral rubble. Our results from observational and experimental data support the hypotheses that *L. variegatus* covers more and with heavier materials than *T. ventricosus*, and that habitat affects covering material preference for *L. variegatus.*

Key Words: Tripneustes ventricosus, Lytechinus variegatus, Thalassia testudinum, *covering behavior, UV radiation*

INTRODUCTION

Sea urchins play an important role in maintaining coral reef ecosystems by grazing algae on the substratum, thus enabling coral colony establishment (Aronson and Precht 2000). This is especially important in Discovery Bay, Jamaica, where hurricane disturbance destroyed much of the coral reef, and created open habitat for algal growth (Woodley et al. 1981). Discovery Bay's back reef features two species of sea urchin, *Lytechinus variegatus* and *Tripneustes ventricosus,* that occupy habitat consisting of both turtle grass (*Thalassia testudinum)* and coral rubble.

Both urchins exhibit a covering behavior, in which they cover their aboral surface with materials from their habitat such as turtle grass, macroalgae, shells, and coral rubble. Preliminary observations suggested that *L. variegatus* and *T. ventricosus* differed in the total amount of aboral surface covered, and that the materials that both species used as covering differed across habitats. In general, *L. variegatus* tended to cover more and used mostly coral rubble (dead coral fragments and shells) to cover while *T. ventricosus* tended to cover less and used mostly turtle grass. Additionally, availability of covering material seemed to affect what each urchin used. We investigated whether these differences in covering behavior were related to species or habitat, using both field observations and laboratory experiments.

Based on our preliminary observations, we expected that *L. variegatus*

would cover a greater percent of its aboral surface than *T. ventricosus*, regardless of habitat. We also expected that *L. variegatus* would use coral rubble to cover more often while *T. ventricosus* would use turtle grass. Similarly, in experiments where each urchin species was presented with an equal mixture of turtle grass and coral rubble, we expected *L. variegatus* to cover more and to preferentially choose coral rubble to cover. We expected *T. ventricosus* to cover less and to preferentially choose turtle grass to cover.

Alternatively, covering behavior may be primarily related to habitat, in which case urchins would cover more with the dominant habitat material. Urchins presented with an equal mixture of turtle grass and coral rubble should therefore display no preference in covering materials. However, if covering behavior is related to original habitat, urchins should cover more with whatever material dominated their original habitat.

METHODS

On the afternoon of 22 February 2006, we observed 144 sea urchins in the west back reef in Discovery Bay, Jamaica across a range of depths between 1 and 3 m. We haphazardly selected 24 sea urchins of each species in each of 3 habitats: 1) mostly (>70%) turtle grass, 2) 50:50 turtle grass and coral rubble, and 3) mostly (>70%) coral rubble. We recorded the percent of aboral surface covered, and what percent of covering materials consisted of turtle grass or coral rubble.

On the morning of 22 February 2006, we collected six *L. variegatus* individuals and six *T. ventricosus* individuals for lab manipulations from each of three habitat types: 1) mostly turtle grass (>70%), 2) 50:50 turtle grass and coral rubble, and 3) mostly coral rubble (>70%), from the west back reef. From 10:30 to 14:30 on 23 February 2006, we observed the covering behavior of each urchin in outdoor tanks (24 x 36 x 64 cm) with running seawater, in direct sunlight. Each tank had a sandy bottom (~1 cm deep), and contained the same covering material: 30 blades of turtle grass, (~15 x 1.5 cm^2 per blade) collected from turtle grass beds in the west back reef, and 30 pieces of coral rubble (rubble and shells ~2-3 cm diameter) collected from the aboral surface of sea urchins during data collection in the west back reef. Incident light intensity was similar across trials (1075 - 1584 $\mu mol\ s^{-1}\ m^{-2}$) and water temperatures varied between 28.5 and 30.0°C.

We placed a single sea urchin into the middle of the tank and recorded the percent of aboral surface covered and the percent of covering material consisting of turtle grass or coral rubble after 15 minutes. We tested the light-blocking capacity of grass versus coral rubble by placing each covering material over the light meter to see how much light was blocked.

We analyzed the effects of species and habitat on percent aboral surface covered and percent turtle grass making up the total covering material using two-way ANOVA. We ran each of these tests on both our experimental and observational data. We arcsine-transformed our proportion data to meet homogeneity of variance assumptions and used JMP 5.0.1 for all analyses.

RESULTS

Observational and experimental data showed similar trends. *L. variegatus* had a higher total percent aboral surface cover than *T. ventricosus* (Fig. 1, Table 1). Habitat did not affect total percent cover for either species. *T. ventricosus* used turtle grass for more of its total covering material than *L. variegatus* (observational: $F_{1,138} = 36.13$, $P < 0.0001$; experimental: $F_{1,30} = 5.39$, $P = 0.03$). Only *L. variegatus* displayed a difference in percent turtle grass cover of the total covering material across habitat, covering with the highest percentage of turtle grass in the mostly turtle grass habitat, and the lowest percentage of turtle grass in the mostly coral rubble habitat (observational: $F_{2,138} = 5.86$, $P < 0.01$; experimental: $F_{2,30} = 3.46$, $P = 0.04$). When used as a covering material *T. testudinum* blocked 82% of ambient light, while coral rubble (rocks and shells) blocked 99% of ambient light.

