SELECTIVITY OF COVERING MATERIAL IN TWO SEA URCHINS, *TRIPNEUSTES VENTRICOSUS* AND *LYTECHINUS VARIEGATUS*

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Abstract: Many sea urchin species exhibit covering behavior, and several explanations for this behavior have been posed. One hypothesis is that urchins cover to protect themselves from harmful UV radiation. If this is true, then urchins should select covering materials that block light using photoreceptors on their aboral epidermis. To test this, we gave two species of urchins (*Tripneustes ventricosus* and *Lytechinus variegatus*) grass strips, clear plastic strips, and black plastic strips and recorded the percentage of strips they held on to after 30 seconds. While *Tripneustes* did prefer black covering strips to clear, *Lytechinus* made no distinction between the two. This suggests that the two species have different mechanisms for covering, and that *Tripneustes* requires covering material that blocks sunlight. *Lytechinus* may prefer grass to unnatural plastic strips, which suggests that covering is a cryptic behavior.

Key words: black plastic, clear plastic, light, *Thalassia testudinum*

INTRODUCTION

Many sea urchin species exhibit covering behavior, where shells, algae, leaves, or other debris are heaped on the aboral surface of the body. Several explanations for this behavior have been posed and tested. Covering may provide camouflage from predators, protection from toppling in heavy surge (Lees and Carter, 1972), shielding from suspended sediment (Richner and Milinski 2000), or protection from UV light (Lees and Carter 1972, Adams 2001, Butcher et al. 2002). While none of these has been shown definitively to be the explanation for covering, light has been shown to be a cue that induces urchins to cover, such that urchins cover more in full sunlight than partial sunlight or darkness (Kehas and Theoharides 2003).

In this study, we examined the selectivity of urchins for covering material. If urchins display a preference for covering materials that block light, this would suggest a mechanism where urchins use photoreceptors on their aboral epidermis to select covering materials. If this is the case, then urchins may select covering material to shield sunlight. Alternatively, urchins may display no preference for light-blocking materials, picking up any material that they can move onto their aboral surface. This would suggest a mechanism where urchins detect and select covering material using only tactile sensors. The lack of preference for light blocking material would suggest that other explanations for covering behavior are more probable than shielding from sunlight. We tested this on the urchins *Tripneustes ventricosus* and *Lytechinus variegatus* by comparing covering behavior when urchins were presented with opaque and translucent covering materials.

METHODS

On 25 - 26 February 2004, we collected ten *T. ventricosus* and seven *L. variegatus* urchins from the West Back Reef at Discovery Bay, Jamaica. Between 1330 and 1630, we placed each urchin in an individual tub with running seawater in full sunlight. Each urchin was presented with three kinds of covering material, one at a time: 2 x 4 cm strips of black plastic, clear plastic, and turtle grass (*Thalassia testudinum*; to serve as a control for the effects of using

plastic). Plastic strips were scored with a sharp probe to make a rougher surface to which tube feet could attach. While translucent covering materials are not normally available to urchins in nature, they allow examination of the mechanism behind this behavior. However, it is of some interest to note that *Tripneustes* will cover with opaque plastic in nature; one individual on the East Back Reef had most of its aboral surface covered with green plastic (R. Quinn Thomas, pers. obs.).

We offered each strip to the urchin using forceps and allowed the urchin to hold and feel the strip with its tube feet. After 30 seconds, we recorded whether the urchin had accepted the strip by continuing to hold it with its tube feet, or whether the urchin had rejected the strip by pushing it aside or allowing it to float away. We repeated this procedure on each urchin using five strips of each kind of covering material, for a total of 15 strips per urchin, presented in a random order. We calculated the proportion of strips accepted by each urchin for each kind of covering material and arcsine-transformed these values for statistical analysis.

Results

Tripneustes favored black strips over clear strips (paired-t = -4.58, df = 9, P = 0.001), grass over clear strips (paired-t = -3.36, df = 9, P= 0.008) and did not distinguish between grass and black strips (paired-t = -0.48, df = 9, P = 0.64; Fig 1). *Lytechinus* showed no preference between clear strips and black strips (paired-t = 0.76, df = 6, P = 0.76), tended to prefer grass over clear strips (paired-t = -2.27, df = 6, P = 0.06), and had no strong preference for grass over black strips (paired-t = -1.92, df = 6, P = 0.10; Fig 1).

For each treatment, the two urchin species did not differ significantly from one another in their preference for grass strips (t = 0.14, df = 15, P = 0.89), black strips (t = -1.01, df = 15, P = 0.33), or clear strips (t = 0.21, df = 15, P = 0.83).

Discussion

While *Tripneustes* did prefer the black strips to clear strips, *Lytechinus* made no distinction between the two. It is possible that the species have different mechanisms for selecting covering material, or that the purpose of covering differs for the two species. For *Tripneustes*, it may not be sufficient to simply cover; the covering material must block light. This provides evidence that photoreceptors are used in the selection of covering material in *Tripneustes*. Furthermore, this is consistent with the hypothesis that *Tripneustes* covers itself to shield sunlight, possibly protecting itself from harmful UV rays.

Lytechinus appeared to be less discriminating in its choice of covering material. However, we did see a trend where *Lytechinus* preferred grass material over black or clear plastic. *Lytechinus* may have rejected the plastic material

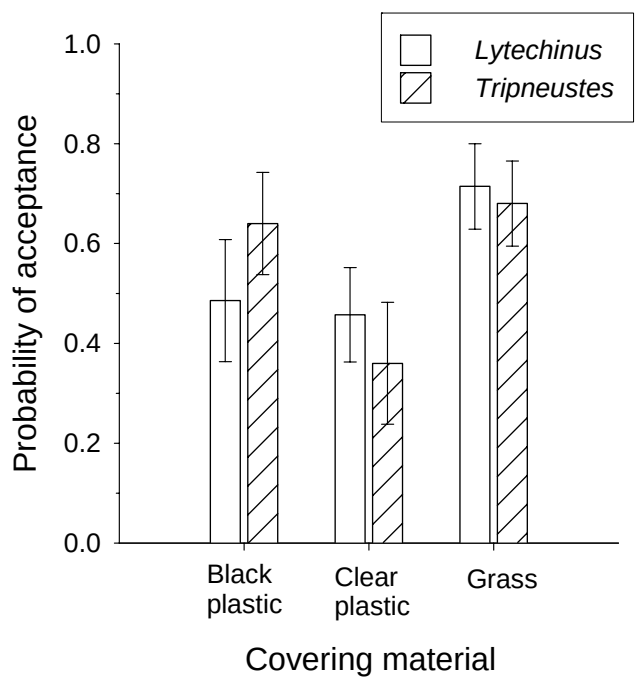

Figure 1. Mean (± SE) probability of acceptance (number of strips accepted out of five) of three types of covering material for ten *Tripneustes ventricosus* and seven *Lytechinus variegatus* urchins.

simply because it was a foreign, introduced material. Another possibility is that *Lytechinus* chooses material that allows it to blend in to its natural substrate (turtle grass). This idea should be tested in the field.

The different preferences for covering material shown by *Lytechinus* and *Tripneustes* may be linked to a difference in the cost and benefits of covering between the two species. For example, urchin tube feet that hold on to covering material are also used for respiration. Therefore, interference with respiration may be a cost of covering. Future studies should examine the costs of covering, and how they vary among species.

Overall, it appears that light is an important factor in the covering behavior of some sea urchins. *Tripneustes* covers more in full than reduced sunlight (Kehas and Theoharides 2003) and, as shown here, selects covering material that reduces sunlight on its aboral surface. There may be other benefits to covering, like protection from surge, and future studies could determine whether covering for these reasons affects the selection of covering material.

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SUBSTRATE SELECTION OF TWO SEA CUCUMBER SPECIES AND THEIR EPITHELIAL ALGAE COMMUNITIES

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Abstract: Two species of sea cucumber (*Isostichopus badionotus* and *Holothuria mexicana*) occur in Discovery Bay, Jamaica, and some individuals have macroalgal communities growing on them. We hypothesized that habitat differentiation may allow these two species to exist on similar resources, and we also tested for patterns in body algae growth. We found little evidence of habitat differentiation, but macroalgae was found almost exclusively on *H. mexicana*. There was no relationship between macroalgae coverage and habitat type. It is possible that differences in epithelial characteristics between the two sea cucumber species result in a disparity in suitability for algal colonization and growth.

Key words: Holothuria mexicana, Isostichopus badionotus, *macroalgae, niche differentiation*

INTRODUCTION

Two species of diurnally active holothurians occur in the backreef lagoon at Discovery Bay, Jamaica. Both species, *Holothuria mexicana* (donkey dung) and *Isostichopus badionotus* (three-rowed), are deposit feeders in shallow water (Hammond 1982). However, little else is known about the ecology of either species. Though *H. mexicana* and *I. badionotus* do not occupy separate temporal or food niches, it is possible that there is some other form of ecological differentiation between the two species. For example, these two species of sea cucumber may occupy different substrates and so be able to coexist in the same environment.

Casual observations revealed that some sea cucumbers have macroalgae growing on them. To our knowledge, no studies have examined this phenomenon on sea cucumbers, though this association has been identified in other marine organisms (e.g., Ballantine et al. (2001) identified 30 species of macroalgae growing on spotted scorpionfish, *Scorpaena plumieri*). We tested for interspecific and habitat-related patterns in the macroalgal communities associated with *H. mexicana* and *I. badionotus*.

METHODS

We sampled the sea cucumber community in the backreef lagoon at Discovery Bay, Jamaica on 24 - 26 February 2004. For all sea cucumbers located along three 150 m transects, we recorded species, percent macroalgae coverage on dorsal half of body, and depth at which the cucumber was found. We estimated the percent of four different substrate types in each cucumber's habitat (a 1 m radius circle around the cucumber); substrate categories were bare sand, seagrass, rock/coral, and macroalgae. We haphazardly selected nine sea cucumbers with percent algal coverage ranging from 5 to 80%, and identified the epithelial macroalgal species on each.

RESULTS

The substrate around *H. mexicana* consisted of a significantly higher percentage of rock/coral than that around *I. badionotus* ($t = 2.03$, $df = 34$, $P = 0.05$). Amounts of other substrate types did not differ between the two species (sand: $t = -1.4$, $df = 34$, $P = 0.17$; grass: $t = -0.28$, $df = 34$, $P = 0.78$; macroalgae: $t = 0.19$, $df = 34$, $P = 0.85$; Fig. 1).

Sixteen of 19 *H. mexicana* had some macroalgae growth on the body (mean coverage of all 19 = 27%; range 0 - 95%), while only one of 17 *I. badionotus* showed algae growth (5% coverage on this individual). For *H. mexicana*, percent of body algal coverage was not correlated with depth (r = 0.04) or percent of macroalgae in the surrounding substrate (r = -0.06). Seven of ten macroalgae species identified were found on multiple cucumbers (Table 1). Macroalgal species richness on an individual cucumber ranged from two to six.

Table 1. Species and frequency of occurrence of macroalgae growing on nine cucumbers examined (eight *H. mexicana* and one *I. badionotus*). Asterisk (*) denotes algal species found on both sea cucumber species; all other species were found only on *H. mexicana*.

Species	Occurrence (# cucumbers)
Laurencia intricata	8*
Dictyota cervicornis	6
Lobophora variegata	3
Hypnea valentiae	2*
Laurencia filifornis	2
Cladophora prolifera	2
Polysiphonia sp.	2
Ceramium sp.	1
Gelidiella acerosa	1
Amphiroa fragilissima	1

DISCUSSION

Mean percent cover of rock/coral was significantly higher for habitats in which *I. badionotus* were found than for *H. mexicana* habitats; however, this substrate type was only a small component of the overall habitat substrate composition for both species. Furthermore, there was substantial overlap in the ranges of habitat

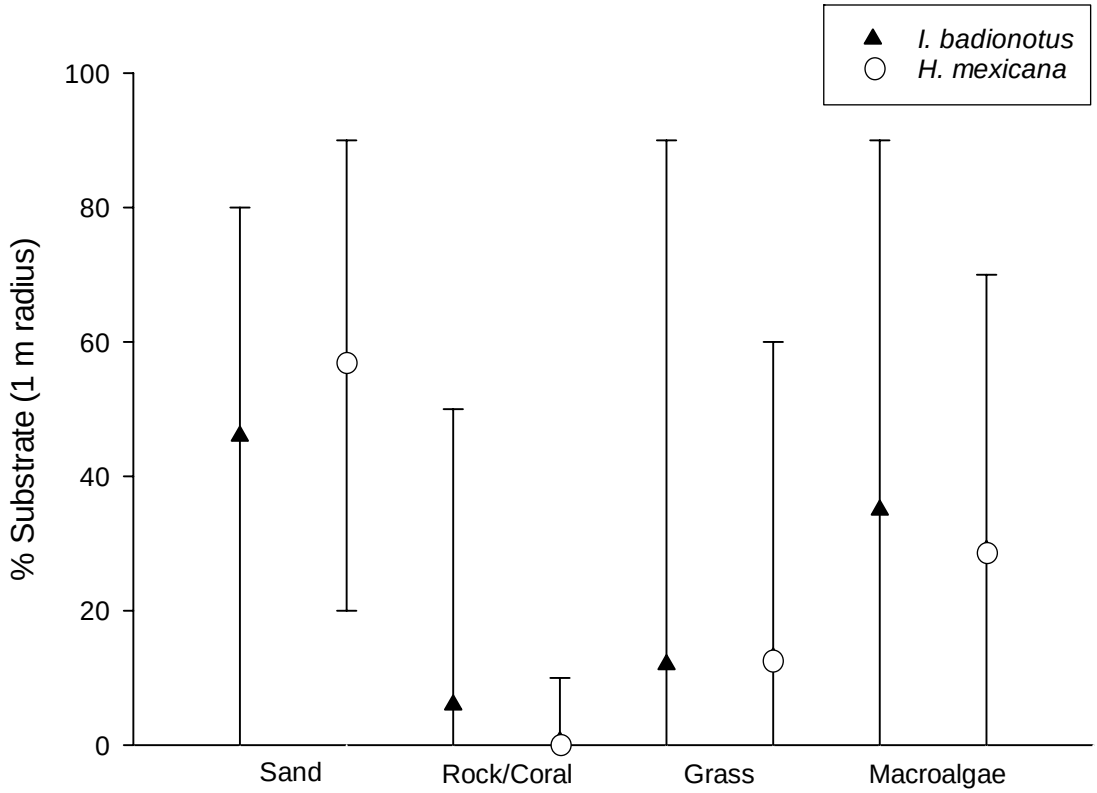

Figure 1. Mean microhabitat composition in a 1 m radius circle around each sea cucumber (circles and triangles represent means; bars represent maximum and minimum). *H. mexicana*: n = 19; *I. badionotus*: n = 17.

types in which the two species were found (Fig. 1). Thus, *H. mexicana* and *I. badionotus* did not differ in their microhabitat distributions, suggesting that there is no niche partitioning by habitat type between these two species. Also, it is unlikely that the two species have temporal or food resource niche partitioning, because they are both primarily nocturnal feeders and both ingest sediment (Hammond 1982). Because we found no evidence for niche partitioning, it is possible that resources for sea cucumbers at Discovery Bay are not limiting, and the populations are instead regulated by other mechanisms such as predation.

A majority of *H. mexicana* had algal communities growing on them. In contrast, algae were only found on a single *I. badionotus*, suggesting that there is some mechanism preventing algal colonization and/or growth on *I. badionotus.* Many fish possess a mucopolysaccharide layer on their epithelial cells that prevents algal growth, though scorpionfish harbor a high diversity of macroalgae species, which may enhance their cryptic appearance (Ballantine et al. 2001). It seems that a similar range of responses to algal growth exists in sea cucumbers. Conceivably, *I. badionotus* produces a compound that limits algal growth, while *H. mexicana* may benefit from improved camouflage. Future studies could compare epithelial characteristics of the two sea cucumber species to determine if this is the case. Furthermore, potential costs and benefits of algal growth to sea cucumbers should be examined.

The community of algae growing on the sea cucumbers was surprisingly diverse. Clearly, numerous species are capable of colonizing and growing on sea cucumbers, though we found a wide range of occurrence frequency: the most common macroalgae species was found on eight of nine cucumbers, while three species were found on only one of nine. Further studies could examine whether sea cucumber algae communities are a reflection of the surrounding algae community (i.e., whether relative abundances of algae species are similar on cucumbers and surrounding substrate), or if there are characteristics of certain algae species that are conducive to growth on sea cucumbers. For example, algal species that are commonly found on loose rocks or coral rubble may be better able to grow on sea cucumbers, which offer a superficially similar substrate. Also, it is possible that various successional stages of algae communities found on sea cucumbers contribute to the diversity of algae observed. This sea cucumber-macroalgae system is an unexplored relationship and merits further study.

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FACTORS AFFECTING TROPICAL FISH COMMUNITIES ON PATCH REEFS

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Abstract: Tropical reefs are known to support diverse and abundant populations of fish. These fish are divided into resident and transient communities that differ in their use of reefs and are affected by competition, substrate complexity, and food availability. We examined the effects of *Diadema antillarum*, reef complexity, and macroalgal cover on resident, transient, and total fish communities on patch reefs. Transient fish abundance and species richness decreased with increasing *D. antillarum* abundance while resident fish abundance increased with increasing substrate complexity. Macroalgal cover was not related to community composition.

