Invertebrate colonization of artificial substrate in a coral reef ecosystem

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Abstract: We examined the colonization of artificial substrata in different habitats and depths over time as an important first step toward understanding the relationship between invertebrates and refuge. We predicted that artificial substrate in the west fore reef of Discovery Bay, Jamaica, would have higher abundance and diversity of colonists than that at Pear Tree Bottom, due to the greater availability of macroalgal refuge harboring more potential colonists at the west fore reef. We also predicted that the greatest invertebrate abundance and diversity would be found at an intermediate depth (where disturbance is intermediate), and that abundance, diversity, and evenness of colonists would likely increase over time. Although macroalgae presence, depth, and colonization time did not affect invertebrate abundance and diversity, they did affect evenness and size of invertebrates, suggesting that disturbance level may affect the community structure of marine invertebrates.

Key Words: amphipod, copepod, depth, intermediate disturbance hypothesis, macroalgae, ostracod, polychaete, refuge colonization, succession

Introduction

Coral reefs in the Caribbean region, such as Discovery Bay, Jamaica, have been negatively affected by stresses that are both natural (e.g., Hurricane Allen 1981, *Diadema* crash 1983) and anthropogenic (e.g., overfishing, eutrophication). As a result, coral reef composition has shifted from dominance by hard corals to dominance by macroalgae over the last 30 years (Nystrom 2000). This transition has reduced populations of algal herbivores and open substratum available for colonization by sessile marine invertebrates (Nystrom 2000). Though macroalgae are thought to be an important refuge for invertebrates (Glastris et al. 2001), the implications of increasing macroalgal refuge for invertebrates on coral reef ecosystems is unknown. Here we examine the colonization of artificial substrates in different habitats and depths over time as an important first step in understanding the relationship between invertebrates and refuge space.

We hypothesized that artificial substrate placed in areas of naturally high macroalgal cover would be colonized more quickly than those in sites of low macroalgal abundance, due to the greater availability of macroalgal refuge harboring more potential colonists. Thus, we predicted that artificial substrates in the West fore reef, an area with high macroalgal cover, would have higher abundance and diversity of colonists than Pear Tree Bottom, where percent macroalgae cover is low.

Depth may affect colonization characteristics though differences in wave and current action and light availability. Wave and current disturbances may hinder colonization of refuge space at shallow depths, and a reduction in photosynthetically active radiation (PAR) at deeper depths may limit primary production decrease with water depth, and therefore resources for invertebrates. Based on Connell's (1978) intermediate disturbance hypothesis and the fact that PAR and corresponding potential for primary production decreases with water depth (Begon et al. 1996), we predicted that the greatest invertebrate abundance and diversity would be found at an intermediate depth. Furthermore, we predicted that abundance, diversity, and evenness of colonists will increase over time. In addition, we tested differences in the structure of refuge space by comparing colonization in highly complex and more simple substrates.

Methods

We used mop heads and PVC pipes as artificial substrates. We cut 18 mop heads into halves (one mop head half was one mop unit). We used cable ties to cinch one end of the 36 mop units tightly and tied two 1.5 m lengths of rope to each of the cable ties (Style A, Fig. 1). The tops and bottoms of the remaining eight mops were cinched tight with cable ties and a 1.5 m length of rope was tied to each of the ties (Style B, Fig. 1). We then constructed six PVC pipe units. Each unit was composed of four 10 cm x 1 cm PVC pipes duct taped together. We also taped metal bolts on opposite ends to weight each unit and attached flagging (Fig. 2).

We haphazardly placed mop units in 10 m x 5 m plots without visible *Diadema* presence in the West fore reef (M1) of Discovery Bay, Jamaica, on 4 March 2001. Plot 1 was at approximately 3 m, Plot 2 was at 9 m, and Plot 3 was at 15 m. Each plot contained nine "A" mop units. We tied the two ropes of each mop unit to opposite pieces of substrate. We collected four mop units from each plot after three days and five mop units from each plot after five days. We placed each mop in a ziplock plastic bag before removing it from its attachment site, and transported the bags back to the laboratory.

To asses differences in placement of the artificial substrates, we placed mops that were either suspended above or secured against substrate at a haphazardly chosen 12 m plot without visible *Diadema* presence. On 7 March 2001, we secured four "B" mop units flush against rubble substrate so that the mop units would be relatively undisturbed by currents and wave action. The remaining four "B" mop units were tied to opposite pieces of substrate so that they would be suspended and subjected to more disturbance. We collected these mops after two days and brought them back to the laboratory.