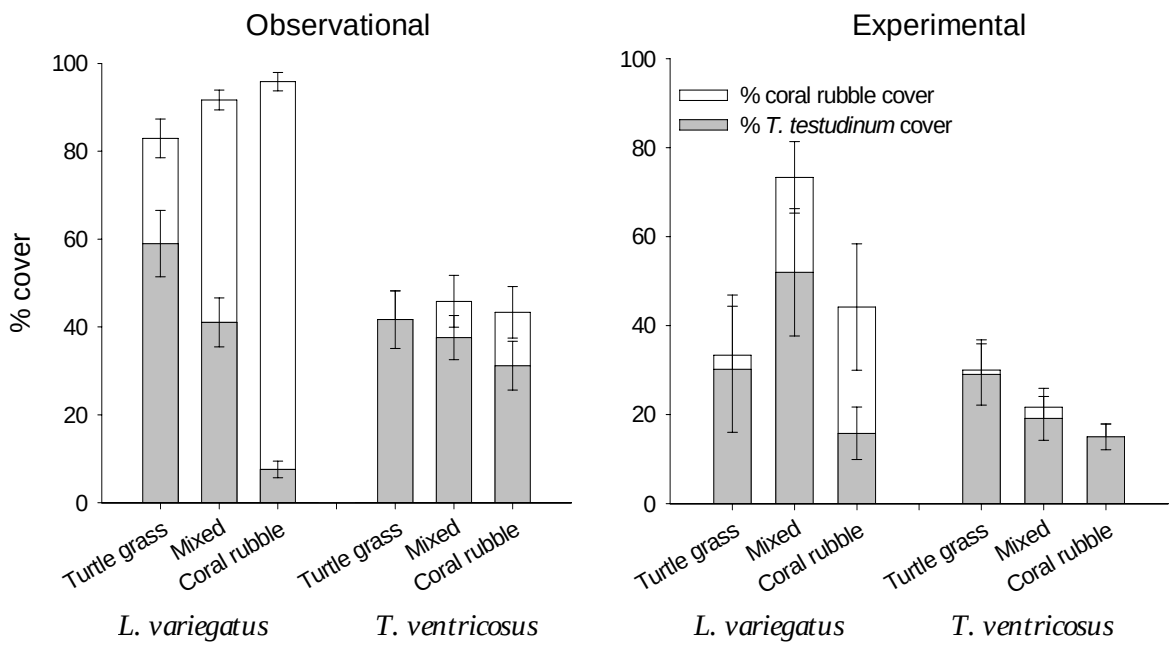

Fig. 1. Covering behavior of *T. ventricosus* and *L. variegates* across three habitats (mostly turtle grass, mostly coral rubble, and 50:50 turtle grass and coral rubble), based on observational and experimental studies (in tanks with equal amounts of turtle grass and coral rubble) at Discovery Bay Marine Lab, Jamaica. Total bar height represents total percent cover of aboral surface (mean ± SE). Stacked bars (mean ± SE) represent percent of total cover made up of turtle grass (gray) and percent of total cover made up of shells (white). See Table 1 for statistical analysis.

Table 1. Observational and experimental data: ANOVA showing the relationships between habitat and percent total covering, and habitat and percent turtle grass covering, for two species of sea urchin at Discovery Bay, Jamaica.

	Percent Total Covering			Percent Grass Covering		
Observational	DF	F	P	DF	F	P
Species	1, 30	10.02	0.004	1, 30	5.39	0.03
Habitat	2, 30	1.82	0.18	2, 30	0.38	0.69
Species * Habitat	2, 30	1.74	0.19	2, 30	3.46	0.04
Experimental	DF	F	P	DF	F	P
Species	1, 138	132.63	<0.0001	1, 138	36.13	<0.0001
Habitat	2, 138	1.60	0.2	2, 138	15.16	<0.0001
Species * Habitat	2, 138	1.14	0.32	2, 138	5.86	0.004

DISCUSSION

L. variegatus covered more than *T. ventricosus* and used coral rubble more than turtle grass, demonstrating that covering behavior depends on species. Species' covering material preferences may be related to urchin pigmentation and the ability of covering materials to block light. Lees and Carter (1972) demonstrated that UV radiation can cause mortality in *Lytechinus anamesus.* Kehas et al. (2004) demonstrated that sea urchins with less pigmentation cover more in response to UV radiation. Because *L. variegatus* is lighter colored and appears less pigmented than *T. ventricosus*, its covering behavior (heavier materials and greater percent covered) may indicate greater susceptibility to UV radiation.

Holding covering materials to the aboral surface requires energy, and may also reduce sea urchin respiration by reducing the number of aboral podia available for gas exchange (Kehas et al. 2004). Urchins often drop their covering material at night and cover less in low light intensities (Kehas et al 2004; Millott 1955), so the benefit of increased cover must outweigh these costs.

Coral rubble blocked more light than turtle grass. For *L. variegatus,* the benefits of extra UV protection may outweigh the combined costs of holding coral rubble: decreased respiration and increased energetic demand. If *T. ventricosus* is less susceptible to UV radiation, it may preferentially cover with turtle grass because it incurs a lower energetic cost. An experiment testing each species' relative susceptibility to UV radiation would effectively test this hypothesis.

Although sea urchin species had the greatest effect on covering behavior, *L. variegatus* covering behavior in the experiment corresponded with its original habitat. This may be due to a behavioral acclimatization to original habitat. We also observed in the field that *L. variegatus* covering behavior corresponded to the covering materials available in its immediate habitat. This suggests that the costs and benefits of covering with certain materials change according to habitat. *L. variegatus'* costs of searching for heavy coral rubble in a turtle grass bed may outweigh the benefits of increased protection. Investigating the costs of searching for covering materials and relative benefits offered by each material would test this hypothesis.

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POTENTIAL BENEFITS OF JUVENILE COLORATION IN DAMSELFISH

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Abstract: Adult damselfish aggressively defend general-purpose territories on coral reefs against both conspecific and heterospecific fish. In contrast to the drab coloration of adults, juvenile damselfish are brightly colored. To explore the potential benefits of juvenile coloration, we examined the conspecific and heterospecific interactions of adults across two damselfish species: Threespot (*Stegastes planifrons*) and Beaugregory (*Stegastes leucostictus*). Adult damselfish may recognize the bright coloration of juvenile conspecifics and identify them as individuals which should not be attacked. Therefore, we hypothesized adult damselfish will be less likely to attack conspicuously colored juvenile damselfish. Furthermore, damselfish may also attack small, colorful fish less than other heterospecific fish visitors because their bright colors resemble juvenile coloration. We observed the number and type of encounters between adult damselfish and other fish. Adult damselfish attacked juvenile conspecifics less frequently than heterospecifics, and small, colorful heterospecifics less than other categories of heterospecifics. This result suggests that small size and bright coloration reduce the frequency of attacks, and that the specific coloration pattern of juveniles may further reduce the frequency of attacks by conspecific adults.

Key Words: Threespot Damselfish, Beaugregory, juvenile coloration, conspecific, heterospecific

INTRODUCTION

Because coral reefs provide habitat for many species of fish with overlapping resources, reef fish have different strategies, including territory establishment, to exploit limited resources and to compete successfully with other fish. Damselfish (Family:Pomacentridae) are known to establish individual territories (Humann 1991), which provide shelter from predators, nest sites for eggs, and food resources in the form of algal gardens (Robertson et al. 1981). Damselfish are pugnacious defenders of these territories, protecting them from both intruding conspecific and heterospecific fish.

Juveniles of these territorial damselfish exhibit bright coloration, which differs dramatically from the uniformly drab coloration of adults. The benefit of this conspecific dichromatism, and more specifically, conspicuous juvenile coloration, is not completely understood. The bright coloration may make juveniles recognizable to adult conspecifics as individuals which should not be attacked (Deloach 1999, Conte 2000). However, given the spatial overlap of adults and juveniles, this benefit of lessened aggression towards juveniles is not self-evident. Our hypothesis, based on Deloach's observations on juvenile coloration, states that conspicuous coloration allows adults to recognize their juveniles, and acts to reduce aggression against juveniles. If our first assumption is correct, and adults attack their juveniles less, we would further hypothesize that adults may also attack small, colorful fish

less than other heterospecific fish visitors since these fish resemble their juveniles. To explore potential benefits of juvenile coloration and bright coloration in general, we examined conspecific and heterospecific interactions of adult Beaugregory (*Stegastes leucostictus)* and Threespot (*Stegastes planifrons)* damselfish in Discovery Bay, Jamaica.

METHODS

We observed 11 adult Beaugregory and 5 adult Threespot Damselfish territories on 22 - 24 February 2006, in the back reef near the Discovery Bay Marine Lab. We chose adult damselfish territories where juveniles were also present. In each territory, we monitored a focal adult for 20 minutes, recording the number of encounters the focal adult had with other fish and the category of each fish encountered. We categorized encountered fish as: (1) adult conspecific, (2) juvenile conspecific, (3) small, colorful heterospecific, (4) large, colorful heterospecific, (5) small, drab heterospecific, or (6) large, drab heterospecific; where small heterospecifc fish were smaller and large heterospecific fish were larger than the focal adult damselfish. We defined each encounter as either an "ignore" (when the adult damselfish did not appear to respond to the presence of the encountered fish) or an "attack" (when the adult damselfish attempted to drive an intruding fish out of its territory).