Key words: Diadema antillarum, *macroalgal cover, reef complexity, resident species, topographic chain method, transient species*

INTRODUCTION

Tropical patch reefs support abundant and diverse communities of both resident and transient fishes. Resident species primarily reside in a specific area of the reef to take advantage of local resources, while other species roam across reefs, most likely expending more energy to find the best resources available. These fish communities are affected by a suite of biotic and abiotic factors, in particular competition for resources, substrate complexity, and food availability.

The reefs in Discovery Bay, Jamaica, are not pristine; the depletion of large predatory fishes by overfishing in particular has led to an abundant population of long-spined black urchins, *Diadema antillarum*. These urchins consume a large amount of macroalgae at night (Sammarco 1982), and hide in holes and crevices during the daytime. *D. antillarum* is therefore a strong competitor with most fishes for both space and food on patch reefs, and thus its presence or abundance may affect both resident and transient fish communities. We predicted that increased *D. antillarum* abundance would decrease abundance and richness in overall resident and transient fish communities. One common reef fish, the threespot damselfish may be an exception because they are capable of evicting urchins from their territories (Williams 1979). We predicted that increased threespot damselfish abundance would be correlated with decreased urchin abundance.

We also hypothesized that substrate complexity would affect only the resident fish community, such that resident abundance and richness would increase with complexity. We expected no changes in transient species because they are less reliant on the physical structure of reefs. Macroalgae may be an important resource for herbivorous fish as well as for carnivores which eat small invertebrates in algae. We expect to see an increase in the species abundance and richness for both transient and resident fish species in areas of high macroalgal cover. We also expect to see decreased macroalgal cover with increasing *D. antillarum* density because *D. antillarum* is known to be a voracious herbivore.

METHODS

We sampled patch reefs in the back reef area north of the Discovery Bay Marine Laboratory, Jamaica on the afternoons of 25 - 26 February 2004. We chose reefs that were predominantly boulder coral (*Montastrea*), roughly 3 m in length, 1.5 m deep, and surrounded by turtle grass or sand. We counted the number of *D. an-*

tillarum on each reef and counted the number and types of fish species that lived on or crossed over the reef area during a 20 minute sample period. We also noted whether each fish species was transient or resident (Appendix 1). We calculated a reef topographic complexity index at the widest point across each reef: complexity = (1 - length / 3D length) using the chain method of Aronson and Precht (1995). We estimated the percentage of macroalgal cover for each patch observed.

RESULTS

As *D. antillarum* abundance increased on patch reefs both the abundance (n = 8, r = 0.96, P = 0.0002) and richness (n = 8, r = 0.79, P = 0.02) of transient fishes decreased significantly (Fig. 1 and Fig. 2, respectively). Urchin abundance did not affect the abundance (n = 8, r = 0.57, P = 0.14) or richness (n = 8, r = 0.39, P = 0.34) of the resident community. Threespot damselfish abundance had no effect on abundance of *D. antillarum* (n = 8, r = 0.25, P = 0.55).

The abundance of resident fishes (n = 7, r = 0.91, P = 0.004) increased with increasing reef complexity, while the abundance of transient fishes was not affected (n = 7, r = 0.48 P = 0.28; Fig. 3). The richness of the resident (n = 7, r = 0.13, P = 0.44) and transient (n = 7, r = 0.48, P = 0.78) fish communities did not change with in-

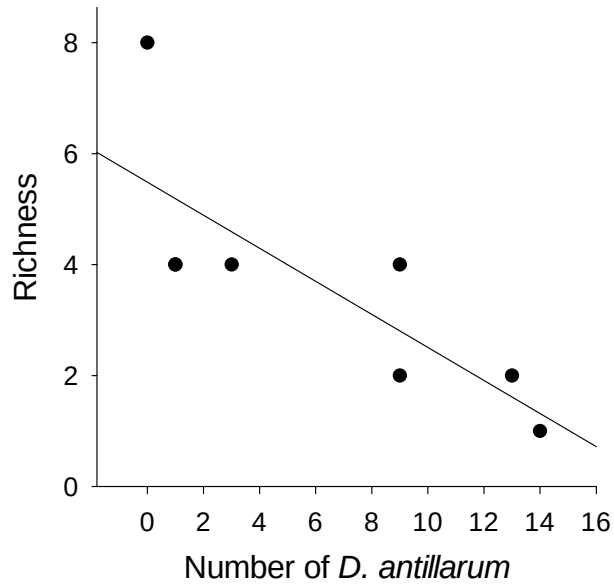

Figure 2. Effects of *D. antillarum* on richness of transient fish communities on patch reefs.

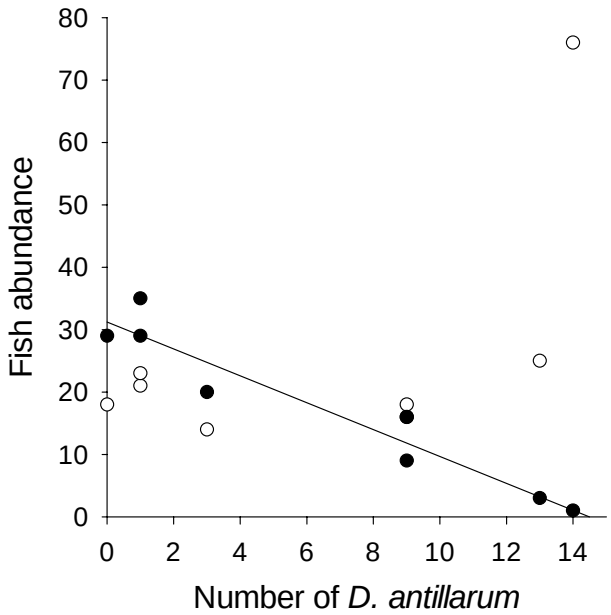

Figure 1. Effects of *D. antillarum* on abundances of resident and transient fish on patch reefs. Open circles = resident fish; line, filled circles = transient fish. Only the significant trend is shown.

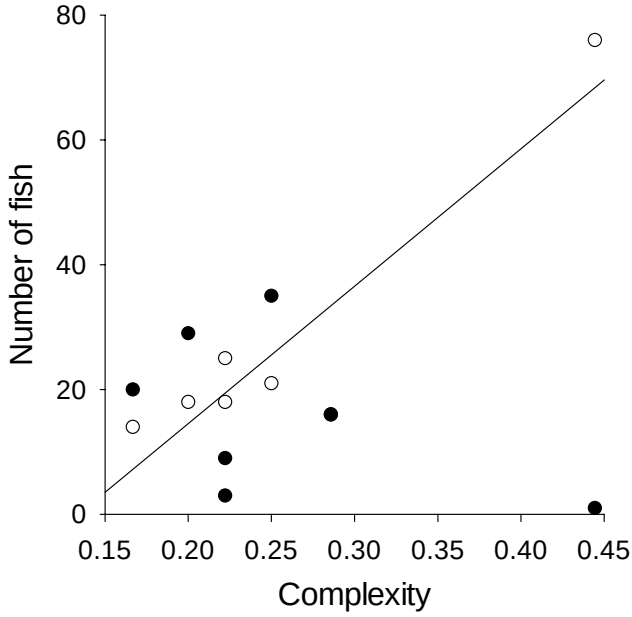

Figure 3. Effects of substrate complexity on abundances of resident and transient fish on patch reefs. Solid line, open circles = resident fish; filled circles = transient fish. Only the significant trend is shown.

creasing reef complexity.

The percent macroalgal cover on patch reefs was not affected by the abundance of *D. antillarum* ($n = 8$, $r = 0.17$, $P = 0.67$). The percent macroalgal cover did not affect the abundance or richness of residents or transients ($n = 8$, all $P \geq 0.26$).

Discussion

Both *D. antillarum* and substrate complexity affect the fish community on patch reefs: *D. antillarum* caused a decrease in transient species abundance and richness, and reef complexity increased resident species abundance. Overall, macroalgal cover did not influence any aspects of the fish communities, nor was macroalgal cover affected by *D. antillarum* density. Because we did not categorize types of algae on patch reefs, we were unable to evaluate the effects of different algal species on fish community. Presumably, fish communities will vary according to the availability of their preferred algal food source. *D. antillarum* may selectively feed on a few algal species and therefore do not affect total macroalgal cover.

Due to the high mobility of transient species, close proximity of patch reefs, and variability in the number of *D. antillarum* on patch reefs, transient fish can choose the best reefs for foraging. They may avoid patches with *D. antillarum* because the urchins lower abundance or quality of available food. On the other hand, residents are not affected by *D. antillarum*, suggesting that the urchin does not limit their food or habitat availability. Surprisingly *D. antillarum* abundance is not affected by threespot damselfish abundance; they seem to coexist on patch reefs without substantial interactions.

Transient fish typically swim from one reef to another, rather than using the reef for refuge, and so may not be a determining factor in reef choice. Resident fish are more reliant on their home reefs to provide cover, and are most abundant on reefs with the highest complexity. The richness of resident fish was unrelated to complexity, suggesting that the same species occur on most patch reefs. Complexity therefore affects total abundances of residents, but not species composition.

While abundance of competitors and reef complexity did affect the resident and transient fish communities on patch reefs, there may be additional factors which contribute to the diversity and abundance of fishes in these habitats. Reefs experience a high level of temporal and spatial variation which may influence these fish communities. Additionally, interspecific interactions undoubtedly influence fish populations. Further studies could investigate other variables that affect these diverse fish communities.

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Appendix 1. Resident and transient species observed on patch reefs in the back reef north of Discovery Bay Marine Lab, Jamaica.

Resident species	Age	Total observed
Foureye butterflyfish	adult	3
	juvenile	0
Blue tang	adult	0
	juvenile	1
French grunt	adult	0
	juvenile	65
Beaugregory	adult	1
	juvenile	6
Bicolor damselfish	adult	0
	juvenile	3
Sergeant major	adult	1
	juvenile	0
Threespot damselfish	adult	56
	intermediate	27
	juvenile	10
Barred hamlet	adult	0
	juvenile	1
Indigo hamlet	adult	1
	juvenile	0
Hybrid indigo/ barred hamlet	adult	1
	juvenile	0
Harlequin bass	adult	0
	juvenile	1
Dusky squirrelfish	adult	1
	juvenile	0
Longjaw squirrelfish	adult	1
	juvenile	0
Longspine squirrelfish	adult	1
	juvenile	0

Resident species	Age	Total observed
Squirrelfish	adult	1
	juvenile	0
Bridled goby	adult	14
	juvenile	0
Gold spot goby	adult	1
	juvenile	0
Blennies	adult	13
	juvenile	0
Porcupine fish	adult	1
	juvenile	0
Goldentail moray	adult	1
	juvenile	0

Appendix 1 (Continued).

Transient species	Age	Total observed
Doctorfish	adult	0
	juvenile	1
Ocean surgeonfish	adult	1
	juvenile	11
Redband parrotfish	adult	1
	juvenile	0
Striped parrotfish	adult	18
	juvenile	85
Stoplight parrotfish	adult	7
	juvenile	2
Bluehead wrasse	adult	2
	juvenile	2
Slippery dick	adult	1
	juvenile	3
Spotted goatfish	adult	7
	juvenile	0

PATTERNS OF DISTRIBUTION OF THREE BRITTLESTAR SPECIES (ECHINODERMATA: OPHIUROIDEA) ON CORAL REEFS

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Abstract: Three common species of brittlestars occur under coral rubble in Discovery Bay, Jamaica. We studied the patterns of intraspecific and interspecific distribution of these species. We found that there is a relationship between rubble size and brittlestar abundance. We also found that brittlestars are distributed randomly with respect to conspecifics and interspecifics. This may attest to the success of brittlestars in minimizing both intraspecific and interspecific competition.

Key words: co-occurrence, coral, Ophiocoma echinata, Ophioderma appressum, Ophiocoma pumila, *Poisson, rubble*

INTRODUCTION

Brittlestars are ubiquitous on coral reefs, with more than 1,800 species worldwide. They tend to be cryptic in their habits, avoiding light and seeking refuge in dark crevices during the day (Kaplan 1982). In Discovery Bay, Jamaica, 14 species can be found occurring under rubble (Sides 1981). Our study focuses on the three most common species: *Ophiocoma echinata, Ophioderma appressum,* and *Ophiocoma pumila.* Paine and Platt (1999) studied the coexistence of these species under rubble in the back reef of Discovery Bay. They found that *O. echinata* was found less frequently with other species than with conspecifics, while *O. appressum* was found more frequently with other species. However, their study did not distinguish whether patterns of coexistence were due to tendencies to avoid conspecifics, tendencies to co-occur with other species, or a combination of both.

To better understand distribution patterns of brittlestars under rubble, we studied the intraspecific distribution of the three common species in the back reef at Discovery Bay to determine whether they are clumped, overdispersed, or randomly distributed with respect to conspecifics. We also analyzed patterns of co-occurrence between the three brittlestar species. In this way, we expected to determine if intraspecific and/or interspecific interactions drive the patterns we observed.

METHODS

On 25 - 26 February 2004, we overturned 76 pieces of coral rubble in the back reef of Discovery Bay, Jamaica, in water depths of 1.5 - 2 m. Each haphazardly selected rubble fragment was within a size range that could be overturned by a single snorkeler. We recorded the dimensions of each fragment and the abundance of each species of brittlestar present.

We calculated expected Poisson distributions for each of the three species and compared that with the observed distributions to determine whether brittlestar occurrence is a random event (meaning that the presence of one brittlestar does not affect the probability of another being present). We used contingency tables to determine whether patterns of co-occurrence between the three species deviated from random.

RESULTS

Of the 76 rubble pieces that we turned over, 65 sheltered brittlestars. A maximum of seven brittlestars was found underneath one rubble fragment. Size of rubble fragments ranged from 100 - 1140 cm^2.

The distribution of brittlestars did not differ significantly from a Poisson distribution for any of the three species (*O. echinata:* $\chi^2 = 1.75$, df = 2, P = 0.41; *O. appressum:* $\chi^2 = 2.25$, df = 1, P = 0.14; *O. pumila:* $\chi^2 = 1.32$, df = 1, P = 0.25; Fig. 1). Various subsets of rubble fragments of narrower size ranges, in which the area-abundance relationship was not significant, also did not differ significantly from a Poisson distribution. Thus, the relationship between rubble size and brittlestar abundance did not influence our comparison to the Poisson distribution. Patterns of co-occurrence also appeared to be random (*O. echinata* and *O. appressum:* $\chi^2 = 3.00$, df = 1, P = 0.08 , *O. appressum* and *O. pumila*: $\chi^2 = 2.62$, df = 1, P = 0.11, *O. pumila* and *O. echinata*: $\chi^2 = 1.35$, df = 1, P = 0.24; Table 1). We found a positive lin-

Table 1. Observed frequencies of *O. echinata*, *O. appressum*, and *O. pumila*. Values in parentheses are expected frequencies under the null hypothesis of no association between species.

		O. echinata	
O. appressum		Present	Absent
	Present	20 (17)	3 (6)
	Absent	36 (39)	17 (14)

		O. appressum	
O. pumila		Present	Absent
	Present	4 (6)	16 (14)
	Absent	19 (17)	37 (39)

		O. pumila	
O. echinata		Present	Absent
	Present	12 (15)	44 (41)
	Absent	8 (5)	12 (15)

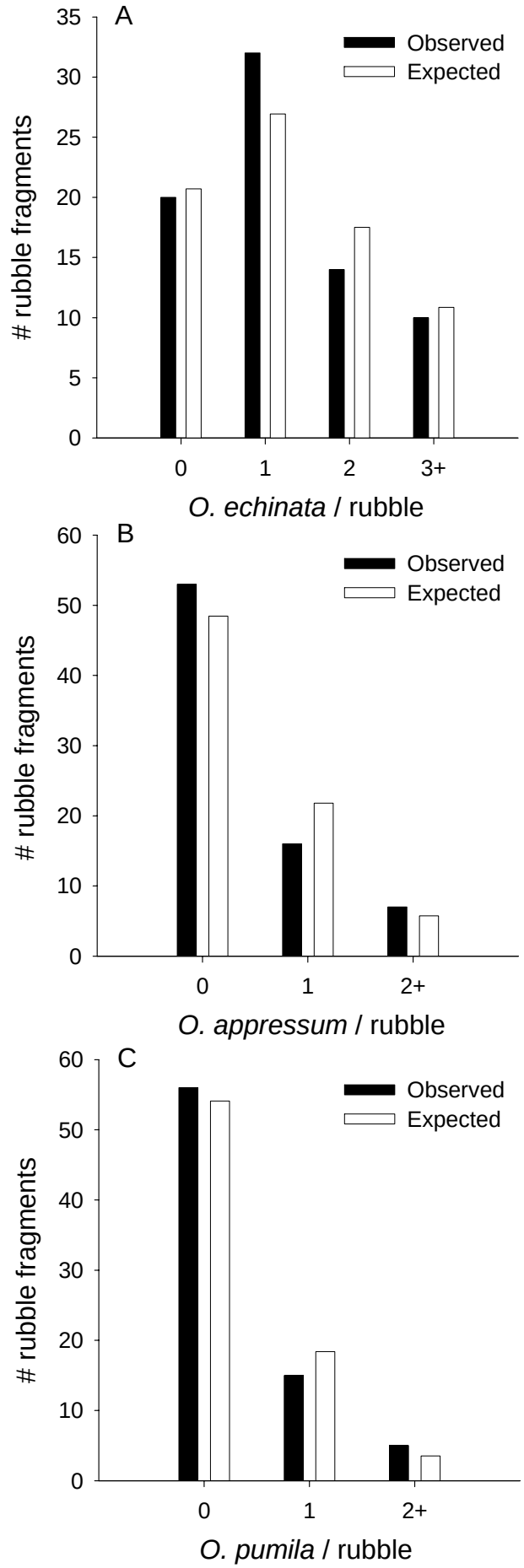

Figure 1. Observed and expected distributions of brittlestars under rubble fragments. Expected values calculated from a Poisson distribution. (A) *O. echinata*: mean = 1.3. (B) *O. appressum*: mean = 0.4. (C) *O.pumila*: mean = 0.3.

ear relationship between size of rubble and abundance for *O. echinata* and *O. appressum*, but not for *O. pumila* ($r^2 = 0.12$, P = 0.002; $r^2 = 0.11$, P = 0.004; $r^2 = 0.0014$, P = 0.75, respectively; Fig. 2). Total brittlestar abundance also increased linearly with rubble size ($r^2 = 0.18$, P = 0.0001).