To compare complex substrate to simple substrate, we placed nine "A" mop

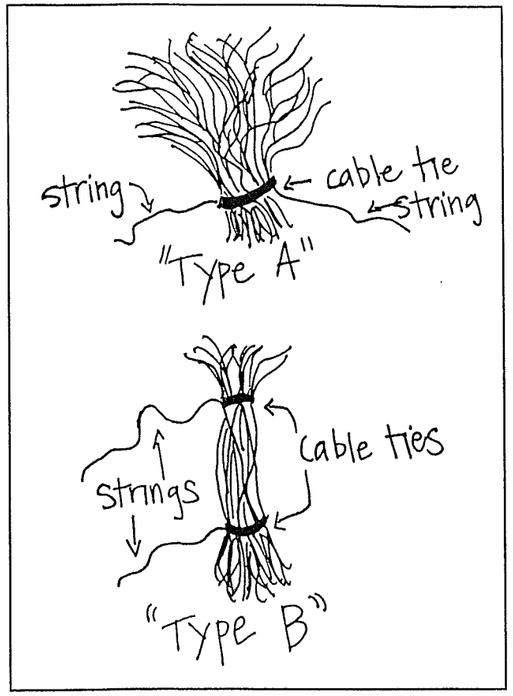

Fig. 1. Illustration of mop treatments. Mops bound at one end (A) were attached to the substrate at depths of 3 m (n = 9), 9 m (n = 9), and 15 m (n = 9) near the M1 dive site at Discovery Bay, Jamaica and at a depth of 3 m (n = 9) at Pear Tree Bottom, Jamaica. Mops bound at both ends (B) were attached against the substrate (n = 8) and suspended in the water column (n = 8) at a depth of 12 m near the M1 Dive site at Discovery Bay, Jamaica.

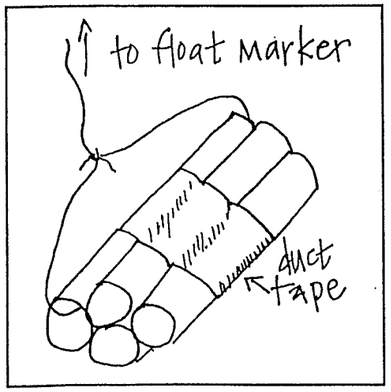

Fig. 2. Illustration of PVC pipe units. PVC pipe units were weighted and left at 3 m (n = 9) at Pear Tree Bottom, Jamaica.

units and six PVC units at a 3 m depth in the fore reef of Pear Tree Bottom (PT) in a 10 m x 5 m plot with visible *Diadema* presence on 4 March. We collected all mops and PVC units after five days and brought them back to the laboratory. Rough seas and poor visibility did not permit collection on day 3 for time comparisons.

In the laboratory, we placed every mop and each PVC unit in separate buckets of salt water. We agitated each mop for two minutes before ringing it dry. The remaining salt water was strained through a 211 μm mesh filter. This procedure was then repeated with a freshwater rinse. We placed the concentrated sample into a container with salt water. We then fixed each sample with formalin (1:10 ratio with salt water) and let it sit for a minimum of one hour. Each sample was filtered again to remove formalin, and slightly diluted with salt water. Using a dissecting microscope we counted and identified all extracted invertebrates to order and estimated their body lengths.

To assess the effects of location on abundance and diversity of mop colonists collected on day 5 at M1 (3 m) and PT (3 m), we used ANOVAs and a Chi-square test. To assess the effects of depth and time, we ran 2-way ANOVAs on mops collected on days 3 and 5 at all depths at M1. We calculated diversity and evenness using the Shannon-Weiner diversity index.

Results

Location

Samples from sites M1 and PT did not differ in abundance (ANOVA, F = 0.18, df = 1, 7, P = 0.69), diversity (ANOVA, F = 3.05, df = 1, 11, P = 0.110), or evenness (ANOVA, F = 2.03, df = 1, 11, P = 0.18) of the colonists communities. Community composition did differ significantly between M1 and PT (χ^2 = 12.96, df = 3, 115, P = 0.005; Fig. 3). More polychaetes were found at M1 and more copepods were found at PT. Invertebrates at M1 were significantly larger than invertebrates at PT (ANOVA, F = 5.30, df = 1, 140, P = 0.023).