We tested the effect individual focal damselfish behavior and encountered fishes' morphological category had on the frequency adult damselfish attacked intruding fish using a two-way ANOVA. We compared the compared the means following the ANOVA using a Tukey-Kramer analysis (JMP5.0.1).

RESULTS

Adult damselfish responded differently to the various morphological classes of intruding fish ($F_{5,71}$ = 20.0, P < 0.0001). The effect of individual focal damselfish behavior was not significant, $F_{15,71}$ = 1.26, P = 0.25). Adult damselfish attacked juvenile conspecifics less frequently per encounter than all other categories (Fig. 1). Small, colorful heterospecifics and adult conspecifics were attacked in about one out of every two encounters, and all other categories of heterospecific fish were attacked with high frequency (>70% of the time; Fig. 1).

DISCUSSION

Bright coloration seems to reduce the frequency of attacks by the adult damselfish, as we found adult damselfish attack juvenile damselfish less frequently than all other categories of intruding fish. They also attack small, colorful heterospecifics less than other categories of heterospecifics. However, the difference in the frequency of attacks on juveniles and on

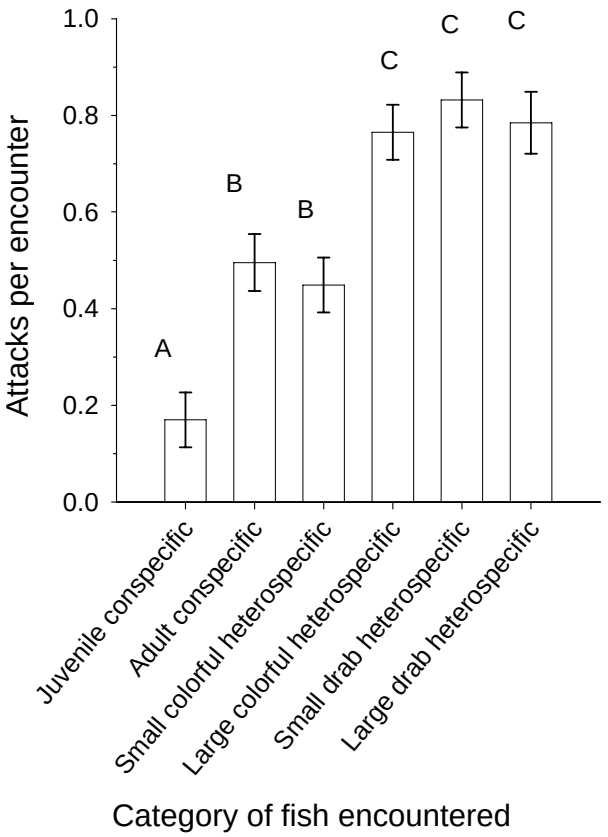

Figure 1: Attacks per encounter by adult damselfish on different categories of fish in Discovery Bay, Jamaica (mean $\pm$ 1 SE). Frequencies of attacks that are significantly different at $\alpha = 0.05$ are represented by different letters (A, B, C; based on Tukey HSD test). Data were collected on 16 individual damselfish. The effect of individual focal damselfish behavior was not significant.

small, colorful heterospecifics suggests that there are additional mechanisms that adult damselfish use to identify conspecific young. Adults may be able to recognize specific color patterns, body shape, or chemical cues of conspecific juveniles. They may attack all conspecific juveniles less in order to avoid attacking their own offspring.

There is also evidence that adults are able to distinguish between species of some fish. For example, we observed squirrelfish utilizing crevices within adult Threespot Damselfish territories without any attack by Damselfish while other colorful fish (blue head wrasse and parrotfish) were attacked. The damselfish apparently distinguished the large, colorful squirrelfish (which do not share a food niche with the damselfish) from other colorful fish--including parrotfish (which share a food niche) and Bluehead wrasse (which prey on damselfish eggs). If damselfish have evolved the ability to recognize non-competitors from competitors and predators, it is possible that they are also able to distinguish the distinctive features of juvenile conspecifics from similar bright color patterns of other small fish species. Given the overlap in food resources between adult and juvenile damselfish, the question of why adult damselfish should attack their juveniles less remains unresolved. However, it is reasonable to assume that adults simply may not consider their juveniles to be competitors.

Previous studies in Discovery Bay examining how size and color of intruding fish affect territory defense of damselfish also found that juvenile coloration decreased adult aggression (Conte 2000). However, in this study, tests using model fish showed different results (decreased aggression towards all colorful fish) than our results. Therefore, we suggest further studies examine the specific mechanisms of recognition in adult damselfish using live fish manipulations, and model fish with different coloration and patterns. Future tests could determine what specific juvenile features adult damselfish are able to recognize, as well as the relative importance of these features in identifying conspecific juveniles as non-competitors.

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DIEL ZOOPLANKTON VARIATION IN A CARIBBEAN BACK-REEF

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Abstract: Many zooplankton populations exhibit diel vertical migration (DVM), a behavioral adaptation where zooplankton minimize exposure to predators by ascending into the water column at night to feed and retreating to the benthos during the day. We predicted zooplankton on a Caribbean back-reef would exhibit DVM. Thus, we predicted that abundance in the upper water column would be greater during the night, and that this trend would be especially strong for larger zooplankton which are subject to more intense visual predation. After sampling in the afternoon and evening we found more zooplankton during the night than day; additionally we found that large copepods, decapod larvae, and polychaete larvae were more abundant at night. Thus, these data supported both predictions.

Key Words: zooplankton, diel vertical migration, copepods

INTRODUCTION

Many marine organisms are either entirely planktonic, or have evolved a complex life cycle which includes a planktonic larval stage. These planktonic organisms are susceptible to intense predation and have therefore evolved behavioral mechanisms to reduce predation pressure while feeding. Such a mechanism is diel vertical migration (DVM), in which these organisms rise into the water column to feed at night and seek refuge in the benthos from visual predators during the day.

We hypothesized that zooplankton on the back-reef of Discovery Bay, Jamaica would exhibit DVM. Therefore, we predicted that zooplankton abundance would be greater at night than during the day. Additionally, because larger zooplankton may be more susceptible to diurnal visual predation, we predicted that among and within taxa this trend would be specially pronounced for large individuals.

METHODS

We collected zooplankton on 25 February 2006 along a 20 meter transect approximately 20 meters south of the reef crest in the west back-reef of Discovery Bay, Jamaica. We collected four day samples from 1400 – 1500 and four night samples from 2200 – 2300 by swimming approximately 0.5 m/s along the transect with a completely submerged (~.5 m below water surface and ~.5 m above substrate) 153 μm mesh net (26 cm diameter). The volume of water filtered for each sample was about 1.06 m^3. We immediately preserved collected samples in the field in 10% formalin sea water and counted and measured all zooplankton in each sample under dissecting microscopes within 24 hours. To examine differences between night and day in overall zooplankton abundance, as well as within size classes of abundant taxa, we used one-way ANOVA on log (x + 1) transformed data.