DISCUSSION

The pattern of brittlestar abundance matches the Poisson distribution, and thus, appears to be driven by random processes. That is, the presence of one brittlestar does not influence the probability of the presence of another. Contrary to the results of Paine and Platt (1999), we found that no two species tended to co-occur less or more frequently than by chance. This suggests that there is no competitive exclusion or facilitation between these three brittlestar species.

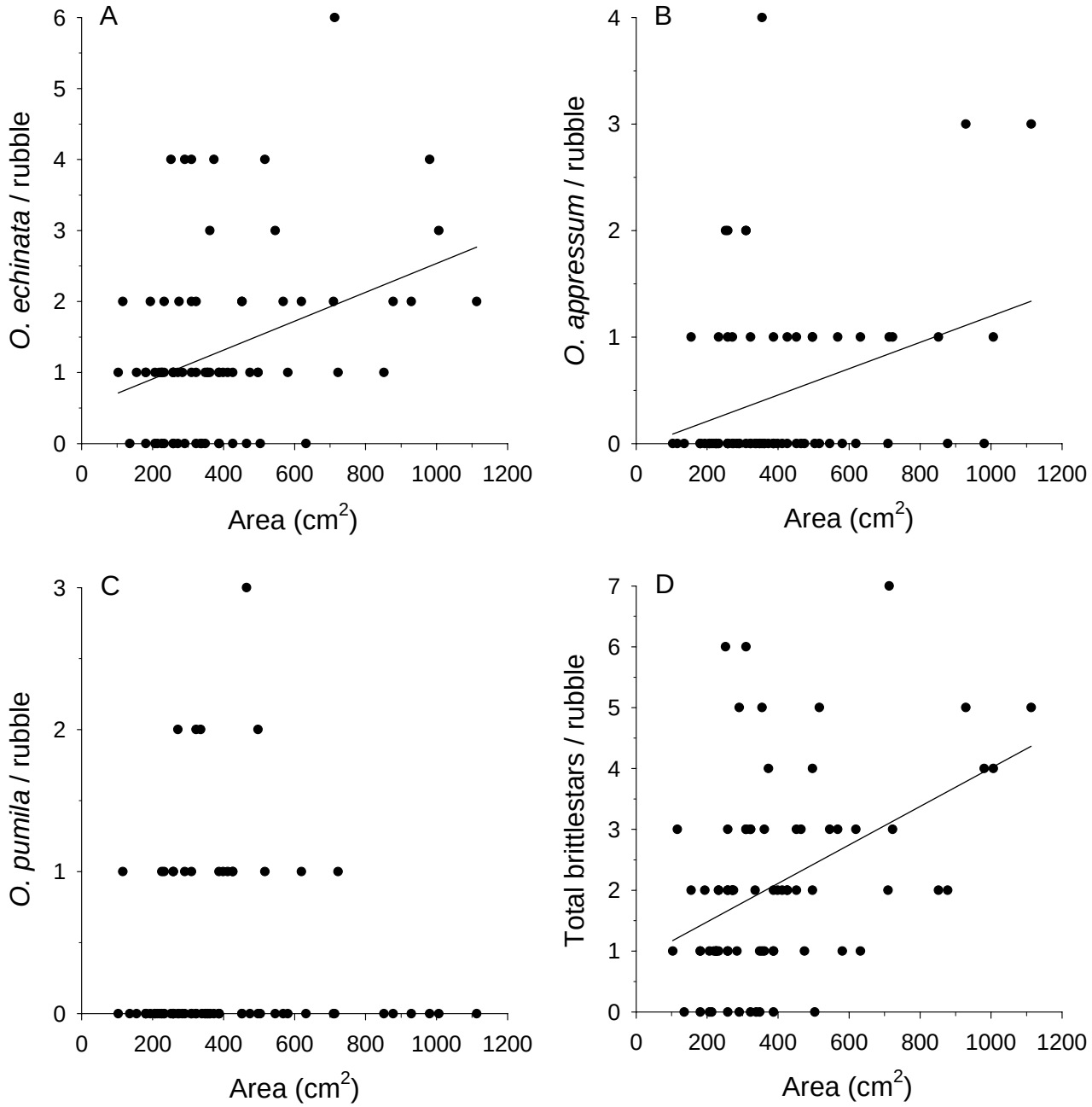

Figure 2. The relationship between brittlestars per rubble fragment and area of rubble fragment. (A) *O. echinata*: y = 0.50 + 0.13x. (B) *O. appressum*: y = -0.04 + 0.008x. (C) *O. pumila*: no significant relationship. (D) Total: y = 0.85 + 0.02x.

The relationship between rubble size and brittlestar abundance in *O. echinata* and *O. appressum* suggests that either larger fragments are capable of housing more individuals (with space being limiting), are encountered more often by colonizing individuals, or are preferred more. However, we can eliminate the first possibility of space limitation because the pattern of brittlestar distribution matches the Poisson distribution. They are not over-dispersed as one would expect if space were limiting. We can also reject the second possibility of unequal encountering rates, since we would expect to see this relationship in all three species, but it is not the case for *O. pumila.* Therefore, it seems that preference for larger rubble fragments is the most reasonable explanation for the relationship between rubble size and abundance. Larger fragments may provide better refuge from predators because they allow brittlestars to retreat farther from exposure at the edge. However, *O. pumila* seems to utilize different spaces within rubble fragments than *O. echinata* and *O. appressum*. We observed *O. pumila* pressing themselves into small crevices, unlike the other two species which tended to occupy the space underneath the rubble. Thus, *O. pumila* may obtain refuge in a different manner.

Patterns of brittlestar dispersal appear largely driven by random processes. However, preference for larger rubble fragments may also play an important role. Future studies examining the role of habitat preference and predation in brittlestars may improve our understanding of patterns in brittlestar distribution.

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COMPARISON OF INFAUNAL COMMUNITIES IN CRYPTIC AND EXPOSED SPONGES AT DIFFERENT DEPTHS

ELIZABETH V. WILSON, BRENDA M. WHITED, SARA M. HELLMUTH AND JILL L. HARRIS

Abstract: Sponges are sources of refuge and food for microfauna in coral reefs. Characteristics of infaunal communities in exposed sponges are well studied, but infaunal communities in cryptic sponges have not been examined. We compared infaunal communities in cryptic and exposed natural sponges at three depths. In addition, we ran a controlled experiment to evaluate the effects sponge orientation (oriented towards water column = exposed and oriented into substrate = cryptic) on infaunal communities. Abundance of infaunal organisms did not vary with depth or between cryptic and exposed natural sponges. Richness was greater in cryptic sponges, perhaps due to fewer chemical defenses. We found no effect of orientation of synthetic sponges on infaunal community composition. Both abundance and richness were highest at shallow depths, but did not differ between cryptic and exposed sponges. This same pattern may have been obscured in natural sponges by variation among species and growth forms. Cryptic sponges harbor diverse infaunal communities that are similar to communities in exposed sponges.

Key words: abundance, community composition, Discovery Bay, richness, synthetic sponges

INTRODUCTION

Sponges function as important sources of refuge and food for microfauna in coral reef ecosystems (Westinga and Hoetjes 1981). Sponges have two growth orientations: on the bottom of buried coral rubble (cryptic sponges) and emerging into the water column (exposed sponges). Past studies have examined the infaunal communities of single species of exposed sponges (Ferrie et al. 2003, Campbell and Lovette 1990), but no study has examined infaunal communities in cryptic sponges.

Exposed sponges may be more accessible to organisms both in the water column and on the substrate than cryptic sponges that grow under rubble in the substrate. Cryptic sponges may also pump less water or be exposed to less water flow than exposed sponges. Because some infaunal organisms feed on matter pumped through sponges, these sponges may be a poorer quality habitat. Finally, there may be less need for microfauna in cryptic environments to take refuge in sponges because they are already somewhat hidden from predation. Therefore, there may be increased infaunal abundance and richness in exposed sponges than in cryptic sponges. We also predict that the composition of infaunal communities in these two sponge types may differ because of the different quality of habitat and food source they may offer.

The effect of depth on infaunal communities in exposed sponges is disputed. Ferrie et al. (2003) found no differences in infaunal abundance in *Aplysina fistularis* with depth, but Campbell and Lovette (1990) found decreased abundance of organisms in *Ircina strobilina* in deeper (20 m) water. We collected both exposed and cryptic sponges at three depths to compare their infaunal communities and determine whether there were effects of depth, and if these effects were similar in cryptic and exposed sponges.

Using synthetic sponges to control for variation among natural sponges in growth form, osculum size, atrial volume, and chemical defenses, we tested for effects of sponge orientation (exposed or cryptic) and depth. Experimental sponges differed only in their orienta-

tion (face up in the water column to simulate exposed sponges vs. face down in the sand to simulate cryptic sponges) and in depth. If orientation is the factor driving community differences, then we would expect to see similar patterns in synthetic and natural sponge communities. We also expected to see similar patterns of depth effects in synthetic and natural sponges.

METHODS

We examined the infaunal invertebrate communities in natural sponges collected from Discovery Bay, Jamaica. We collected cryptic and exposed sponges at depths of 1 m in the west back-reef, and 11 m in the fore-reef at M1 and Dairy Bull. We measured the volume of each sponge by water displacement in a graduated cylinder. To extract the infaunal organisms, we cut up the sponges and rinsed them twice in seawater and once in freshwater, filtering the rinse water each time through a 153 μm mesh. We preserved the samples in 10 parts seawater, 1 part formalin. We examined the infauna with dissecting microscopes, recording size and taxonomic category of each organism.

For the experimental portion of our study, we cut synthetic sponges to 50 ml volumes. We tied the sponges to the top and bottom of a ceramic tile using fishing line, and weighted the bottom side of the tile with two bolts (Fig. 1). Top sponges will hereafter be referred to as exposed, and bottom sponges as cryptic. We placed four tiles in the sand at the sand-reef interface at depths of 1 m in the west back-reef and 11 m and 20 m in the fore-reef at M1. We collected the tiles after three days, and examined the infaunal organisms of the synthetic sponges using the same methods as for the natural sponges.

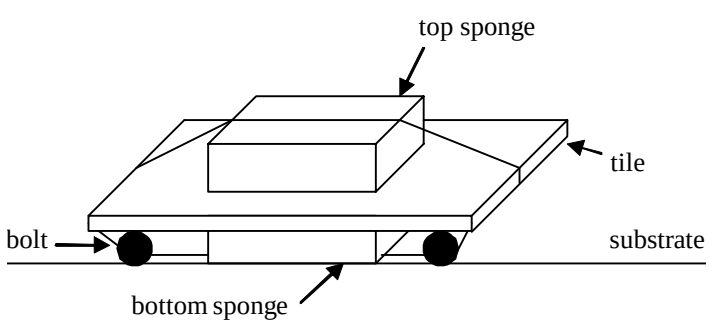

Figure 1. Experimental tiles simulating exposed (top) and cryptic (bottom) sponges with synthetic cellulose sponges. Tiles were placed on sandy substrate.

Two tiles at 1 m and one tile at 20 m were overturned when we collected them. Because the sponges originally on the bottom of these tiles all showed extensive fading while the top sponges did not, we were confident that they had been flipped over for the majority of the three days. We therefore used the final orientation of the sponges for our analyses.

For each sample, we calculated the abundance and taxon richness of infaunal organisms. We analyzed the abundance of organisms in each of five main taxonomic groups (Copepoda, Amphipoda, Isopoda, Polychaeta, and Decapoda) for natural and synthetic sponges at 11 m. We chose 11 m as a representative depth because it was intermediate and no tiles at this depth had been overturned.

RESULTS

There were rich and abundant infaunal communities in natural cryptic sponges. Abundance of infaunal organisms ranged from 0.8 to 7.5 organisms per ml sponge and taxon richness ranged from 0.4 to 2.5 taxa per ml sponge.

Abundance of infaunal organisms in natural sponges did not vary with sponge type (cryptic or exposed) or across depth (Table 1, Figure 2). Taxon richness tended to be higher in cryptic sponges than in exposed sponges, although there were no differences across depth (Table 1, Figure 3).

Abundance of infaunal organisms in synthetic sponges was higher in sponges at 1 m than in sponges at either 11 m or 20 m, but was

not different between cryptic and exposed sponges (Table 2, Figure 4). Taxon richness was higher in synthetic sponges at 1 m than in synthetic sponges at either 11 m or 20 m (Figure 5), but did not differ between cryptic and exposed sponges (Table 2).

The abundance of organisms in each of the five dominant taxonomic groups did not differ between cryptic and exposed natural sponges, or between top and bottom synthetic sponges (Table 3).

DISCUSSION

Living cryptic sponges harbor infaunal communities that are similar to those in living exposed sponges, despite the seemingly less accessible locations of the former. Although abundance of infauna did not differ between cryptic and exposed sponges, there was a trend towards greater taxon richness in the cryptic sponges. Cryptic sponges tend to be more palatable than exposed sponges (Wulff 1997), pos-

Table 1. 2-way ANOVA results comparing abundance of infauna and taxon richness per ml of cryptic and exposed natural sponges at three depths.

	Abundance			Taxon richness		
Treatment	F	df	P	F	df	P
Depth	2.24	1	0.16	0.91	1	0.36
Sponge type	0.37	1	0.55	3.74	1	0.07
Depth x sponge type	1.02	1	0.33	0.04	1	0.84

Table 2. 2-way ANOVA results comparing abundance of infauna and taxon richness per 50 ml of cryptic and exposed synthetic sponges at three depths.

	Abundance			Taxon richness		
Treatment	F	df	P	F	df	P
Depth	18.74	1	**0.0003**	10.75	1	**0.004**
Sponge type	0.19	1	0.66	1.37	1	0.26
Depth x sponge type	0.07	1	0.80	0.75	1	0.40

Table 3. T-test results comparing abundance of infauna by taxa in exposed and cryptic sponges at 20 m. There were no decapods in any natural sponges.

	Natural sponges			Synthetic sponges		
Taxon	t	df	P	t	df	P
Copepoda	0.04	5	0.97	1.07	6	0.32
Amphipoda	-0.36	5	0.73	-1.35	6	0.23
Isopoda	1.15	5	0.30	-0.40	6	0.70
Polychaeta	-0.32	5	0.77	-1.10	6	0.32
Decapoda	NA	NA	NA	-0.66	6	0.54

sibly due to lower chemical defenses. If chemical defenses also have a detrimental effect on infaunal organisms, cryptic sponges may then be a more suitable habitat for infaunal organisms. Our study showed that there was no difference between cryptic and exposed sponges in the abundance of fauna in each of the five classes. This suggests that the increased rich-

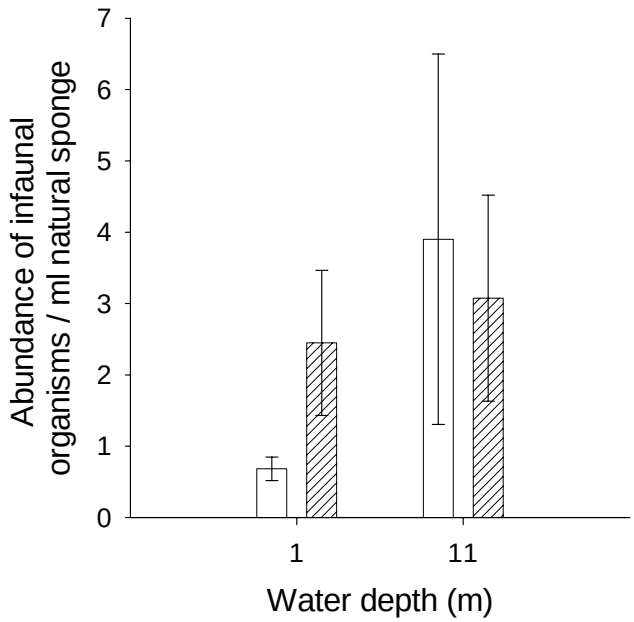

Figure 2. Mean abundance of infauna per ml of natural sponge tissue from two depths at Discovery Bay, Jamaica. Open bars = exposed sponges, hatched bars = cryptic sponges. Sample size above each bar. Error bars show 1 SE.