Depth and Time

At M1, there was no effect of depth or time on colonist abundance (2-way ANOVA, F = 1.69, df = 5, 20, P = 0.18) or diversity (ANOVA, F = 1.05, df = 5, 19, P = 0.42). Evenness was significantly greater after 5 days than 3 days (2-way ANOVA, F = 15.53, df = 1, P = 0.0009; Table 1, Fig. 4). We also found that evenness was affected by depth (2-way ANOVA, F = 6.71, df = 2, P = 0.0063), being greater at 15 m than at 3 m (Table 1, Fig. 5). After five days, there was also a significant difference in invertebrate composition (χ^2 = 21.57, df = 10, 271, P = 0.025), but no single taxon demonstrated an outstanding change. Invertebrate size was significantly greater after 5 days (2.36 ± 0.16 mm) than after 3 days (1.58 ± 0.11 mm) (2-way ANOVA, F = 19.90, df = 1, P < 0.0001). There was no effect of depth on invertebrate size nor was there an interaction between duration and depth (2-way ANOVA, F = 1.11, df = 2, P = 0.33; 2-way ANOVA, F = 2.20, df = 2, P = 0.11, respectively).

Variation due to artificial substrate type

We found no difference in abundance or taxa composition of invertebrates between mops attached to the substrate and those suspended above the substrate (ANOVA, F = 0.56, df = 1, 6, P = 0.48; χ^2 = 3.00, df = 3, 117, P = 0.39, respectively). Invertebrates were significantly larger in mops attached to the substrate than those suspended above the substrate (ANOVA, F = 5.05, df = 1, 140, P = 0.026). We found no significant difference in size of organisms between mops and PVC pipe substrate placed at PT (ANOVA, F = 1.43, df = 1, 118, P = 0.23).

Other observations

We found several invertebrates not found by Glastris et al. (2001) in a recent examination of natural macroalgal inhabitants at Discovery Bay. Of note were one of order

Table 1. Mean diversity (H ± 1 SE), mean evenness (J ± 1 SE), number of taxa, and number of invertebrates found at the West fore reef (M1), Discovery Bay and Pear Tree Bottom (PT), Jamaica.

Location	Depth	N	Day	Mean H	Mean J	# Taxa	# Invertebrates
M1	10	4	3	1.54 ± 0.12	0.35 ± 0.12	6	59
M1	10	4	5	1.38 ± 0.17	0.77 ± 0.06	8	68
M1	30	4	3	1.47 ± 0.06	0.66 ± 0.10	12	167
M1	30	5	5	1.60 ± 0.16	0.83 ± 0.04	9	173
M1	50	4	3	1.21 ± 0.25	0.76 ± 0.08	9	70
M1	50	4	5	1.64 ± 0.05	0.90 ± 0.03	10	86
PT	10	5	5	1.14 ± 0.14	0.79 ± 0.03	8	74
PVC (at PT)	10	4	5	1.12 ± 0.21	0.83 ± 0.04	9	46

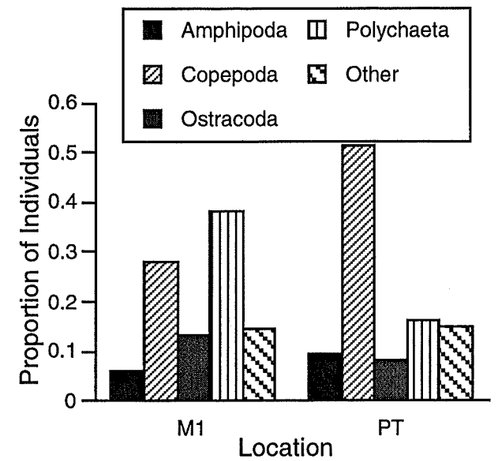

Fig. 3. Proportion of individuals found within the four most common orders (and "Other" for rare orders) at the West fore reef, Discovery Bay (M1), and Pear Tree Bottom (PT), Jamaica.

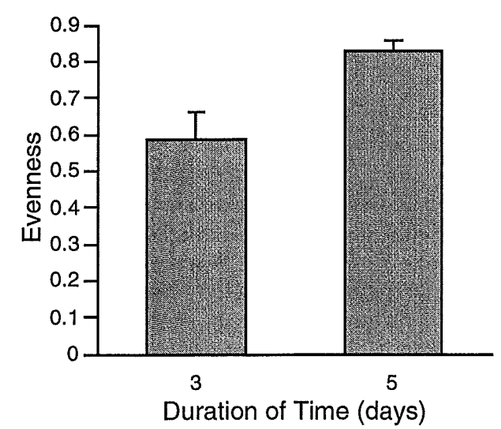

Fig. 4. Mean evenness (J ± 1 SE) of taxa for mops exposed for 3 days (n = 12) and those exposed for 5 days (n = 13) at the West fore reef of Discovery Bay, Jamaica.