RESULTS

In total, we sorted 482 zooplankton (Table 1). These numbers are much lower than in previous years (Hunter et al. 2005, Iwamoto et al. 2003). However, visual surveys of the area revealed few zooplankton, so we do not believe this change is a result of sampling error.

In general, there were more zooplankton in the night samples (97 ± 22 organisms/m^3) than in the day samples (24 ± 6 organsims/m^3; $F_{1, 6} = 13.60$, $p = 0.01$). Copepods made up 82% of the day samples and 21% of the night samples. Night samples were primarily composed of polychaete larvae (40%), decapod larvae (19%) and isopods (11%).

We found differences in abundances between day and night samples for the three most abundant taxa that we identified. There were more large copepods (> 1mm) at night than during the day ($F_{1, 6} = 23.67$, $p = 0.0028$), but there were no differences between night and day for other copepod size classes (Fig. 1a) or for copepods overall ($p > 0.5$). There were many more decapods overall at night ($F_{1, 6} = 92.92$, $p < 0.0001$). Only a few decapods in the smallest size class were found during the day (Fig. 1b). There were also more polychaete larvae overall at night ($F_{1, 6} = 100.82$, $p < 0.0001$). Only a few polychaetes in the smallest size class were found during the day (Fig. 1c).

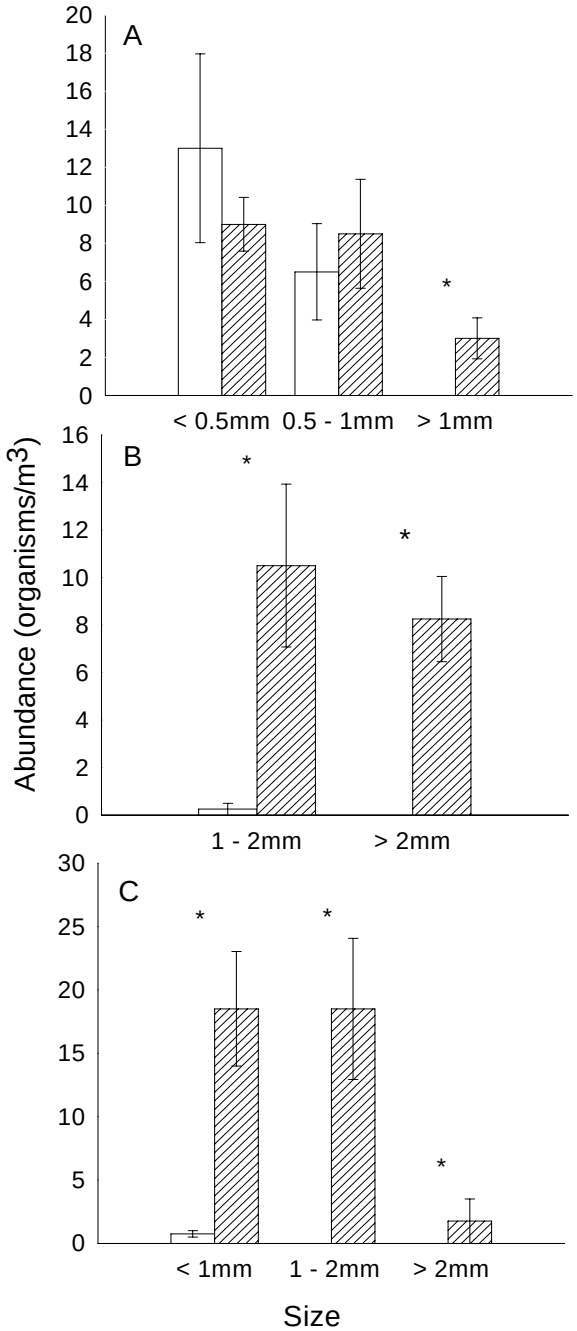

Figure 1. Abundance (mean ± SE) of copepods (A), decapod larvae (B), and polychaete larvae (C) in samples collected during the day (light bars) and at night (shaded bars) at Discovery Bay, Jamaica. Individuals in each taxa were divided according to size class. Asterisks indicate significant differences ($p < 0.05$).

Table 1. Total number of zooplankton in samples collected during the day and at night.

Taxa	Day	Night
Copepods (< 0.05mm)	52	36
Copepods (0.5 - 1mm)	26	34
Copepods (> 1mm)	0	12
Decapods (1 - 2mm)	1	42
Decapods (> 2mm)	0	33
Amphipods (< 1mm)	2	1
Amphipods (1-2mm)	1	9
Amphipods (> 2mm)	0	4
Isopods (< 1mm)	5	12
Isopods (1 - 2mm)	1	26
Isopods (> 2mm)	1	5
Mysids (2 - 4mm)	0	0
Mysids (4 - 6mm)	0	2
Fish larvae (< 2mm)	0	3
Fish larvae (2 - 4mm)	0	3
Fish larvae (> 4mm)	0	1
Polychaete larvae (< 1mm)	3	74
Polychaete larvae (1 -2mm)	0	74
Polychaete larvae (> 2mm)	0	7
Cumacean Shrimp	2	4
Other (Gastropods, Ostracods)	1	5
Total	95	387

DISCUSSION

Many zooplankton in Discovery Bay undergo a diel vertical migration, with larger size classes showing the greatest disparity between day-time and night-time abundances. The increased prevalence of large zooplankton at night is consistent with higher daytime predation as a selective pressure for DVM, with large zooplankton likely being more vulnerable to visual predators.

Zooplankton abundances, particularly copepods, were far lower than in previous studies that used similar methodology (Hunter et al. 2005, Iwamoto et al. 2003). Copepods made up 94% of night samples in 2003, 63% in 2005, but only 21% in our study. This may be the result of a continuing decline over time in copepod abundance and dominance. However, rough weather on the day we collected data is also a possible cause of decreased copepod and overall zooplankton numbers. The weather may have directly affected zooplankton; additionally, it may have had indirect effects, as it forced us to sample further from the reef crest than in past years, over a substrate of patch reef and sand.

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DISTRIBUTION AND SOURCES OF FISH SPECIES RICHNESS IN WEST DISCOVERY BAY

WILLIAM F.J. STORK, CHRISTINA MAY, CATRINA A. LINDGREN,
ERIK E. STANGE, AND THE 2006 FSP CLASS

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

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, α- and β-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:

$$y = \frac{K * x}{d + x}$$

[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:

$$\log(E[S_n]) = h\log(n) + k$$

[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.