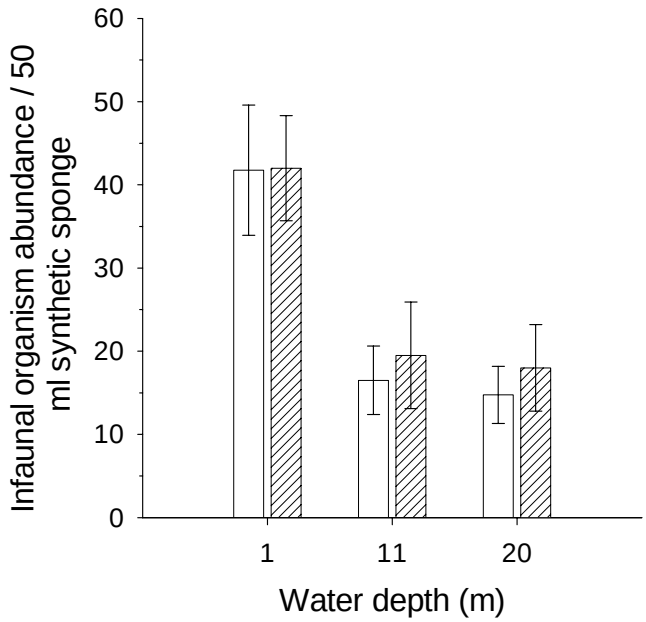

Figure 4. Mean abundance of infauna per 50 ml of synthetic sponge from two depths at Discovery Bay, Jamaica. Open bars = top sponges, hatched bars = bottom sponges. N = 4 for each bar. Error bars show 1 SE.

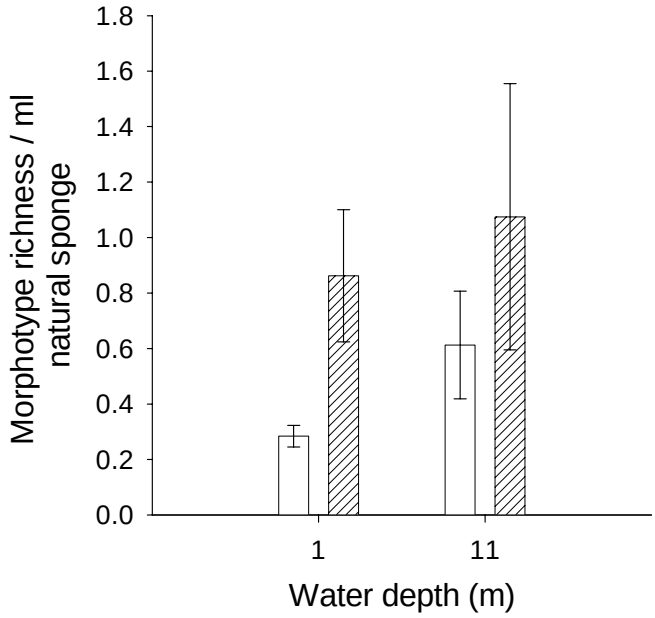

Figure 3. Mean taxa richness per ml of natural sponge from two depths at Discovery Bay, Jamaica. Open bars = exposed sponges, hatched bars = cryptic sponges. Sample size above each bar. Error bars show 1 SE.

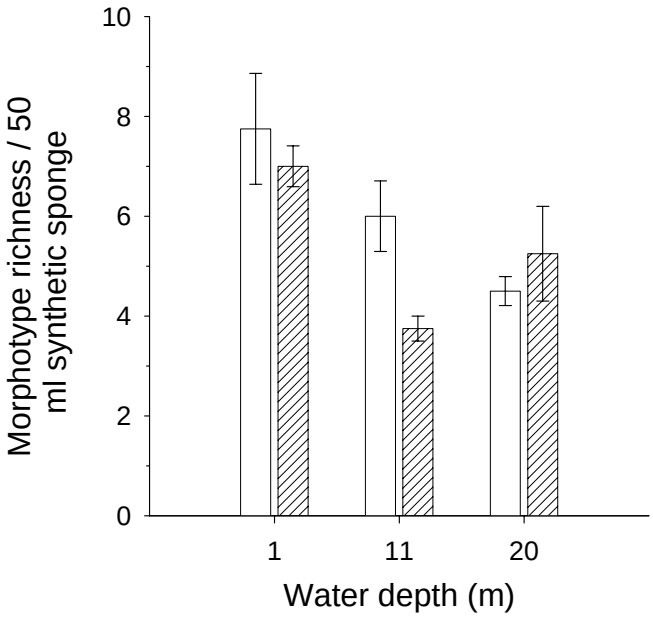

Figure 5. Mean taxon richness per 50 ml of synthetic sponge from three depths at Discovery Bay, Jamaica. Open bars = top sponges, hatched bars = bottom sponges. N = 4 for each bar. Error bars show 1 SE.

ness in cryptic sponges is a result of differences at a finer taxonomic scale of classification.

Unlike natural sponges, synthetic sponges showed no difference in taxon richness based on sponge orientation. It is possible that orientation does not influence community richness, or that our experimental design did not effectively simulate differences between cryptic and exposed sponges. Additionally, the difference in richness patterns between natural and synthetic sponges may have been caused by functional differences. Natural sponges provide both habitat and feeding opportunities to their associated infaunal communities, whereas synthetic cellulose sponges provide only habitat. Some organisms that feed in natural sponges may have been absent from the synthetic sponges, thereby reducing differences between communities occupying top and bottom synthetic sponges.

We found significantly higher abundance and taxon richness in synthetic sponges at the 1 m depth, but this pattern was not observed in natural sponges. Variations among natural sponges may have obscured the depth related patterns we observed in our synthetic sponges. Campbell and Lovette (1990) found that abundance and richness of the infaunal communities in the tube sponge, *Ircina strobilina*, were highest at shallower depths; however, Ferrie et al. (2003) found that the infaunal communities of the tube sponge *Aplysina fistularis* showed no patterns with depth. Thus, species-specific trends with depth in infaunal sponge communities may have obscured overall trends present in natural cryptic and exposed sponges.

Our study shows that cryptic sponges harbor infaunal communities that are similar to those in exposed sponges. However, many characteristics potentially affecting infaunal communities in both cryptic and exposed sponges vary both within and among sponge species. Further studies could examine the effects of toxicity, growth form, osculum size, flow rate, and other factors on infaunal communities.

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PREDATION AND SURGE STRESS AS FACTORS IN THE DISTRIBUTION OF TWO COMATULID CRINOID SPECIES

HEATHER E. LAPIN AND LUKE M. EVANS

Abstract: Two comatulid crinoid species of the genus *Davidaster* (formerly genus *Nemaster*) are abundant in the Caribbean at Discovery Bay, Jamaica: *D. rubiginosa* and *D. discoidea*. We tested the hypotheses that their populations are limited to depths below 10 m due to high predation pressure or due to high surge stress, and that the two species are differentially affected by surge stress. We found no evidence of predation. *D. rubiginosa* appears to be more resistant to surge than *D. discoidea*. Its arms were more likely to be extended, rather than curled, in high surge. Also, it occurred high on coral promontories, while *D. discoidea* was found low on these promontories. Finally *D. rubiginosa* was relatively more abundant than *D.discoidea* at shallow depths, and less abundant than *D. discoidea* at deeper depths. D. *rubiginosa* also seems to prefer areas of higher water movement, and may be limited at deeper depths where water movement may be low.

Key words: Davidaster discoidea, Davidaster rubiginosa, *living fossils, resistance to surge*

INTRODUCTION

500 million years ago, tropical reefs looked very different. Up until the Mesozoic period 250 million years ago, sessile sea lilies (Echinodermata: Crinoidea) were abundant at all depths, forming thick depositional layers in the fossil record (Macurda and Meyer 1983). It is hypothesized that their sudden disappearance from waters above 100 m is linked to the radiation of predatory teleost fish in the Mesozoic period. Now, only members of Comatulidae, a more derived, non-stalked, mobile order, remain in shallow waters (Meyer and Macurda 1977).

Two comatulid crinoid species of the genus *Davidaster* (formerly genus *Nemaster*) are abundant in the Caribbean at Discovery Bay, Jamaica: the smaller, more slender and delicate, gray-colored *D. discoidea,* and the often orange-colored, more robust *D. rubiginosa* (Hendler et al. 1995). During the day, these crinoids hide their disc-shaped calyx in crevices in coral promontories along the reef and extend their arms, catching passing plankton in the water current (Macurda 1973). These species, however, are only abundant at depths below about 10 m. Like their stalked sea lily ancestors, these crinoids may be limited to these depths because of predation pressure.

Another hypothesis is that intolerance to high surge stress limits them to calmer, deeper waters. Macurda (1973) found both species to be rheophobic (current-avoiding); however, Andrea (1979) found *D. rubiginosa* to be slightly rheophilic (current-seeking) and so surge may affect these two species differently. If the more robust *D. rubiginosa* is able to tolerate higher wave stress, then we expect it to extend its arms during times of high surge while *D. discoidea* would have a more protective posture, curling its arms. Additionally, we expect *D. rubiginosa* to be more abundant than *D. discoidea* at shallower depths. Lastly, we predicted that at shallower depths, *D. discoidea* would be found lower on promontories than *D. rubiginosa* to avoid surge stress, but that at deeper depths, where there is less surge stress, there would be no difference in relative height on promontories between the two species.

METHODS

We sampled the crinoid population in

Discovery Bay, Jamaica on 3 - 8 March 2004, at Mooring 1, Dancing Lady and Dairy Bull reefs. *D. rubiginosa* and *D. discoidea* were identified using *Reef Creature Identification* (Humann 1992).

Tests of predation hypothesis

We collected two *D. rubiginosa* and one *D. discoidea* from Mooring 1 on 3 March 2004 and tethered them for 24 hours at approximately 1 m on the west back reef and noted any evidence of predation. We also released these same crinoids amidst a "feeding frenzy" started by crushing up a *Tripneustes ventricosus* and attracting predatory fish to the area. Any predation on the crinoids was noted. On 8 March 2004 we collected two *D. rubiginosa* and brought them down to about 10 m at Dancing Lady reef. We created another "feeding frenzy" and observed any predation.

Tests of surge stress hypothesis

We surveyed the crinoid population at depths ranging from about 8 to 20 m. At all depths we followed a compass bearing and recorded every observed crinoid from both species along that transect for approximately 30 minutes. We measured the relative height (low, mid level, or high) at which the crinoids occurred on the promontories and whether their arms were fully extended or curled (defined as having arms either curled up or completely hidden in a crevice).

Surge was bidirectional; we measured the level of surge by timing how long it took a piece of synthetic sponge to move 15 cm in one direction. Water surge was then grouped into 3 categories for analysis; low (3 - 4.9 cm/sec), medium (5 - 8 cm/sec), and high (> 8 cm/sec). Depths were also categorized for analysis: shallow (< 13 m), medium (between 13 and 16 m) and deep (> 16 m).

RESULTS

Tests of predation hypothesis

After 24 h there was no visible sign of predation on the tethered crinoids. When crinoids were presented to fish (two sergeant majors, one squirrelfish and three threespot damselfish) along with *T. ventricosus* at 1 m depth, fish fed on urchin parts, but not on crinoid parts. When the same test was done at 10 m, one initial phase yellowhead wrasse, three juvenile bluehead wrasse, and one juvenile spanish hogfish were present; all ate pieces of urchin. The yellowhead wrasse took one bite of a *D. discoidea* arm, but spat it out. No other feeding on the crinoids was observed.

Tests of surge stress hypothesis

As surge varied between days due to weather, we were able to measure a range of levels (3 - 15 cm/s). Surge, independent of depth, did not affect arm extension in *D. rubiginosa*, although there was a trend for arms to be more curled at high surge ($G = 4.72$, $df = 2$, $P = 0.094$; Table 1). Surge did affect arm extension in *D. discoidea*. Arms were generally extended at low surge and curled at higher surge ($G = 30.64$, $df = 2$, $P < 0.0001$; Table 1). No crinoids were observed shallower than about 9 m in the areas we sampled. *D. rubiginosa* was relatively more abundant at shallower depths than *D. discoidea*, while *D. discoidea* was relatively more abundant at deeper depths ($G = 16.77$, $df = 2$, $P < 0.0001$; Table 2). *D. rubiginosa* was found relatively higher on promontories than *D. discoidea* ($G = 26.59$, $df = 2$, $P < 0.0001$; Table 3). However, there was no significant relationship between relative height on promontories and depth for either *D. rubiginosa* or *D. discoidea* ($G = 5.53$, $df = 4$, $P = 0.24$ and $G = 6.11$, $df = 4$, $P = 0.19$, respectively; Table 4).

Table 1. Number of crinoids observed with arms extended or curled at low, mid and high wave surge for *D. rubiginosa* and *D. discoidea*.

	D. rubiginosa		*D. discoidea*	
Surge	# extended	# curled	# extended	# curled
Low (3 - 4.9 cm/s)	9	1	37	1
Mid (5 - 8 cm/s)	10	9	5	8
High (> 8 cm/s)	3	1	0	3
Total	22	11	42	12

Table 2. Number of *D. rubiginosa* and *D. discoidea* observed at shallow, mid and deep depths.

Depth	*D. rubiginosa*	*D. discoidea*
Shallow (< 13 m)	15	7
Mid (13 - 16 m)	27	34
Deep (> 16 m)	6	30
Total	48	71

Table 3. Total number of *D. rubiginosa* and *D. discoidea* observed low, mid and high on coral promontories at all depths.

Relative height on promontory	*D. rubiginosa*	*D. discoidea*
Low	6	32
Mid	13	21
High	21	6
Total	40	59

DISCUSSION

The results of our predation tests do not support the hypothesis that these comatulid crinoids are absent from shallower depths due to predation pressure. At Discovery Bay, there may be no or few natural predators of these crinoids. This could be due to chemical defenses, which have been found in Great Barrier Reef crinoids (Macurda and Meyer 1983), or to the morphology of the organisms, which are mostly hard skeleton and have little nutritive value (Meyer and Macurda 1977). However, our results do not rule out predation entirely. It is possible that diurnal crinoid predators were not present, as Discovery Bay is overfished and

Table 4. Number of *D. rubiginosa* and *D. discoidea* observed at low, mid and high on coral promontories at shallow, mid and deep depths.

	D. rubiginosa			*D. discoidea*		
	Relative height on promontory			Relative height on promontory		
Depth	Low	Mid	High	Low	Mid	High
Shallow (< 13 m)	3	7	5	6	1	0
Mid (13 - 16 m)	3	4	12	13	6	3
Deep (> 16 m)	0	2	4	13	14	3
Total	6	13	21	32	21	6

lacks many fish species which normally occur on coral reefs, or that predators are nocturnal and thus excluded from our study. Crabs, for example, have been observed as predators (Macurda and Meyer 1983), and may be primarily nocturnal.

High surge clearly affects *D. discoidea* more than *D. rubiginosa*. This can be seen by the arm extension of *D. rubiginosa* and curling of *D. discoidea* during high surge. *D. rubiginosa* (more rheophilic) was found to be relatively more common at shallower depths than *D. discoidea* (more rheophobic). Surge stress is greater at shallow depths (Andrea 1979), and so our results support the hypothesis that the two species are affected by surge stress differently. The fact that *D. rubiginosa* is not found at depths less than 9 m and that it is found in crevices would suggest that there is some upper threshold surge level above which it cannot tolerate. *D. discoidea* may have a similar upper surge threshold which is less than that of *D. rubiginosa*.

The finding that *D. rubiginosa* was found relatively higher on promontories across all depths than *D. discoidea* also corresponds to the rheophilic and rheophobic nature of the two species. *D. rubiginosa* tends to be higher on the promontories at greater depths but was found at all heights at shallow depths. *D. discoidea* tends to be lower on the promontories at shallower depths but was found at all heights at deep depths. As surge decreases with depth, *D. rubiginosa* may have to be relatively higher on promontories to meet its water movement demands. Conversely, in shallow water *D. discoidea* may have to be relatively lower on promontories to escape heavy surge.

These results support the hypothesis that these two species of crinoids are unable to tolerate the high surge found at shallow depths and are limited to deeper, calmer areas. Future studies could compare relative abundances of these two species between sites with different levels of surge stress (i.e., a protected cove vs. the fore reef). Determining if these comatulid crinoids are chemically defended, and if such chemicals are unpalatable to fish or other predators, could more conclusively rule out predation as a factor in crinoid distribution.

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THE EFFECT OF SCHOOL SIZE AND COMPOSITION ON AGGRESSIVE BEHAVIOR IN THE TERRITORIAL THREESPOT DAMSELFISH, *STEGASTES PLANIFRONS*

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Abstract: Threespot damselfish exhibit territoriality to protect algal resources and brooding space. The resources within a damselfish territory are also used by other fish on the reef. Fish invading the territory use schooling as a method of overwhelming the ability of the damselfish to defend its territory. We predict that as school size increases, the likelihood that a damselfish will chase the school will increase, the likelihood that a school will return to the territory will increase, and the time from territory invasion to damselfish attack will decrease. Additionally, there is some debate on whether damselfish show more aggression towards ecologically similar species (i.e., those with greater overlap in resource use). We tested these ideas by observing interactions of intruding fish with territorial *Stegastes planifrons* (threespot damselfish) on the back reef of Discovery Bay, Jamaica. The probability of being chased and probability of returning both increased with school size, but time spent in territory was unaffected by school size. Type of fish did not affect any of these response variables. It appears that school size is an important determinant of damselfish aggressive behavior toward other fish.