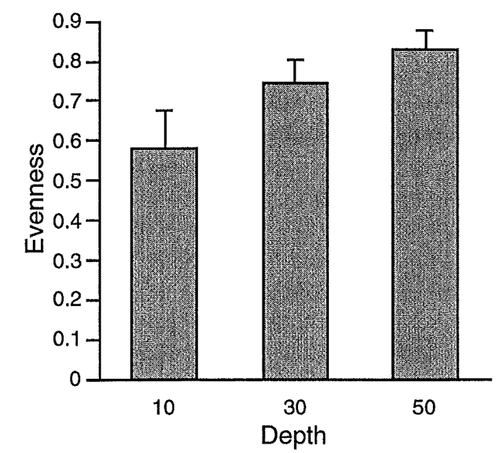

Fig. 5. Mean evenness (J ± 1 SE) of taxa at 10 feet (n = 9), 30 feet (n = 8), and 50 feet (n = 8) on the West fore reef, Discovery Bay, Jamaica.

cirripedia, a barnacle larva, two very small fish (10-15 mm), and one leptostrocan shrimp. Mean sizes of all invertebrates sampled were consistent with the size range of invertebrates found by Glastris et al. (this volume) in three macroalgal species. Whereas those authors found an approximate mean size range from 1.50 to 2.40 mm, we found a comparable mean size range from 1.48 to 2.19 mm.

Discussion

The study of Glastris et al. (2001) suggests that macroalgae host a rich assemblage of invertebrates. Based on our observation that the West fore reef has more macroalgae and thus might already host more potential

macroalgal colonists, we predicted that the West fore reef and Pear Tree Bottom would differ in colonization characteristics. Pear Tree Bottom is dominated by coral buttresses and *Diadema* patches whereas the West fore reef is dominated by algae-covered rubble. The lack of difference in invertebrate assemblage characteristics suggests that coral is also an important refuge for invertebrates and may be an important source of colonists that could disperse to new substrates during times of disturbance (Able 1984). Differences in substrate, as well as predation pressure and resources, may explain why invertebrate size and composition differed between locations. Any other potential differences between locations may have been masked by wave and current disturbance generated by a three-day storm, since both locations used for comparison were at a 3 m depth where wave action was high.

This storm may have also exaggerated the potential effects of disturbance on depth. Mops found at shallower depths appeared most affected by the storm, as they were the most tattered and had the lowest evenness. If disturbance occurs frequently, colonization will not advance beyond the pioneer stage, and the diversity of the community as a whole will be low because pioneer species will dominate (Connell 1978, Begon et al. 1996). Successional species may not have had an opportunity to colonize our mops at shallow depths because of the storm's constant disturbance. Our results suggest that disturbance may affect the colonizer community composition of the coral reef. The storm may have been great enough to cause disturbance to mops placed at 9 m. In addition, the mops placed at 9 m may have not been at an "intermediate" depth as we intended, as evenness continued to increase with depth. Since evenness continued to increase after our designated "intermediate" depth at 9 m, a greater range of depths should be used to test the intermediate disturbance hypothesis (Connell et al. 1978).

The larger body size of colonists found in mops after 5 days versus 3 days may be explained by larger predators that recognize the mops as a source of food and begin to colonize them. Small copepods and other small plankton may colonize first, followed by larger, and perhaps less mobile, invertebrates. The lack of effect of time on abundance of invertebrates in the mops is surprising, but may be explained by slow colonization rates. A time scale of 3 to 5 days may be too short to observe succession in the refuge space we provided. Further study looking over a longer temporal scale would be of interest.

The greater size of invertebrates found in mops attached to the substrate versus those suspended above it may be because those attached firmly to rock provided a more stable refuge for invertebrates seeking cover from predators. Alternatively or in concert with this mechanism, dispersal abilities of larger benthic invertebrates may limit the possibility of colonizing suspended mops. For example, larger invertebrates such as polychaete worms, which were common, would not be able to disperse as easily to suspended mops as would copepods thus explaining the small size of invertebrates found in the suspended mops. Assessments of PVC units for invertebrate colonization also may have been substantially affected by the storm, as the units were not secured to the substrate. As a result, colonists prior to the storm may have been dislodged more easily during the storm than those in the filamentous mops.

The similarity of taxa and body size between our study and that of Glastris et al. (2001) potentially suggests that our artificial substrata adequately mimicked macroalgal structure. However, we have some concern that while structure of these artificial substrata was comparable to natural macroalgae, food resources available to colonists differed and may distort community characteristics. For example, many macroalgal inhabitants eat the algae that form their habitat (Duffy and Hay 1990) and thus may not settle in our mops where microalgae and bacteria may be the primary resources available. Future studies

could remove natural macroalgae, cleanse them of colonists, and return them to the field to better assess colonization on a natural substrate. As macroalgae continue to be an important component of the reef ecosystem at Discovery Bay, understanding these dynamics will provide insight into potential "bottom-up" mechanisms affecting community composition.

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