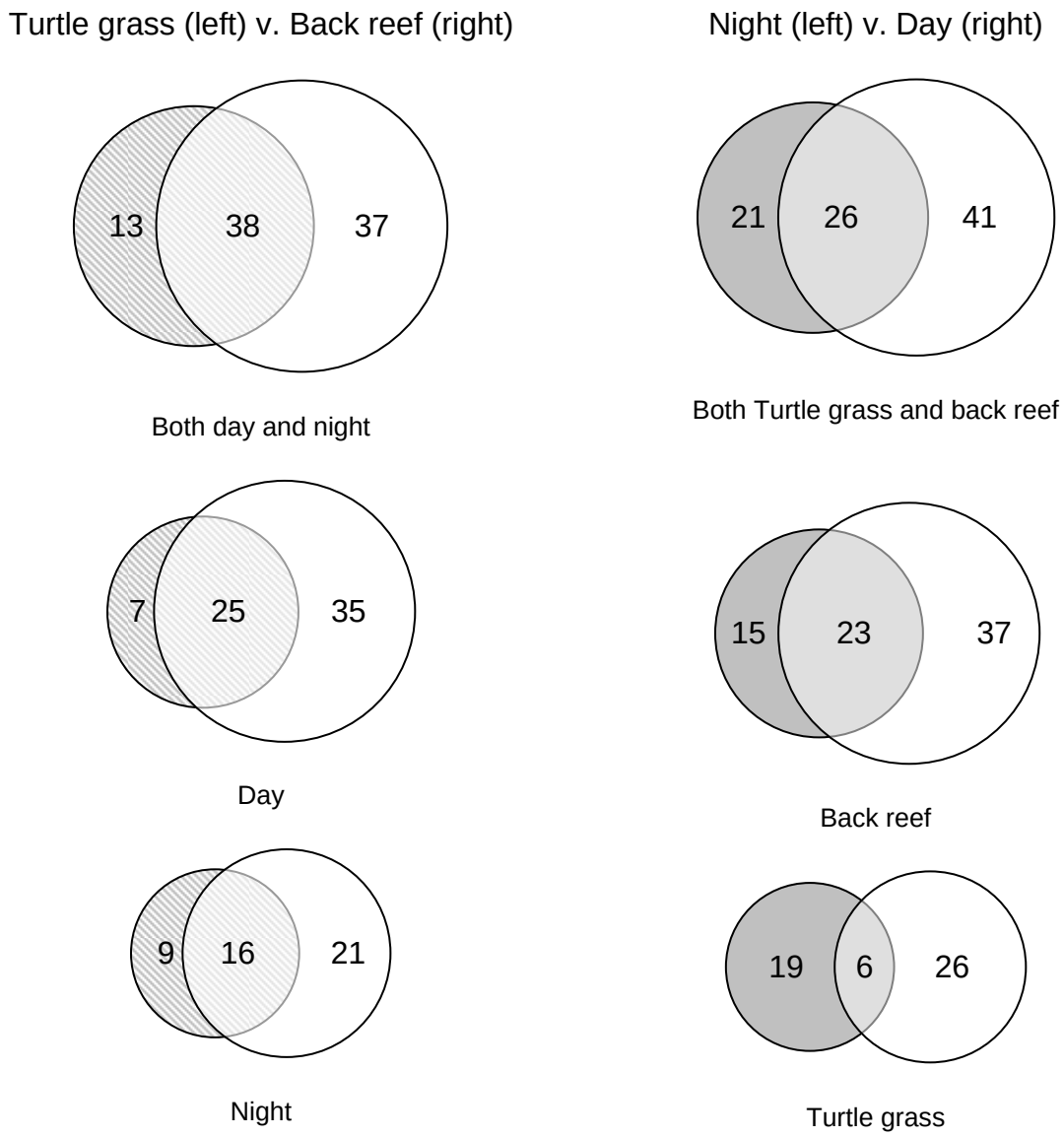

Figure 1. Number of fish species observed during day and night sampling in both turtle grass and back reef habitats in Discovery Bay, Jamaica. Size of circles is proportional to the total number of species observed in each population.

Back reef habitat displayed evidence of higher alpha diversity than turtle grass (mean species per sampled plot ± 1 SE; back reef = 15.69 ± 1.64, turtle grass = 8.38 ± 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], ± 1 SE; back reef = 100.13 ± 2.17, turtle grass = 81.32 ± 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: $\log(E[S_n]) = \mathbf{0.534}\log(n) + 2.858$, $r^2 = 0.990$; turtle grass: $\log(E[S_n]) = \mathbf{0.634}\log(n) + 2.256$, $r^2 = 0.988$; $t_{1,30}$= 4.49, p<0.001, Fig. 2).

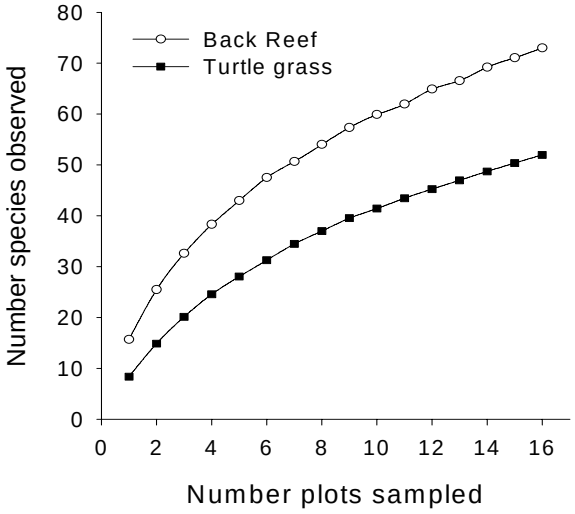

Figure 2. Species-area curves for back reef and turtle grass habitat in Discovery Bay, Jamaica, including both day and night sampling. Points represent the mean number of species found in all permutations of pooled sites, and obscure the standard error bars.

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

	Back reef		Turtle Grass	
Species	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		
Morray, Goldentail				X
Needlefish, Keeltail	X			
Ocean surgeonfish	X	X	X	
Parrotfish, Bluelip	X			
Parrotfish, Bucktooth	X		X	
Parrotfish, Greenblotch	X			

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

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 follwing 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^3 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.

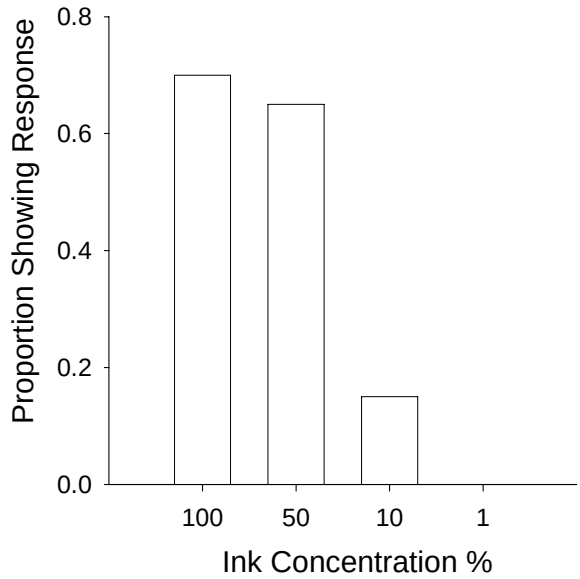

Figure 1. The percentage of *Aplysia dactylomela* that responded to being squirted with ink at different concentrations. A response was defined as a sudden change in behavior that involved withdrawing its head, balling up, or closing its parapodia.

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 noncalcalareous 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.