Key words: algae gardens, interspecific interactions, schooling, territoriality

INTRODUCTION

Damselfish (Pomacentridae) in tropical coral reefs maintain territories to protect food resources and as a substrate on which their eggs mature. These fish maintain gardens of their favored algal species and aggressively chase off fish that may enter the territory to consume the algae or damselfish eggs (Deloach 1999). Intruding fish use schooling as a technique to overwhelm the damselfish and thereby decrease its ability to defend its territory. Foster (1985) found that the feeding rate of A*canthurus coeruleus* (blue tang) individuals in damselfish territories was positively correlated with the size of the school of *A. coeruleus*. Robertson et al. (1976) found that solitary individuals had both a high probability of being attacked and a low feeding rate, whereas schooling fish suffered few attacks and had a higher feeding rate; they suggested that this pattern resulted from the inability of the damselfish to attack all fish simultaneously. Both studies suggest that schooling confers a benefit to fish attempting to invade a damselfish territory.

Though these studies have elucidated the adaptive benefits of schooling for the individuals in the group, the effects of intruding schools on damselfish behavioral response have not been examined. Because larger schools have been shown to be more successful in exploiting territorial resources and thus represent an increased threat to the damselfish, we predicted that *Stegastes planifrons* (threespot damselfish) is more likely to show an aggressive response to schools of increasing size. Additionally, the likelihood of a fish in a school being chased multiple times should decrease with school size because higher numbers of intruding fish will overwhelm the damselfish. Therefore, we predicted that fish in larger schools would be more likely to return after being chased. Finally, damselfish should respond more quickly to the greater threat of the larger school, so we predicted that the time a school spends in a territory before being attacked would decrease with school size.

Additionally, it has been shown that damselfish are more aggressive towards fish which exhibit greater niche overlap with them

(Ebersole 1977). Manson (1978) found that *Acanthurus bohianus* (ocean surgeon) was attacked at a much higher rate than *Holocentrus* spp. (squirrelfish), reflecting the greater dietary overlap of *A. behainus* with dusky damselfish (*Stegastes fuscus*). However, Cressler (1981) found no difference between attacks on parrotfish (*Scarus* spp.) and *Acanthurus* spp., despite parrotfish having a higher degree of dietary overlap. Our study aimed to examine effects of both species and school size on the aggressive behavior of *S. planifrons*.

METHODS

We examined *S. planifrons* territorial behavior on 4 - 8 March 2004 at Discovery Bay, Jamaica, at three sites (East Back Reef, the West Back Reef and Columbus Park). We haphazardly selected damselfish territories and observed the focal fish until we could determine the boundaries of its territory. We then observed all fish entering this territory during a 10 min period. For every territory invasion, we recorded the number and species of intruding fish, the size (relative to the focal damselfish) of the intruder(s), and the time that intruding fish spent in the territory before being chased off or leaving. We also recorded whether the focal damselfish chased away the intruding fish, the number of fish that were chased, and whether the intruding fish immediately returned to the territory after being chased.

To evaluate effects of fish type on damselfish response, we grouped all species into families. Only three families (parrotfish, surgeonfish or wrasse) had a large enough sample size to test for differences among families in whether at least one fish was chased, whether they returned (chi-square tests), and how much time they spent in the territory (Kruskal-Wallis test). We also tested for effects of intruding group size (range one to twelve fish) on whether the fish were chased, whether they returned (logistic regressions), and time spent in territory (linear regression). For groups of two to twelve fish, we also tested the effects of school size on the proportion of schooling individuals chased. All species were included for these analyses, except schools of hardhead silversides and bar jacks that were clearly transients in the territory. Aggressive interactions with neighboring damselfish were not included in any of the analyses.

RESULTS

We observed 42 focal damselfish for a total of 420 min and recorded 248 territorial intrusions by other fishes (Table 1). Fish type (parrotfish, surgeonfish or wrasse) did not affect how much time each individual or group spent in a damselfish territory (Kruskal-Wallis, χ^2 = 0.39, df = 2, P = 0.82; Fig. 1), whether at least one fish was chased (χ^2 = 3.609 df = 2, P = 0.17;

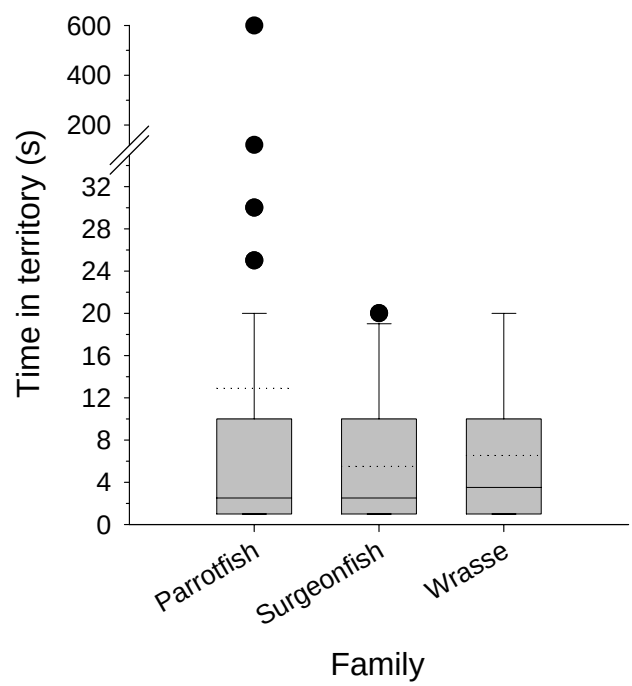

Figure 1. Time spent in damselfish territory before being chased or leaving compared among the three most commonly encountered fish families. Box plots show median and interquartile range. Whiskers show 10th/90th percentiles. Dotted lines are means. Points are outliers.

Table 1), or whether the fish immediately returned to the territory after being chased (χ^2 = 2.42, df = 2, P = 0.30; Table 1).

There was no relationship between school size and time spent in a territory before initiation of damselfish aggression (r^2 = 0.00002, P = 0.95, n = 250), but larger schools showed a marginally significant trend toward a higher probability of being chased (logistic regression: χ^2 = 3.31, df = 1, P = 0.068; Fig. 2). As school size increased, the probability of returning after being chased by a territorial damselfish increased (logistic regression: χ^2 = 14.7, df = 1, P < 0.0001; Fig. 3). There was a significant negative linear relationship between the size of the group and the proportion that were chased (r^2 = 0.15, P < 0.0016, n = 65; Fig. 4).

Discussion

S. planifrons did not respond differently to intruding parrotfish, surgeonfish or wrasse, indicating that either damselfish response is consistent regardless of the nature of the threat or that these three groups present a similar level of threat. Additionally, we found that fish in these three groups were equally likely to return after being chased, which suggests that response to damselfish aggression is similar across groups. However, less frequently encountered fish groups may have a different relationship with damselfish. For example, damselfish at-

Table 1. Total number of observations of fish entering damselfish territories, the number of times at least one fish was chased by the focal damselfish, the number of schools (more than one individual) observed, and the number of immediate returns after a chase.

Group	# observations	# chases	# schools	# returns
Balloonfish	1	0	0	0
Blennies	9	5	1	4
Butterflyfish	3	3	0	1
Croaker	2	2	0	0
Damselfish	33	27	1	5
Eel	1	1	0	0
Goatfish	1	0	1	0
Gobies	3	3	0	1
Grunt	7	6	0	2
Hamlet	2	1	0	0
Parrotfish	112	88	57	26
Jacks	1	0	1	0
Silversides	2	0	2	0
Squirrelfish	8	1	0	1
Surgeonfish	20	14	1	3
Wrasse	44	39	16	16

tacked squirrelfish only one out of eight times, despite squirrelfish often being present in the territory for the entire 10 min observation period.

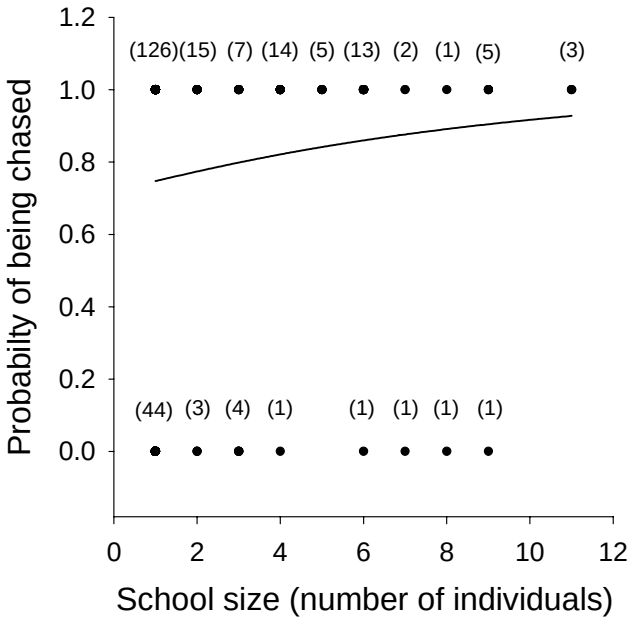

Figure 2. School size versus probability of being chased by focal damselfish. Points show observations and numbers indicate number of overlapping points. Line shows best fit logisitic function.

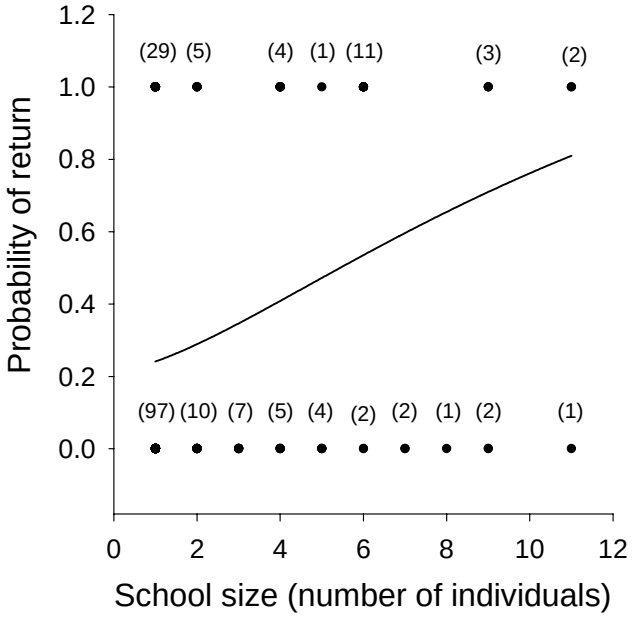

Figure 3. School size versus probability of returning after being chased by focal damselfish. Points show observations and numbers indicate number of overlapping points. Line shows best fit logisitic function.

School size appeared to be a much more important factor than fish type, with increased school size leading to a greater probability of at least one fish being chased. Two potential reasons for this pattern are that damselfish perceive larger schools as a greater threat to their territories and/or that larger schools tend to be more visible (Shannon et al. 2000). However, we found no effect of school size on the time it took a damselfish to initiate an attack after territory invasion. Such a pattern would be expected if visibility of school were important.

Our finding that the proportion of individuals attacked decreased with school size supports the interpretation of Robertson (1976) and Foster (1985) that schooling enhances the ability of individual fish to invade damselfish territories. Furthermore, return rate of invading fish after an attack increased with school size. This finding suggests that individuals in larger schools have a lower probability of being chased multiple times, and therefore are more likely to risk an immediate return.

Though damselfish encountered individ-

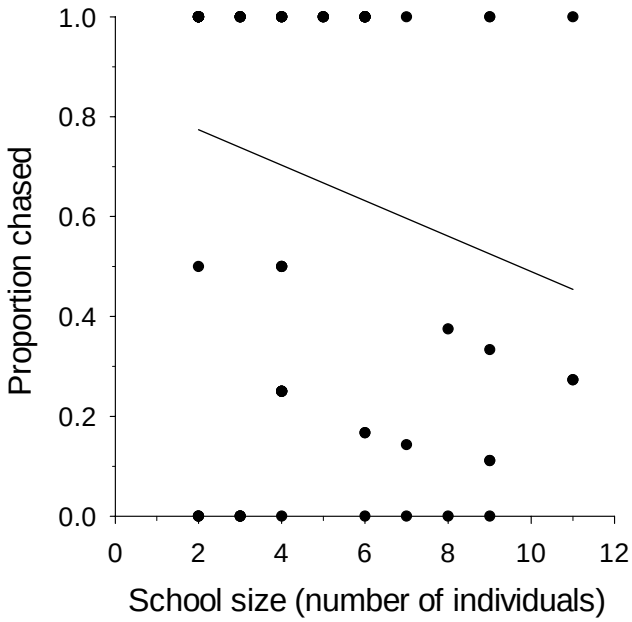

Figure 4. School size versus proportion of individuals reacted to by focal damselfish. Individuals in larger schools have a lower probability of being chased.

ual intruders more often than schools (170 versus 77, respectively), the total number of intruding schooling fish was greater than the total number of intruding individual fish (362 versus 170, respectively). This suggests that the impact of schools on damselfish may be greater than their encounter rate indicates, especially if individuals within schools have a higher feeding rate. Thus, selection pressure on damselfish behavior should be driven in part by interactions with schooling fish.

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Coloration and movement of trumpetfish at Discovery Bay

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Abstract: The trumpetfish (*Aulostomus maculatus*) is a common piscivore in the back reef at Discovery Bay, Jamaica. As a roaming predator, their cryptic coloration and behavior help them blend in with their habitats and ambush prey. Based on results from this observational study, trumpetfish do not often change color, but do vary their patterns of banding with movement and substrate. Energy costs associated with frequent color changes maybe greater than any additional cryptic benefits that might be gained. The movement of trumpetfish varied, with juveniles exhibiting little to no movement, and adults ranging in movement from 0 to 28 m. While trumpetfish showed no reaction to conspecifics, their interactions with other fish ranged from predation events to being chased by two species of damselfish.

Key words: color change, crypsis, interactions, movements

Introduction

The trumpetfish (*Aulostomus maculatus*) is a common piscivore in the back reef at Discovery Bay, Jamaica. These elongate, well-camouflaged predators exhibit varying colorations, patterns, and orientations in the water column (Aronson 1983). Aronson (1983) postulated that the frequency of color morphs in a trumpetfish population will be evenly distributed throughout the population; this theory has been supported in more recent studies (e.g., Braman and Ungerer 1998). Trumpetfish benefit from their varying cryptic morphologies; however, if one were more common than others, Aronson (1983) suggests that prey would learn to avoid the more abundant morph, and thus a negative selection pressure would be placed on that color morph. The ability of trumpetfish to change both their color and their banding patterns while traveling across microhabitats on a reef should allow them to blend in with their surroundings and ambush prey undetected. Despite the potential importance of color and pattern change in trumpetfish, however, little is known about the extent to which individual trumpetfish change coloration or color pattern over time.

We examined the coloration and patterning of trumpetfish, their movement on the reef crest, as well as their interactions with both heterospecific and conspecific fish. We observed trumpetfish through focal studies, and hypothesized that they would exhibit frequent changes in coloration and patterning as they move over varying substrate types on the reef crest. Additionally, we hypothesized that although they are roaming predators (DeLoach 1999), trumpetfish would have relatively small home ranges due to their high density in the back reef and the high abundance of prey species. Finally, we observed interactions of trumpetfish with both conspecifics and other fishes, such as damselfish and potential prey species.

Methods

We conducted our study from 3 - 9 March 2004 in the west and east back reef at Discovery Bay, Jamaica. Trumpetfish can generally be located at the reef crest in Discovery Bay, most often near edge habitats and over-hanging reef structures. Using small floats, we marked locations of trumpetfish on the reef crest and returned several times over one week to determine possible territory ranges. We followed 17 trumpetfish for a period of 30 min each, recording their size, changes in coloration and

markings, approximate territory size, and interactions with conspecific and heterospecific fish. We observed an additional 22 trumpetfish for less than 30 min each but more than 10 min each, and recorded the aforementioned characteristics except for territory size. Because we had no reliable way to mark and identify individual trumpetfish, we cannot say if we saw 39 unique fish or if some were repeated observations.

Results and Discussion

Coloration and patterning

Fish ranged in size from juveniles of < 20 cm to the largest adult of 80 cm. Three color morphs were observed: green, red-brown, and tan, the latter being the most common among adult fish. Of adult fish (> 45 cm), one was green, three were red-brown and 19 were tan colored. Of juvenile fish (< 45 cm), eleven were green, none were red-brown, and five were tan.

In seventeen 30-min observations, only three color changes occurred. While positioned over a patch of red algae, an individual exhibited a red-brown hue, but changed to tan upon relocating to a sandy area. Similarly, a trumpetfish changed from tan to green after moving from the reef to a stationary position over a small patch of turtle grass (*Thallassia testudium*). Another fish shifted from red-brown to tan while moving over the reef structure.

While color changes were rare, trumpetfish often demonstrated changes in pattern by displaying dark vertical bands. Observed fish always displayed bands when stopped over turtle grass and never when in motion. Bands were rarely displayed when fish were stationary over the reef or under reef structure. Bands seemed to provide crypsis over turtle grass, while lack of banding seemed to facilitate crypsis over sand and other substrate. In one instance, a trumpetfish nearly matched a sea rod in coloration, pattern and movement. The juvenile (< 20 cm), tan and lacking banding, mimicked the sea rod by positioning itself vertically with the upright fingers of the gorgonian, and swayed synchronously with the gorgonian.

Trumpetfish in the back reef at Discovery Bay seemed to rely on changes in banding more often than changes in color. Trumpetfish seemed to prefer hunting near small patches of turtle grass and sand within the reef structure, using banding to contribute to the crypsis of the tan and green color morphs most commonly observed in these microhabitats. It is possible that changes in banding are energetically preferred to color changes.

Movement

Trumpetfish moved between 0 and 28 m during the 30-min observation periods. In five cases fish remained stationary (moving < 2 m) for the entire time period. These fish were under overhead cover of reef or close (< 0.5 m) to reef structure. The other 12 fish traveled a mean distance of 13.8 m (± 9.6 SD). Moving fish often stopped and remained stationary for a variable period of time (between 3 s and a number of minutes) while traveling through reef structure and over patches of turtle grass.

Trumpetfish were frequently found at marked sites where at least one conspecific had been previously observed. It was impossible to know whether these were the same individuals or different fish. A trumpetfish with an isopod located on its tail was observed only once despite this distinctive identifying mark. At one site a fish of the same size and coloration was noted in five observations in three consecutive days; however, on the subsequent day, the site was occupied by a much larger fish.

While trumpetfish did move throughout the area of the reef crest, we observed many cases in which both juvenile and adult trumpetfish were stationary. Stationary trumpetfish

were most often in vertical positions or at a 45 degree incline, typically with the anterior end positioned downward. This stationary position generally occurred at reef structure, especially under a ledge or an arch of the reef.

Most of the observed fish moved relatively little (< 10 m), with almost a third of the fish remaining in the same location for the entire 30 min survey. It may be unnecessary for trumpetfish to travel broadly while hunting; their difficulty may not lie in finding potential prey (that are typically abundant) or competing with conspecifics, but in the surprise necessary to capture the prey. In this case, slow exploration and stationary periods of waiting would likely be the most effective hunting tactics.

Heterospecific fish were considerably more active on the reef crest than were trumpetfish. Because trumpetfish hunt throughout the day (DeLoach 1999), they may spread their periods of high activity over a period of hours, or their prey may be so abundant that trumpetfish do not need to travel very far to satisfy their energetic and nutritional requirements. Other fish may need a larger area to support their resource needs, or may school, and thus move about in a group over a wider range than trumpetfish.

Interaction

Some trumpetfish were observed interacting with conspecifics. In ten cases, two adult trumpetfish were in close proximity (< 1 m) to each other, and in five of these cases fish seemed to positively interact by swimming as a pair, usually one following the other. Other trumpetfish showed no reaction to conspecifics. Three juveniles were seen in close proximity to adults, but there was no apparent interaction between the fish.

We also observed trumpetfish interacting with fish of other species, the nature of these interactions ranging from territory defense to symbiotic cleaning. Trumpetfish were chased by territorial damselfish 11 times. Bicolor damselfish (*Stegastes partitus*) reacted the most aggressively to the presence of trumpetfish, while threespot damselfish (*Stegastes planifrons*) generally ignored trumpetfish roaming through their territory. In one instance a dusky damselfish (*Stegastes fuscus*) chased away a trumpetfish. Perhaps the damselfish were protecting themselves from this potential predator. It is interesting to note that the bicolor damselfish, which reacted most aggressively to the presence of trumpetfish in their territory, are a favored prey of the trumpetfish (DeLoach 1999). Threespot damselfish ignored trumpetfish, perhaps because trumpetfish were seemingly passing through their territories, and were not poised to strike (DeLoach 1999).

In several instances on the east back reef, juvenile angelfish were observed cleaning trumpetfish, generally above or near reef structure. We also observed seven predation events in which trumpetfish made pronounced strikes at heterospecifics. Prey fish were generally too small to be correctly identified with the exception of one juvenile (~3 cm) bluehead wrasse (*Thalassoma bifasciatum*). While we do not know how much a given trumpetfish feeds in one day, their day-long feeding behavior (DeLoach 1999) suggests that predation by trumpetfish may be limited to a few periodic events, and it is possible that we did not observe a representative number of these strikes. The only conspecific interactions of trumpetfish involved two trumpetfish swimming together for a period of time, usually with the smaller fish following the larger. These may have been male/female pairs; alternatively, trumpetfish may benefit in some other way from close association with conspecifics, such as increased hunting efficiency. No juvenile fish were seen interacting with other juveniles or with adult fish, possibly supporting the idea that interacting fish were male/female pairs.

Trumpetfish are a unique contributor to the diverse fish life in many reef ecosystems. While this study has provided some general knowledge on their physical characteristics and behavior, future studies could quantitatively examine their color and banding patterns with respect to substrate type, or examine their social structure to a greater degree.

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FEEDING BENEFITS FOR SPOTTED GOATFISH IN MIXED SPECIES SCHOOLS WITH PARROTFISH

PAUL A. MARINO AND R. SCOTT CUSHMAN

Abstract: Heterogeneous schools of juvenile fish utilize turtle grass habitat at Discovery Bay, Jamaica, and commonly include parrotfish as the core fish and spotted goatfish, among other associated fish. We hypothesized that spotted goatfish feeding would be facilitated by parrotfish feeding, but that parrotfish feeding would be unaffected by the presence of spotted goatfish. We surveyed co-occurrence of these two species in 55 schools to test the prediction that goatfish would show a strong tendency to co-occur with parrotfish, but not vice versa. We also observed feeding in 18 schools with both parrotfish and goatfish to test the prediction that goatfish would feed under the parrotfish where flushing activity would increase prey availability. Data supported our hypotheses and suggested that co-feeding of these species is mutually beneficial.

Key words: bluehead wrasse, sea grass bed, spatial partitioning

INTRODUCTION

Turtle grass (*Thalassia testudinum*) beds near reefs are important habitats for the juveniles of many coral reef fish species, including parrotfish (*Scarus croicensis* and *Scarus taeniopterus*) and the spotted goatfish (*Pseudupeneus maculatus*) (Nagelkerken 2002). In the turtle grass beds inshore of the reef crest at Discovery Bay, Jamaica, juvenile parrotfish are abundant and exhibit schooling behavior, which is thought to reduce predation risk and facilitate feeding in damselfish territories. Small numbers of juveniles of several fish species, including spotted goatfish, doctor fish and slippery dicks often associate with these schools (Pouliot et al. 1995). Juvenile spotted goatfish, which use two anterior-ventral barbels to search the sediment for invertebrates, are almost always associated with the parrotfish-dominated schools (Gunderson 1992). For the goatfish, this association may facilitate feeding, reduce predation risk (Pouliot et al. 1995), or both.

We examined the nature of the relationship between juvenile spotted goatfish and juvenile parrotfish. Preliminary observations showed that spotted goatfish only occurred in parrotfish-dominated schools, while parrotfish-dominated schools did not always contain spotted goatfish. Therefore, we hypothesized that goatfish benefit from foraging with a parrotfish school, while parrotfish foraging is unaffected by goatfish. We predicted (1) that goatfish would always co-occur with parrotfish, but parrotfish would occur both with and without goatfish, and (2) that goatfish and parrotfish would spatially partition when feeding, such that parrotfish would feed on the epiphytic tips of turtle grass, while goatfish would forage below and near the sediment. In this arrangement, goatfish would not likely effect parrotfish feeding, but parrotfish biting and movements could facilitate goatfish foraging by dislodging invertebrates from the bases and blades of grass. To test these predictions, we observed schools of juvenile fish in turtle grass beds at Discovery Bay, Jamaica.

METHODS

On the afternoons of 25 and 26 February 2004, we snorkeled imprecise transects in the turtle grass beds of the backreef at Discovery Bay without sampling the same area twice. For every school seen containing juvenile parrotfish, juvenile spotted goatfish, or both, we recorded the number and composition of species. We analyzed the relative abundances of species and

ran a chi-square model to examine the tendency of co-occurrence of goatfish and parrotfish.

We followed some schools until we observed a feeding event, noting where the parrotfish and spotted goatfish were feeding. Relative feeding positions were categorized as either "bottom of turtle grass and sediment" or "top of turtle grass." We ran a chi-square model to examine the tendency of the two species to maintain separate relative feeding positions.

RESULTS

We sampled 55 schools with a mean size of 24 fish (SD = ± 15) per school. Mean proportions of species, based on all 55 schools, showed parrotfish (princess and striped, which are difficult to distinguish in the field) to be the core species. Spotted goatfish, doctor fish, bluehead wrasse, stoplight parrotfish, slippery dick and french grunt were present in decreasing order (Table 1). The ratio of parrotfish to spotted goatfish was approximately 9 : 1.

Parrotfish occurred without spotted goatfish in 18 schools, and both species occurred together in 37 schools. Frequencies of co-occurence were significantly greater than those expected by chance for the goatfish ($P < 0.0001$) but not for the parrotfish ($P = 0.08$; Table 2). In one case, one stoplight parrotfish and one spotted goatfish were seen foraging together.

Feeding events were observed for 18 schools; in 17 of these events, parrotfish fed on the top region of grass blades while spotted goatfish fed below among grass stalks or off the sediment (Fig. 1, Table 3). In one exception to this pattern, the school was swamping a damselfish territory, and spotted goatfish and parrotfish fed in the same regions.

Table 1. Composition of mixed schools (± SE) seen in the west back reef.

Species	Percent composition
Parrotfish	87.0 ± 2.0
Spotted goatfish	8.9 ± 1.7
Doctor fish	2.5 ± 0.7
Bluehead wrasse	2.5 ± 0.7
Stoplight parrotfish	0.3 ± 0.2
Slippery dick	0.3 ± 0.2
French grunt	0.3 ± 0.3

Table 2. Frequency at which spotted goatfish and parrotfish occurred alone and with the other species.

	Alone	Together
Spotted goatfish	2	36
Parrotfish	18	36

Table 3. Frequency at which spotted goatfish and parrotfish fed at the top and bottom regions of *Thalassia testudinum* beds.

	Feeding position			
	Top	Bottom	Both	χ^2 test
Spotted goatfish	0	16	2	
Parrotfish	17	0	1	$P < 0.0001$

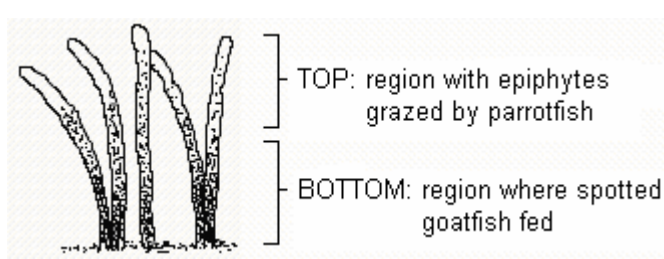

Fig 1. Feeding positions of parrotfish and spotted goatfish in *Thalassia testudinum* beds.

Discussion

Our school composition surveys showed that parrotfish often occurred without spotted goatfish, but spotted goatfish rarely occurred without parrotfish. As hypothesized, this pattern may exist because spotted goatfish benefit from co-occurring with parrotfish. However, it does not indicate whether or not parrotfish benefit from spotted goatfish. Though our data suggest that spotted goatfish have a higher tendency to occur with parrotfish than vice versa, the pattern could only be due to the different abundances of the two groups in the turtle grass habitat. If there are few spotted goatfish relative to parrotfish, and if mixed-species schools form with no particular order, it is likely that some schools would lack the relatively rare spotted goatfish, while few schools would lack the ubiquitous parrotfish.

Feeding was spatially partitioned between the two species in such a way that parrotfish could facilitate feeding for spotted goatfish, but spotted goatfish would have no affect on parrotfish feeding. Parrotfish almost always bit the upper region of grass blades with a heavy epiphyte load, a process which could flush invertebrates from the grass blades or from sediment at the base of disturbed grass stalks. Goatfish, meanwhile, fed among the grass stalks or in the sediment immediately below parrotfish, suggesting that parrotfish may in fact increase prey availability for spotted goatfish.

The relationship between these two fish may be mutualistic. By co-occurring with goatfish, parrotfish may benefit from an augmented school size and its effect on swamping damselfish territories, or deterring predators. Gunderson (1992) suggested that juvenile spotted goatfish benefit from heterospecific schooling, likely by reduced predation risk. Spotted goatfish, however, appear to also benefit from increased prey availability, which contradicts the findings of Pouliot et al. (1995), who suggested that spotted goatfish mostly feed when away from the school. Most of the schools they observed, however, were dominated by bluehead wrasse, not parrotfish. It is possible that spotted goatfish behave differently with wrasse than with parrotfish.

This study highlights the complexity of school dynamics and the range of benefits that may cause fish to form mixed-species schools. In this case, it appears that the relationship may be mutualistic, in which spotted goatfish benefit from increased feeding efficiency, and parrotfish benefit from increased school size. Further studies should investigate the change in feeding efficiency of juvenile spotted goatfish when foraging with and without parrotfish, as well as the roles of other species that occur in these schools less commonly.

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ROCKIN' AROUND THE CHRISTMAS TREE WORM: THE EFFECT OF SURGE ON *SPIROBRANCHUS GIGANTEUS* MORPHOLOGY

SARAH E. B. FIERCE AND ELEANOR E. CAMPBELL

Abstract: Spirobranchus giganteus is a serpulid polychaete that builds calcareous tubes on the surface of live coral heads. These worms are unique among suspension feeders; their spiraled radiole crown requires external current to separate incurrent from excurrent flow. Otherwise, water is moved by cilia along the tentacles and is filtered multiple times, making the system is inefficient. However, this compact spiraled form allows for a large filtering surface area, and *S. giganteus* may trade efficiency for compactness in order to deal with drag from surge. We hypothesized that *S. giganteus* crown morphology would be affected by surge. Since surge decreases with increasing depth, we predicted that the radiole crown would become more elongated with depth. We found that *S. giganteus* crowns were more elongated with depth, supporting the idea that their morphology is affected by drag. The compact spiraled crown of *S. giganteus* may allow this worm to exploit areas with high flow not tolerated by other suspension feeding tube worms. Further studies should assess the effects of predation pressure on crown morphology.

Key words: calcareous tube worms, depth, radiole crown, suspension feeding efficiency

INTRODUCTION

The Christmas tree worm, *Spirobranchus giganteus*, is a tropical serpulid polychaete that lives in calcareous tubes built on the surface of live coral heads (Hunte et al. 1990). These worms suspension feed by extending two spiraled crowns or radioles into the water current. The stacked spiral arrangement of the crowns gives the worm a large but compact filter, but this design is at the cost of some efficiency. Cilia along the radioles and then pinnules generate current, but incurrent flow is not separated from excurrent flow, so water passes through several whorls, and thus, is filtered multiple times. Therefore the worm depends on external flow perpendicular to the crowns to separate incurrent from excurrent flow (Strathmann et al. 1984).

This compact crown morphology may be the result of multiple selection pressures. Strathmann et al. (1984) speculated two possible explanations for *S. giganteus'* unique suspension feeding shape. The tentacles may be compact and close to the tube entrance to decrease the risk of predation, or the compact shape may prevent tentacles from being bent over by drag, thereby decreasing filtering efficiency. Our study examines this second idea that the compact crown shape of *S. giganteus* is an adaptation to cope with drag. We hypothesized that surge would affect *S. giganteus* crown morphology due to a tradeoff between drag and filtering efficiency. Since surge decreases as depth increases, we used depth as a proxy measure for the amount of surge. We predicted that *S. giganteus* crowns would become more elongated with depth, as the danger of radioles being bent would be reduced and elongated crowns may filter more efficiently.

METHODS

We measured 85 Christmas tree worms at Discovery Bay, Jamaica from 3 - 8 March 2004. We swam transects at three sites on the fore-reef (M1, Dancing Lady and Dairy Bull), sampling across a depth range of 3 - 16 m. For each worm in our transects we measured its height from base to tip and its width at the base of one of its

two spiraled radiole crowns. We counted the number of visible spirals, noted the coral species on which the worm lived and recorded water depth.

Radioles at the top of the crown are shorter and perhaps younger than those at the bottom of the crown. Therefore, it seems likely that worms grow by extending their crown axis as radioles increase in length. We assumed that the number of spirals was indicative of worm age. Therefore, we calculated an index of elongation for each worm, standardized for age, by dividing its height by the number of spirals.