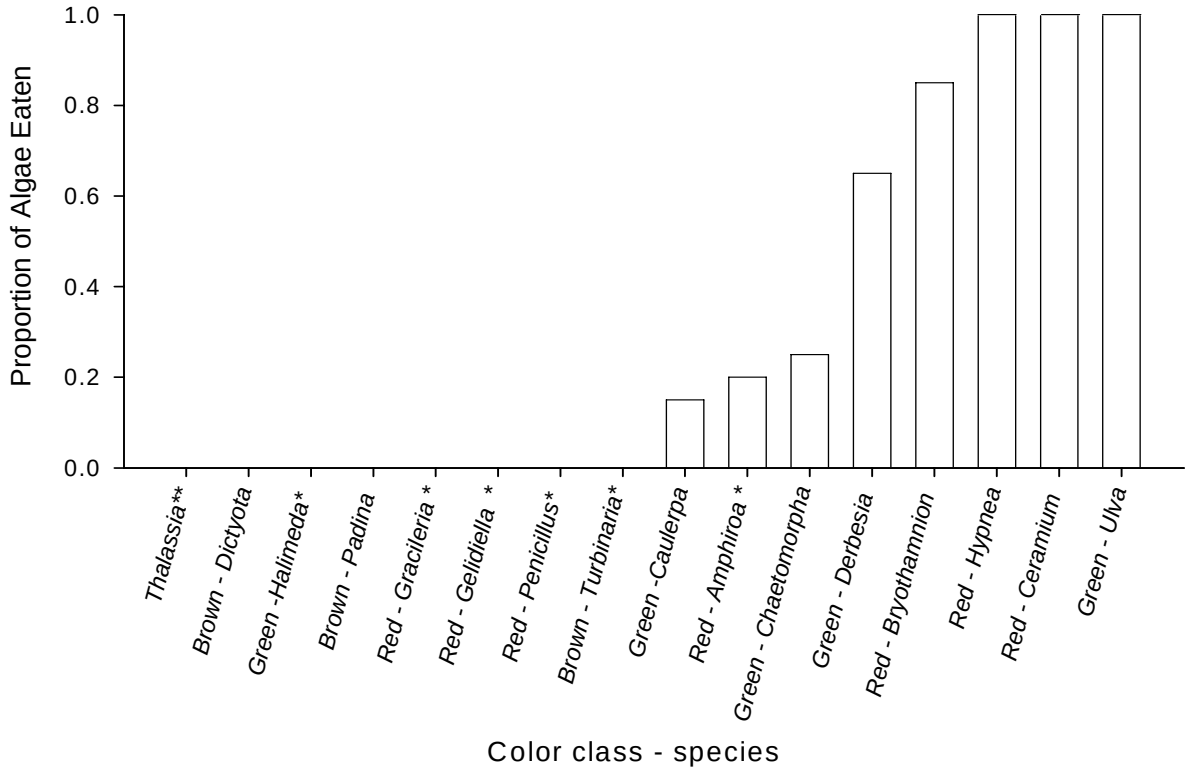

Figure 2. The proportion of algae eaten by *Aplysia dactylomela* after 24 hours in a lab setting exposed to 20 grams of each type of algae. An asterisk denotes calcareous algae, while all others are noncalcareous. ***Thalassia* is a true plant rather than an algae.

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MECHANISMS AFFECTING THE COLONIZATION OF AN ARTIFICIAL SUBSTRATE BY MARINE INVERTEBRATES

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

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 function 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.

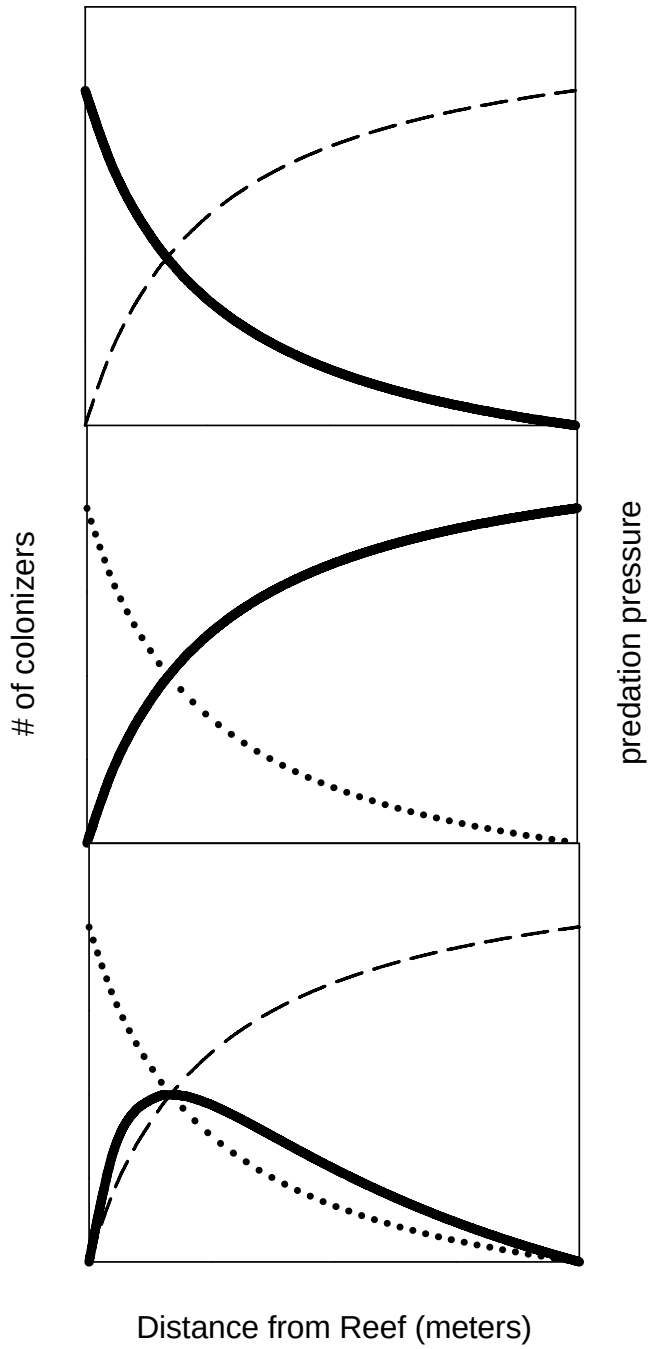

Figure 1. Potential relationship between total invertebrate colonizer abundance (solid line) and A) dominant pre-colonization predation pressure (dashed line) (Note: pattern of colonizer abundance also consistant with dispersal limitation from source), B) dominant post-colonization predation pressure (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 transect to ensure that no other coral reef wall or patch was within 20 m.