RESULTS

Elongation increased with increasing depth ($r^2 = 0.21$, df = 82, $P \leq 0.0001$; Fig. 1). A three-way ANOVA showed that variance in elongation was explained by depth ($F_{1,73} = 13.47$, $P = 0.0005$) and dive site ($F_{2,73} = 3.36$, $P = 0.04$), but not by coral species ($F_{7,73} = 0.2$, $P = 0.98$). There was an increase in *S. giganteus* crown height with increased depth ($r^2 = 0.11$, df = 83, P = 0.002; Fig.2). The number of spirals increased with crown height ($r^2 = 0.63$, df = 83, $P \leq 0.0001$; Fig. 3). Crown height and width were highly correlated ($r = 0.85$, df = 1, $p \leq 0.0001$), so we did

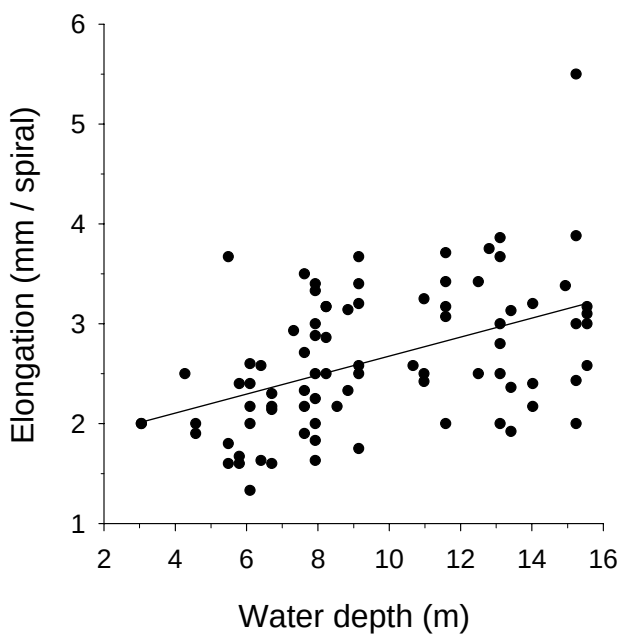

Figure 1. Relationship between elongation of the radiole crown (height / number of spirals) and depth for *S. giganteus* (n = 84). Regression equation: Elongation = 1.73 + 0.09 x Depth.

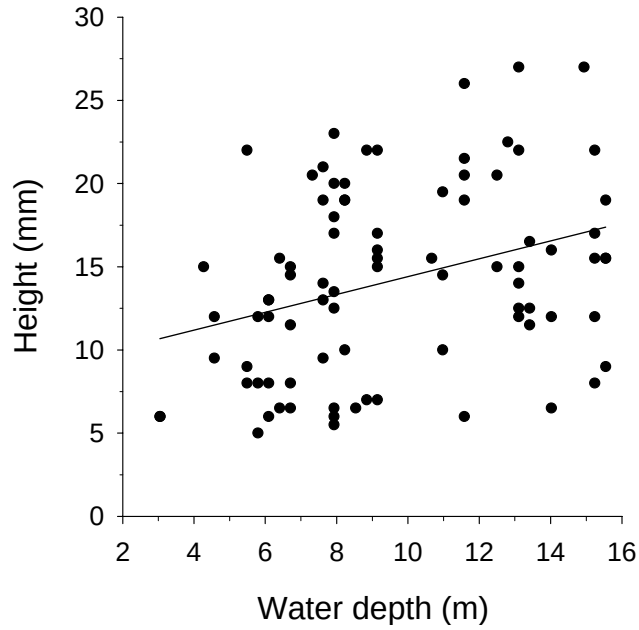

Figure 2. Relationship between height of the radiole crown (from base to tip) and depth for *S. giganteus* (n = 85). Regression equation: Height = 9.05 + 0.54 x Depth.

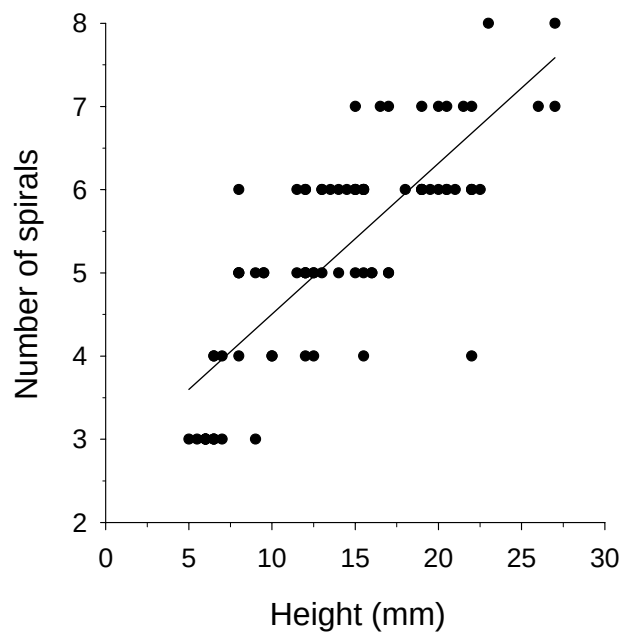

Figure 3. Relationship between the number of spirals in a radiole crown to the height of the radiole crown in *S. giganteus* (n = 84). Regression equation: Number of spirals = 2.69 + 0.18 x Height.

not use width for analyses. There was no relationship between number of spirals and depth ($r^2 = 0.01$, df = 82, P = 0.37), coral species ($F_{7,76} = 1.84$, P = 0.09) or dive site ($F_{2,81} = 0.67$, P = 0.51).

DISCUSSION

The radiole crowns of *S. giganteus* became more elongated with depth, suggesting that crown morphology may be influenced by drag. Although the number of spirals was unrelated to depth, radiole crown height increased with depth, indicating that changes in crown morphology are likely unrelated to age. The increase in number of spirals with crown height supports the assumption that number of spirals is a function of age, since larger worms have more spirals. There was some variance attributable to dive site. However, we could not examine the same range of depths at each site, and the strong effect of depth may have created variance between dive sites that was actually due to depth.

Unlike other suspension feeders, *S. giganteus* is reliant on external current to feed efficiently. A compact spiral crown may allow them to exploit shallow areas where surge is common, while minimizing the potential for their tentacles to be bent over by drag. As surge decreases with depth, the need for compactness decreases, and the worms may take on a more elongated morphology that allows them to expose more surface area to the water column to suspension feed more efficiently.

Differences in radiole crown shape with depth may indicate that *S. giganteus* exhibits morphological plasticity, where elongation of the radiole crown depends on the flow conditions where the worm settles. Alternatively, differential mortality may select for a more compact form in shallow water, and elongation in deep water. In shallow water, worms with elongated crowns may be unable to maintain an upright position to feed in heavy drag, while at deeper depths there is too little surge for worms with more compact crowns to separate incurrent from excurrent flow. In these cases, worms would not be able to feed efficiently and would therefore be less likely to survive.

Other kinds of fanworms are able to suspension feed efficiently just by generating their own current. However, without a compact morphology these fanworms may not be able to withstand as much surge as *S. giganteus*, and may be restricted to more protected microhabitats. Suitable settlement space for tube building worms may be limited on reefs since larvae must settle on patches of dead coral to avoid being eaten by coral polyps (J. Gilbert, pers. comm.). Thus, to avoid competition, *S. giganteus* may be exploiting a unique niche by settling in areas where the current is too strong for other suspension feeding worms. In general, we casually noticed that other suspension feeding worms in the family Sabellidae were not in the same microhabitats as *S. giganteus*. They seemed to be more prevalent in more protected parts of coral mounds, where surge and drag would be reduced. Further studies could look for differences between *S. giganteus* and other fanworm microhabitats to address the possibility of niche differentiation.

Drag appears to be an important determinant of *S. giganteus* morphology. However, this does not exclude the possibility that predation pressure may also influence the compactness of the worms' radiole crowns. We observed that worms quickly retract into their tubes when approached and that worms have a plethora of color patterns even within a coral mound. Since color patterns are unrelated to substrate type or depth (Dickenson and Douzinas 1998), color variation may be a predator confusion tactic. If worms face predation pressure, as this variation in color suggests, then a compact radiole crown may allow for quicker retraction into their tubes

when worms are attacked. Consequently, our finding that worms have more elongated radiole crowns with depth may reflect reduced predation risk with depth. Further studies should examine whether predation pressure on *S. giganteus* influences crown morphology, or if there are other patterns that suggest that predation or other abiotic factors influence the morphology of these organisms.

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FISH HERBIVORY ON TWO GROWTH FORMS OF MARINE PLANTS

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Abstract: A number of complex interacting factors determine marine vegetation morphology. For instance, fish may eat foliose and low-profile forms at different rates, exerting a selection pressure upon these forms. However, debate exists in the literature as to whether the low-profile form benefits the plant by reducing herbivory. Through an *in situ* manipulation of *Thalassia testudinum* blades, we compared the herbivory on prostrate (a proxy for low-profile forms) and vertical (a proxy for foliose forms) blades. We found that herbivorous fish consumed vertical blades ten times more often than prostrate blades. This suggests that prostrate forms are less desirable to fish herbivores and may be a growth strategy to decrease herbivory. Further research could focus on costs of low-profile growth that may offset the herbivory benefit.

Key words: algae, foliose growth form, herbivory defense, low-profile growth form, Thalassia testudinum

INTRODUCTION

Plant morphology is the result of various ecological pressures, such as maximizing photosynthesis and minimizing herbivory. In marine algae, both foliose and low-profile forms exist, and these different growth forms relate to differences in herbivory (Lewis et al. 1987). Prostrate (low-profile) growth forms may be more difficult for herbivores to eat than vertical (foliose) ones because it is mechanically harder to bite a leaf growing against a hard substrate than one with more surface area available in the water column (Lewis et al. 1987, Loren and Tanner 1989). Alternatively, Littler and Littler (1980) suggest that low-profile forms may be more easily accessible to herbivores. This suggestion would lead to higher herbivory rates in prostrate growth forms than vertical growth forms. To resolve these opposing theories, we measured herbivory rates on prostrate and vertical growth forms by using experimentally manipulated *Thallassia testudinum* leaves.

METHODS

We measured herbivory rates on vertical and prostrate *T. testudinum* leaves at Discovery Bay Marine Laboratory, Jamaica. We compared herbivory by using a paired design. Three prostrate leaves and three vertical leaves were attached to a ceramic tile (15.1 x 15.1 cm). Prostrate leaves were held with clothespins on each end and one wrap of 15-lb test fishing line to hold down the leaf center, and vertical leaves were each held in place with a clothespin on one end; this was repeated on 24 tiles. We used approximately 23 cm x 2.5 cm leaf tip sections of *T. testudinum* with roughly equal epiphyte loads. Tiles were randomly divided into three groups of eight tiles and placed in three sites. Each site was a sandy patch surrounded by *T. testudinum,* and all tiles were placed on the edge of the patch. Tiles were left out from 1010 to 1645 on 25 February 2004.

We calculated herbivory as percent of the grass blade missing after sampling. Average percent herbivory for vertical blades and for prostrate blades was calculated for each tile. We arcsine-transformed these data to correct for non-normality and compared transformed average percent herbivory between vertical and prostrate blades using a paired t-test. We determined spatial variation in herbivory rates using a nested one-way ANOVA with site and plate nested within site as effects.

RESULTS

There was evidence of herbivory on both leaf orientation treatments. Per-tile mean vertical blade herbivory ranged from 0 - 78%, while per-tile mean prostrate blade herbivory ranged from 0 - 35%. Most herbivory resulted from scallop-shaped parrotfish bites. Herbivory was over ten times greater on vertical blades than on prostrate blades (paired $t = 5.49$, $df = 23$, $P < 0.0001$; Fig. 1). Herbivory varied significantly within sites (between plates; $F_{21,71} = 6.3$, $P < 0.0001$) and between sites ($F_{2,71} = 18.85$, $P < 0.0001$).

DISCUSSION

While fish were able to feed upon both forms, they preferred vertical grass blades to prostrate ones. This result supports findings by Lewis et al. (1987). As *T. testudinum* was used for both treatments, other factors that might affect herbivory on different macroalgae - such as differential nutrient content or calcification - could be excluded. A low-profile form must therefore be more difficult to feed upon, possibly due to a more difficult feeding position or biting angle for fish. It is also possible that fish search for vertical blades when feeding on turtle grass, which could also explain their preference for vertical blades.

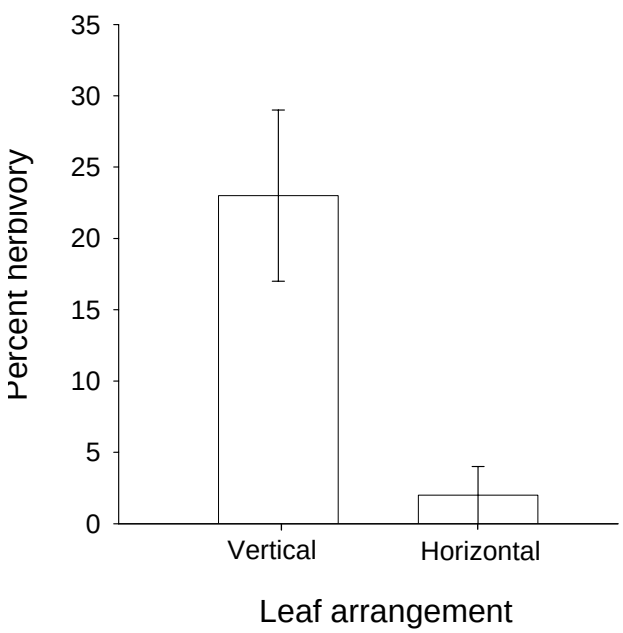

Figure 1. Mean percent herbivory (± SE) on vertical and horizontal blades of *T. testudinum*.

Our results suggest that patterns of herbivory are dependant on herbivore behavior, as there was spatial variation in herbivory rates. Though we did not examine in detail how herbivory rates varied across the back reef, we found significant variation across large (between sites) and small (within sites) spatial scales. Herbivory is patchy throughout the turtle grass habitat, which might be expected from schooling herbivores such as parrotfish. The mechanism for foraging patterns of herbivores could be examined in further detail.

Our results demonstrate that a low-profile form is beneficial to the plant as it decreases herbivory. As both low-profile and foliose forms are found in nature, this suggests a cost-benefit tradeoff to the prostrate form. The decrease in exposed surface area in a low-profile alga may decrease photosynthetic rates or nutrient uptake; alternatively, it may decrease mechanical wave stress and damage. Further studies could examine such potential costs and benefits of a low-profile growth form, as many ecological factors, biotic and abiotic, influence growth form.

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THE GREAT ZOOPLANKTON DIE-OFF OF 2004

ELEANOR E. CAMPBELL, SARAH E. B. FIERCE, HEATHER E. LAPIN AND SHARON J. MARTINSON

Abstract: Many zooplankton exhibit diel vertical migration; they seek refuge from planktivorous fish in the benthos during the day, but rise into the water column at night to feed. We studied a zooplankton community during day versus at night and compared abundances and size classes of various taxa. Surprisingly, there was no difference between day and night zooplankton abundance. Furthermore, total abundances were significantly lower than those found in previous studies. Zooplankton were approximately two times larger at night than during the day, driven by the larger abundance of decapod larvae at night. The largest and smallest size classes of copepods, however, were more abundant during the day. These results contradict the diel pattern of zooplankton abundance found in previous studies. We speculate that zooplankton have patchy distribution horizontally in the water column. Habitat heterogeneity of zooplankton resources such as refuge and food could cause spatial variance in abundance. It is also possible that there has been a large decrease in zooplankton abundance in the back reef in the past year.

Key words: demersal zooplankton abundance, diel vertical migration, habitat heterogeneity

INTRODUCTION

Many zooplankton exhibit diel vertical migration; they are found in the benthos during the day, but rise into the water column to feed at night. This migratory behavior is thought to provide protection from predation by planktivorous fish that rely on vision to locate food during the day, but are less active and efficient at night. In addition, zooplankton size may influence their vulnerability to visual predators, such that predation risk increases with the size of the individual. In this study, we explored diel patterns of abundance, composition, and size structure of the zooplankton community in Discovery Bay, Jamaica. We predicted that we would find a lower abundance of zooplankton in the water column over a tropical coral reef during the day than during the night. We also predicted that we would find a greater abundance of larger individuals and taxa at night.

METHODS

We collected five replicate zooplankton samples both during the day (1330 to 1430) and at night (2200 to 2300) on 28 February 2003 near the reef crest in the West back reef of Discovery Bay, Jamaica. Samples were collected by towing a plankton net (153 μm mesh, 26 cm diameter) for 40 m back and forth along a 20 m transect at a depth of 20 - 40 cm. The volume of water filtered in each replicate sample was ~1.06 m^3. Collected samples were preserved in 10% formalin in the field and zooplankton taxa were later identified and counted in the lab using dissecting microscopes. We categorized the zooplankton into copepods, amphipods, isopods, decapod larvae, mysids, polychaete larvae, fish larvae, medusae, arrow worms, larvaceans, and cumacean shrimp. We assigned size classes for copepods (< 0.5 mm, 0.5 - 1 mm, > 1 mm), amphipods (< 1 mm, 1 - 2 mm, > 2 mm), isopods (< 1 mm, 1 - 2 mm, > 2 mm), decapod larvae (1 - 2 mm, 2 - 3 mm), mysids (2 - 4 mm, 4 - 6 mm), polychaete larvae (< 1 mm, 1 - 2 mm, > 2 mm), and fish larvae (< 2 mm, 2 - 4 mm, > 4 mm).

We analyzed the differences in zooplankton abundance and size between day and night using an ANOVA model, with sample nested within time (sample as a random effect).

RESULTS

There was no difference between day and night zooplankton abundance ($F_{1,8}$ = 0.64, P = 0.43). We found a total of 656 zooplankton during the day and 399 zooplankton during the night. There was little variance in abundance between samples of the same time of day ($F_{8,60}$ = 0.27, P = 0.97). There was no difference in abundance for any of the taxa sampled (all P > 0.007; with Bonferroni correction for multiple tests, α = 0.05, critical P = 0.0007), although copepods tended to be more abundant during the day ($F_{1,8}$ = 12.2, P = 0.008; Fig. 1).

Overall average zooplankton size was approximately two times larger at night than during the day; night zooplankton had a mean size of 1.52 mm ± 0.21, and day zooplankton were 0.78 mm ± 0.19 ($F_{1.8}$ = 6.87, P = 0.02). This result was driven by increased decapod abundance during the night (182 at night, 2 during the day), as decapods are large (1-3 mm). There was no difference overall in zooplankton size between samples at the same time of day ($F_{8,60}$ = 0.44, P = 0.88).

Copepods, a relatively small zooplankton category(< 1.5 mm), showed diel differences in size-class distributions. Copepods smaller than 0.5 mm ($F_{1.8}$ = 18.3, P = 0,003) and larger than 1 mm ($F_{1.8}$ = 12.2, P = 0.008) were more abundant during the day, while the abundance of zooplankton in the middle size class was similar day and night ($F_{1.8}$ = 1.64, P = 0.24; Fig. 2).

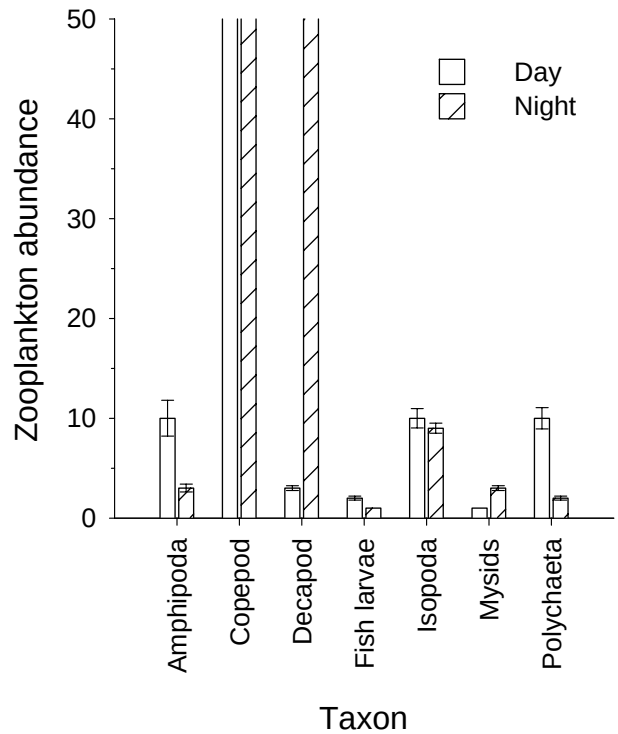

Figure 1. Zooplankton abundance between taxa in the day versus the night. Copepod day abundance was 627 ± 11.96 and night abundance was 205 ± 21.04. Decapod night abundance was 183 ± 11.96. Graph was capped to allow comparison between less abundant zooplankton.

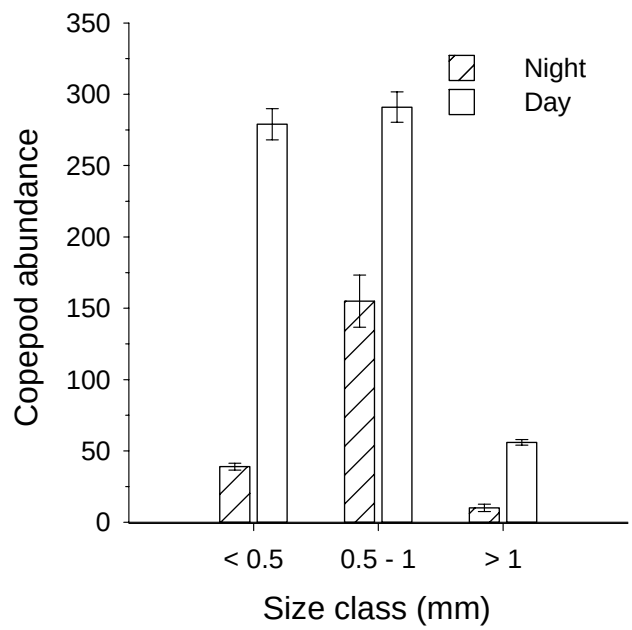

Figure 2. Copepod size class abundance during the day versus at night.

DISCUSSION

We found very low overall zooplankton abundance (orders of magnitude less than in three previous years; Fagan et al. 2002, Iwamoto et al. 2003, Pickhardt et al. 1999), with no significant difference between day and night abundance. The trend of greater zooplankton abundance during the day than at night is inconsistent with the findings of other diel zooplankton pattern studies. This is especially surprising as

there was little moonlight (four days waxing past the new moon), and we expected that zooplankton would be more abundant in darker night conditions when visual predators are disadvantaged.

We speculate that zooplankton have a patchy distribution horizontally in the water column. This may be caused by habitat heterogeneity of zooplankton resources, such as refuge and food, that could lead to spatial variance in abundance. Perhaps we saw low zooplankton abundance because there was little refuge available to zooplankton in our sampling area. Further studies should look for horizontal patchiness in zooplankton abundance, and determine if local abundance is affected by available refuge, or other factors that vary spatially across their range.

The average zooplankton size was larger at night versus the day. This pattern was driven by decapod larvae, which are large and much more abundant at night. Copepods, the most abundant and smallest zooplankton, had a higher abundance of the largest and smallest size classes during the day versus the night, while the middle size class did not change. The largest copepod size class was smaller than all the other zooplankton taxa. Therefore, we expected them to be more abundant during the day, as they are not easily seen by visual predators. The increased abundance of large copepods during the day, however, may be an artifact of low sample size. Perhaps there were such low levels of abundance overall that finding a few of the largest copepods could lead to a statistically significant result.

The results of this study suggest that there may have been a large decrease in zooplankton abundance in the back reef in the past year. Alternatively, zooplankton abundance may experience endogenous population fluctuations on some temporal scale, or fluctuate in response to some exogenous perturbation.

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DIEL PATTERNS OF CORAL REEF FISH COMPOSITION AND ABUNDANCE IN FOUR HABITATS

ELIZABETH V. WILSON, STEPHEN T. WELLER, R. QUINN THOMAS, SARA M. HELLMUTH, PETER N. CHALMERS AND JULIA M. BUTZLER

Abstract: In this study, we explore the role of spatial and temporal resource partitioning as potential factors contributing to the maintenance of diversity of fish on a coral reef. We surveyed the fish community of Discovery Bay, Jamaica in four different habitats during two different times of day. We calculated species richness and evenness to compare the day and night fish communities. We also used richness and evenness to compare the day and night fish communities within each habitat, and to compare the fish communities within each habitat during each sampling period. We observed a total of 60 fish species, and a total of 1002 individuals. We found that both species richness and evenness varied with time of day and habitat. This study shows that coral reef fish partition themselves both spatially and temporally, possibly contributing to the high diversities of fish observed on coral reefs.

Key words: abundance, back reef, coral reef fish, day, night, patch reef, richness, sand, turtle grass

INTRODUCTION

The coral reef fish community is recognized as being highly speciose (Horn 1989, Harmelin-Vivien 2002). Many theories have been proposed to explain the general pattern of high species diversity, such as intermediate levels of disturbance, a highly diverse regional species pool and resource partitioning (Begon et al. 1990). Resource partitioning encourages high diversity by allowing many species to occupy the same geographic area through the separation of resources; because species are utilizing different resources, direct competition is prevented (Begon et al. 1990).

Resource partitioning can occur both spatially and temporally. A species can avoid interacting with another species with which it competes by avoiding overlap in space (e.g., feeding grounds) and/or time (e.g., feeding time). In this study, we explore the role of spatial and temporal resource partitioning as potential factors contributing to the maintenance of diversity of fish on a coral reef. We hypothesize that the species composition, richness and evenness will differ temporally (between day and night) and spatially (between habitat: sandy bottom, turtle grass beds, patches reefs, and the back reef).

METHODS

On 26 February 2004, we surveyed the fish community of Discovery Bay, Jamaica. Eight pairs of observers each conducted 10-min surveys in four habitat types (back reef, patch reef, turtle grass bed and sand patch) both in the day (0830 - 0930) and night (2030 - 2130). Observers recorded fish species composition and abundance observed during each time interval. The data collected by each observer pair were combined to estimate overall abundance and richness in each habitat at both night and day.

We calculated species evenness for each treatment using

$$J' = (H' / H' max) = -\Sigma(p_i * log (p_i)) / log (k),$$

where p_i is the proportion of observations in category i, and k is the total number of species observed (Zar 1984). We then used Chi square tests to compare overall species richness found in the day versus the night, to compare species richness within each habitat between both sampling periods, and to determine if species richness within each sampling period varied between habitats.

RESULTS

We observed a total of 60 fish species, with 29 species found only during the day, 15 found only during the night, and 16 found in both day and night samples (Figure 1, Appendix 1). A total of 1002 individuals were observed, 85% during the day and 15% during the night. Species richness was lower at night than in the day; however, when examined at a finer scale (e.g., habitat), this difference was only significant for patch reefs (Table 1, Fig. 2). The number of species found in patch reefs during the day was three times greater than the number found at night. Species richness also differed significantly among habitats during the day, but not at night (Table 1). Overall, evenness tended to be higher at night; when examined at a finer scale, we found that sand patches had the highest evenness at both day and night (Table 2, Fig. 3).

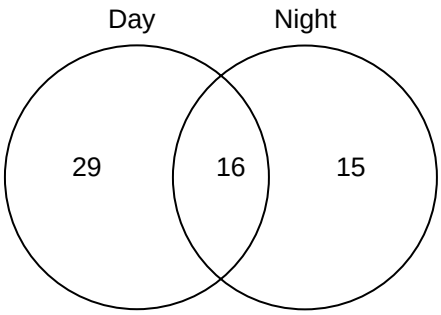

Figure 1. Number of fish species found in the day, night, and in both censuses in four habitats of the back reef of Discovery Bay, Jamaica.

Table 1. Chi-square statistics for diel and habitat comparisons of species richness. Significant differences are marked with an asterisk (*).

Treatment	χ^2	df	P
Overall (day vs. night)	2.58	1	0.11
Day patch reef vs. night patch reef	6.72	1	0.01*
Day back reef vs. night back reef	0.40	1	0.53
Day turtle grass vs. night turtle grass	0.93	1	0.34
Day sand vs. night sand	0.22	1	0.64
Between habitats (within day)	11.23	3	0.01*
Between habitats (within night)	4.24	3	0.24

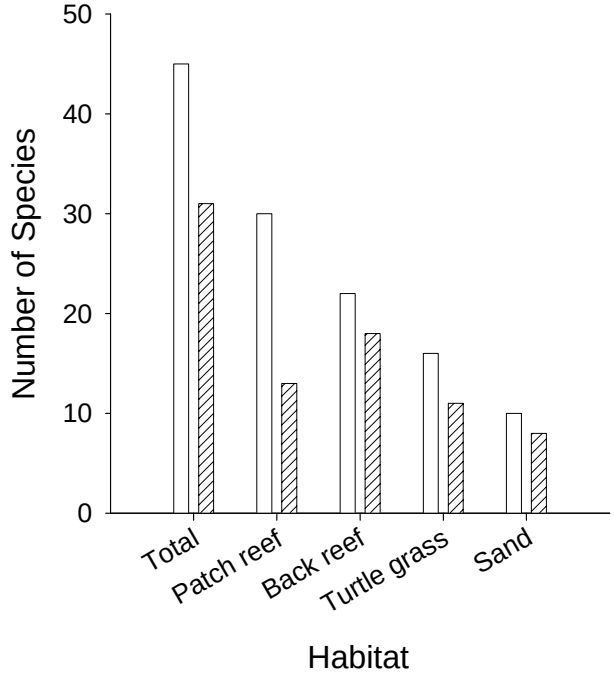

Figure 2. Species richness for each habitat type during the day (open bars) and night (hatched bars). Night and day richness differed significantly in patch reefs. Richness was significantly different among habitats during the day but not at night.

Table 2. Evenness values for diel and habitat comparisons.

	Day	Night
Sand bed	0.6164	0.8277
Turtle grass bed	0.7569	0.8637
Patch reef	0.7231	0.6806
Back reef	0.9145	0.9138
Total	0.6705	0.8468

DISCUSSION

Species richness tended to be higher during the day than at night, suggesting that there may be either more niches available to fish, or there are more resources available during the day. However, this pattern was only significant in the patch reef habitats. Previous studies have suggested that during the day, fish are more prevalent in areas that provide a refuge from predators such as patch reefs (Nagy et al. 2000). It is possible that many different species are concentrated on patch reefs during the day to avoid predation, subsequently dispersing at night to areas of less cover.

Species evenness was greater at night than during the day, indicating that there are fewer dominant species at night. The bluehead wrasse, french grunt, threespot damselfish, hardhead silversides and striped parrotfish were dominant during the day, each comprising at least 10% of the total species seen during the day, whereas these same species were very rare at night (Appendix 1). These particular fish feed on very different resources (e.g., the striped parrotfish feeds on algae and the bluehead wrasse feeds on invertebrates) thereby possibly allowing them to co-occur at higher abundances than if they all fed on the same resource. In contrast, most species found at night were primarily feeding on demersal zooplankton, prohibiting any one species to dominate.

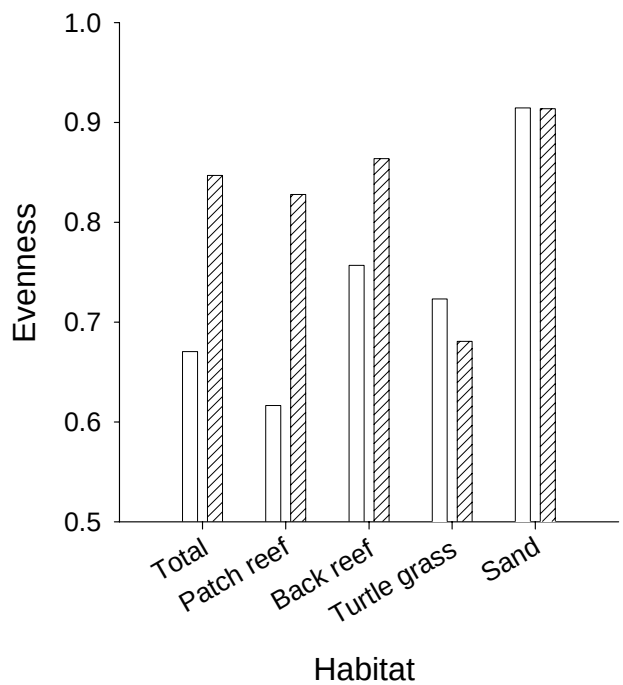

Figure 3. Evenness for each habitat type during the day (white bars) and night (hatched bars).

This study shows coral reef fish partitioning themselves both spatially and temporally, possibly contributing to the high diversities of fish observed on coral reefs. Further studies could test whether fish during the day are exploiting a higher diversity of feeding niches than those found at night, which might explain the higher species richness observed during the day.

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Appendix 1. # individuals of fish species observed at each location and time on 26 February 2004, Discovery Bay, Jamaica.

	Day				Night			
Species	Back	Patch	Sand	Turtle	Back	Patch	Sand	Turtle
Balloonfish	1	1		1	4	1	2	1
Banded jawfish			1					
Bar jack			2					
Barracuda				1				
Barred cardinalfish					2		3	
Barred hamlet				1				
Beaugregory	5	7	8	14	1			
Bicolor damselfish	20	3						
Bigeye								20
Blackbar soldierfish		1						
Blackear wrasse				2				
Blue tang	6	7			1			
Bluehead wrasse	75	10		30				
Bridled goby		5	9	3			5	
Clown wrasse		2						
Cocoa damselfish		1	4					
Doctorfish	11	3		4				
Dusky cardinalfish						2		
Dusky damselfish	25	2		1	2	1		
Dwarf herring					11			
Eyed flounder		1		1				
Fairy basslet		1						
Flamefish					2			
Foureye butterflyfish		1		1				
French grunt	11	65		40				
Glasseye snapper								1
Goldentail moray eel	1	1	3					
Hardhead silverside	100	1050	40	300	1040	1550	1350	740
Indigo hamlet	2	1						

Appendix 1. Continued from previous page.

	Day				Night			
Species	Back	Patch	Sand	Turtle	Back	Patch	Sand	Turtle
Longjaw squirrelfish	1				2	4		1
Longspine squirrelfish					4		2	
Mottled mojara			5					
Night sergeant					3			
Ocean surgeon	6	5		3	1	1		
Palehead blenny	1							
Porcupine fish					2		1	1
Purplemouth moray eel					1	1		
Redband parrotfish	2			1		1		
Reef squirrelfish	2	1			2	1		
Sergeant major	4							
Sharpnose puffer								1
Sharptail eel	1							
Slippery dick	10			1				
Spotfin butterflyfish		1						
Spotted goatfish		5		11				
Spotted scorpionfish	1							
Squirrelfish	8	6			14	11	2	6
Stoplight parrotfish	25	7				1		
Striped parrotfish	49	122		56				1
Threespot damselfish	36	51	3	20		2		
Trumpetfish					1			
Twospot cardinalfish					2	1		
Yellow stingray							4	1
Yellowfin mojarra			2					4
Yellowhead wrasse		1						
Yellowtail damselfish		4						
Yellowtail parrotfish							8	1
Yellow-tail hamlet		3						