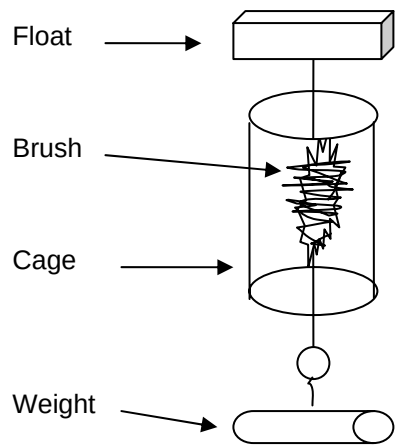

Figure 2. ACS device

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 μm 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^2 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:

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

[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

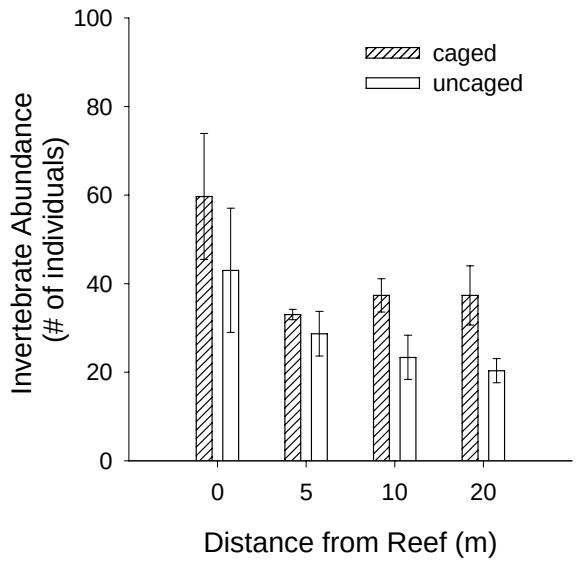

Figure 3. Mean invertebrate abundance (± 1 SE) after 72 hours on caged and uncaged artificial colonization sites placed at 0, 5, 10 and 20 m from large coral reefs in Discover Bay, Jamaica. Abundance decreased significantly with distance from reef ($F_{3,16}$ = 3.25 P = 0.05) and was significantly higher 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 polycheate) (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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Research advisors: Faculty and graduate students. Faculty editor: John J. Gilbert

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 π x length x 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 rugosity = complexity / [(2 x height) + (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^2 to 16.6 m^2 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^2) 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).

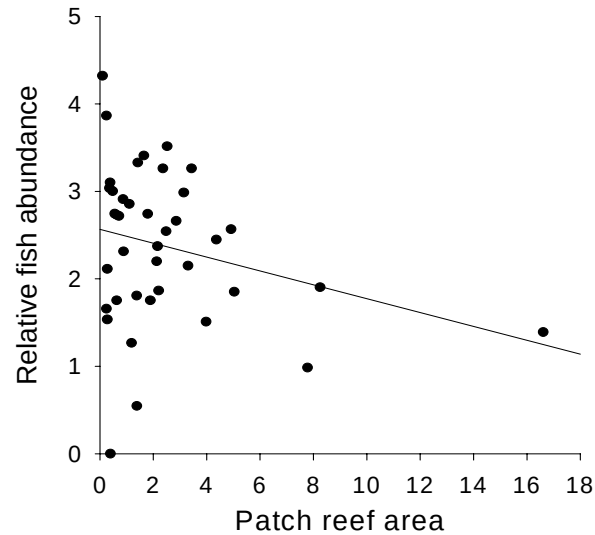

Figure 1. Relative fish abundance, *Ln [(fish abundance / patch reef area) + 1]*, as a function of reef patch area in the back reef off of Discovery Bay Marine Laboratory, Jamaica. Relative fish abundance decreases with increasing patch reef area (r^2 = 0.12, df = 37, P = 0.03).

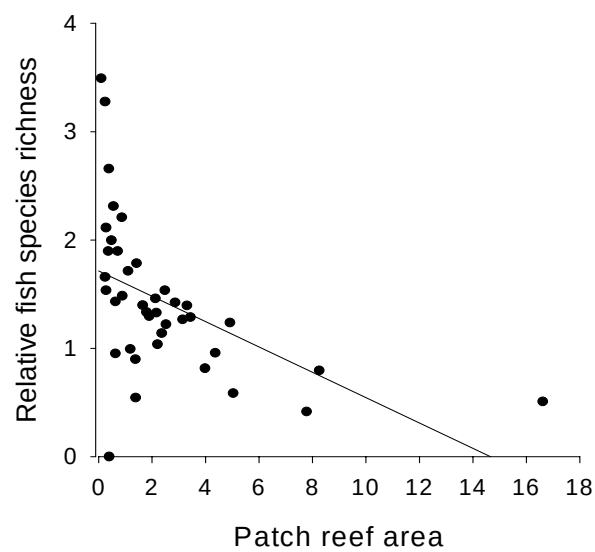

Figure 2. Relative fish species richness, *Ln [(fish species richness / patch reef area) + 1]*, as a function of reef patch area in the back reef off of Discovery Bay Marine Laboratory, Jamaica. Relative fish species richness decreases with increasing patch reef area (r^2 = 0.32, df = 37, P < 0.001).

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 (fish abundance + 1)]*, and (C) Gini diversity index [*Ln (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	$F_{1,39}$	P
Area	**42.7**	**7.63**	**0.01**
Complexity	2.91	0.52	0.48
Distance	12.2	2.18	0.15
Area*Complexity	**24.0**	**4.29**	**0.05**
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	$F_{1,39}$	P
Area	**8.69**	**12.4**	**0.001**
Complexity	0.27	0.38	0.54
Distance	0.92	1.32	0.26
Area*Complexity	**4.65**	**6.65**	**0.01**
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	$F_{1,38}$	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, it's 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, dealin 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 ± SE; 4.4 ± 5.28 individuals/m^2) than in the algal zone (0.1 ± 5.64 individuals/m^2; $F_{1,13}$ = 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 ± 166 individuals/100 m^2) than the algal zone (670 ± 177 individuals / 100 m^2; $F_{1,13}$ = 7.61, $p < 0.02$; Fig. 1). This relationship was driven largely by

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

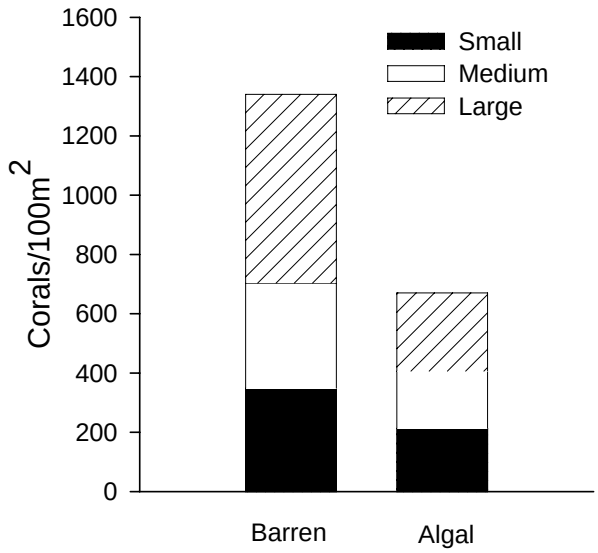

Figure 1: Coral densities and percent composition of total corals by size class pooled across transects at two dives sites in barren (n=4 at M1, n=4 at Dancing Lady) and algal (n=4 at M1, n=3 at Dancing Lady) zones along the west fore reef, Discovery Bay, Jamaica. There was significant difference in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

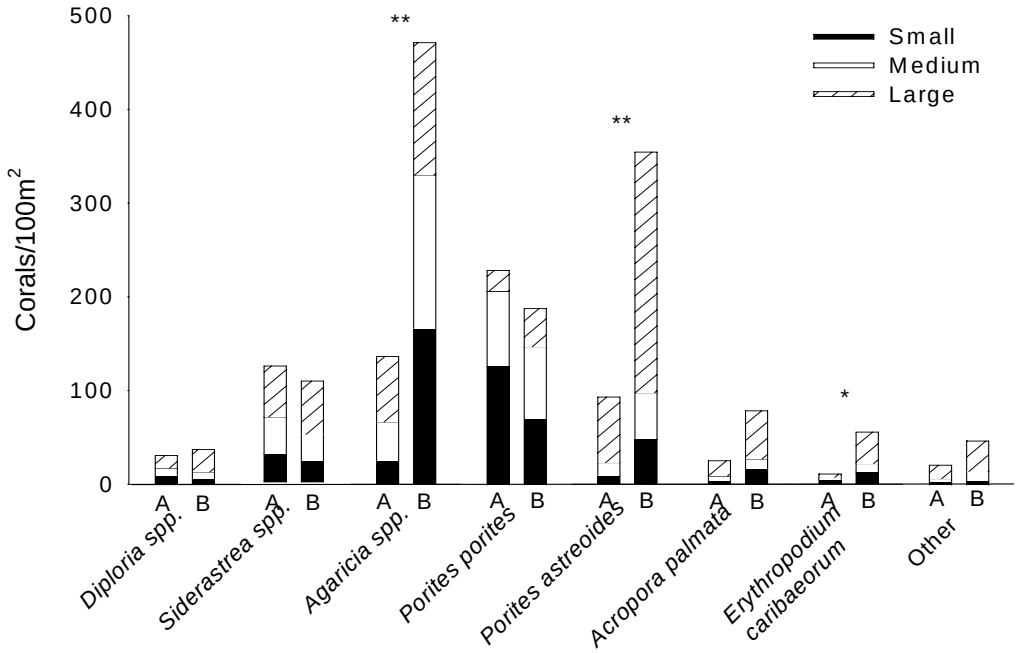

Figure 2: Density of different coral species by size class pooled across transects at two dive sites in algal (A) (n=4 at M1, n=3 at dancing Lady) and barren (B) (n=4 at M1, n=3 at Dancing Lady) zones along the west fore reef, Discovery Bay, Jamaica. * denotes significant difference in total counts of 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
Diploria spp.	barren	9	12	38	4.71	0.09
	algal	13	11	19		
Siderastrea spp.	barren	36	45	91	2.81	0.25
	algal	42	55	76		
Agaricia spp.	barren	266	262	226	34.81	< 0.0001
	algal	35	58	98		
Porites porites	barren	114	123	65	26.38	< 0.0001
	algal	178	112	31		
Porites asteroides	barren	77	79	411	1.27	0.53
	algal	13	19	98		
Acropora palmata	barren	26	17	82	1.34	0.51
	algal	5	7	23		
Erythropodium	barren	21	14	54	4.24	0.12
caribaeorum	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: $r2 < 0.0003$, $p > 0.97$).

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 ± SE/ 100m^2) 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 ± 54.0	213 ± 50.5	3.35	0.09
Medium	355 ± 48.3	193 ± 51.6	5.27	0.04
Large	637 ± 80.3	264 ± 85.8	10.05	0.007

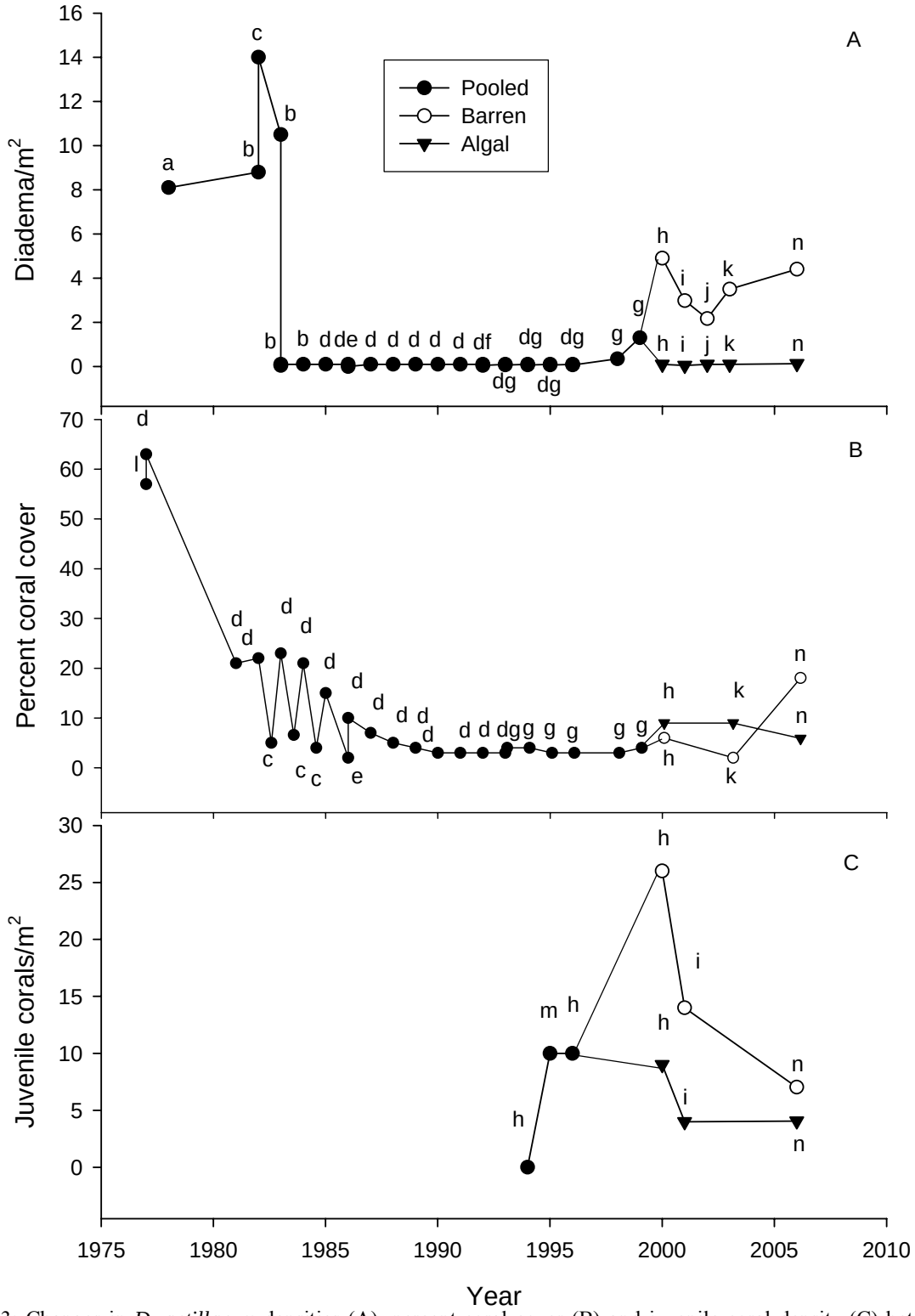

Figure 3: Changes in *D. antillarum* densities (A), percent coral cover (B) and juvenile coral density (C) between 3 and 7 meters depth on the west fore reef, Discovery Bay, Jamaica. Letter above each data point corresponds with its source: (a) Carpenter 1981, (b) Hughes et al. 1985, (c) Liddell and Ohlhorst 1986, (d) Hughes 1994, (e) Hughes et al. 1987, (f) Balser 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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