

The Impact of Mangrove Prop-Root Epibionts on Juvenile Reef Fishes: A Field Experiment Using Artificial Roots and Epifauna

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Abstract A field experiment was established in Bocas Del Toro, Panama to examine the relationship between sessile organisms living on mangrove prop roots and fish communities. Artificial mangrove roots (AMR) with different sets of artificial (AE) or real epibionts were established in five different locations in two separate years. Fish species in each plot were identified, counted, and their size estimated by visual census for 15 days in each replicate. In the artificial mangrove plots, the treatments with the most heterogeneous structure had significantly greater abundance of most families and species richness of fish in both years of the experiment. AMR plots with AEs attracted a more abundant and diverse fish assemblage than those with live epibionts, which had lower three-dimensional structure. All of the AMR plots had significantly greater fish abundance than comparable plots of sea grass alone. The location of the replicate also made a significant difference to fish abundance. The data indicate that prop-root epibionts can enhance fish abundance and diversity in mangroves,

although the relationship may depend on the specific nature of the epibionts and fishes present.

Keywords Artificial mangrove root · Artificial epibiont · Juvenile reef fish · Mangroves as fish habitat · Habitat heterogeneity

Introduction

Mangroves and other shallow-water tropical habitats are believed to function as nursery habitats for reef fish, sheltering large numbers of juvenile fish among the prop roots to a varying degree (Parrish 1989; Nagelkerken et al. 2000, 2002; Faunce and Serafy 2006). The presence of mangroves increases abundance or biomass and enhances fish communities on nearby reefs and fisheries (Dorenbosch et al. 2004, 2005; Mumby et al. 2004; Manson et al. 2005).

The importance of mangroves as a fish nursery habitat may relate to the relationship between habitat and predator efficiency. Several studies have suggested that there is a trade-off involved for prey species in shelter habitats; the densest habitats reduce predator foraging most efficiently, but are also not always the best habitats for the prey species themselves to forage (Crowder and Cooper 1982; Gotceitas and Colgan 1989). Predators themselves may grow more slowly in very densely structured habitats (Spitzer et al. 2000). The majority of studies on this topic, however, have examined habitat density, while only a few have discussed habitat shape or impacts of shape on trophic interactions (Beukers and Jones 1998; Warfe and Barmuta 2004).

The relationship between habitat complexity and fish communities, with or without predators, has also drawn attention, with most authors agreeing that a more heterogeneous or rugose habitat increases diversity or abundance in

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fish communities (Luckhurst and Luckhurst 1978a, b; Caley and St. John 1996; Gratwicke and Speight 2005a, b). A habitat that is conducive to a greater abundance of smaller prey species is also conducive to a greater abundance of predators as well (Stewart and Jones 2001).

The mangrove prop root habitat contains far more than just roots and fish. In many areas, particularly in the Caribbean, a diverse epibiont community of sessile organisms, e.g., algae, sponges, etc., live directly on the roots themselves. These organisms have been determined to be important to the mangrove forest, protecting the roots from harmful infestations (Sutherland 1980; Ellison and Farnsworth 1990). Their loss potentially has severe ecological or economic implications (Ellison 2008).

The importance of these organisms to fish habitat has rarely been addressed. Kieckbusch et al. (2004) examined trophic relationships between primary producers, noting the role of algae as a base of the food web in these areas. Epibionts themselves are prey for several mangrove-utilizing species (e.g., *Holocanthus* spp.), and some types are prey habitat for others (Cruz-Rivera and Paul 2006). However, given the diversity of body shape and function of mangrove root epibionts, their importance may extend beyond primary food webs or as a physical protective barrier for the trees. Many of these organisms are large enough to substantially increase structural heterogeneity in the mangroves, and epibiont communities can demonstrate enough diversity to change the character of a mangrove habitat at a small scale.

A number of field experiments have used a variety of artificial structures to simulate mangrove habitat and examine hypotheses about why mangroves attract juvenile fish. These studies have examined the role of structure, root density, shade, feeding opportunities, or behavior in attracting fish to mangroves in both Caribbean and Pacific mangroves (Laegdsgaard and Johnson 2001; Cocheret de la Moriniere et al. 2004; Meager et al. 2005; Verweij et al. 2006a; Nagelkerken and Faunce 2007). Only one laboratory study (Meager et al. 2005), examined mangrove habitat complexity beyond vertical structures, also taking into account highly heterogeneous woody debris.

The present study used a combination of artificial mangrove roots (AMRs) and artificial epibionts (AEs) to experimentally examine the potential importance of mangrove epibionts to fish habitat in a field setting. We tested the idea that both the amount of structure (surface area) as well as the total number of AEs would both be important in attracting fish. We hypothesized that (a) treatments with both the highest number of individual structures and the greatest overall volume of surface area would attract the greatest diversity and highest densities of fishes, and (b) all plots with heterogeneous structure would attract higher densities than control plots. We also hypothesized that in

the absence of variation in structural heterogeneity created by the AEs, any differences would disappear. The structural heterogeneity was hypothesized to have the greatest influence on densities of smaller fish.

Materials and Methods

Site Description

The experiment was established near the town of Bocas Del Toro, Isla Colon, Bocas Del Toro Province, Panama (Fig. 1). The shorelines in the study area are almost exclusively fringing red mangroves *Rhizophora mangle*, with occasional individual white mangroves, *Laguncularia racemosa* behind them. The *R. mangle* abut extensive beds of the marine grass *Thalassia testudinum*, frequently interspersed with *Porites porites* and other species of shallow-water corals. The closest coral reef is 200 m away. The majority of the human population is found in nearby Bocas del Toro town, or the port of Almirante on the mainland. The rest of the area is sporadically settled, although there has been clearing of *R. mangle* fringes on many islands and the mainland. Artisanal and subsistence fishing is a major source of income in the area, including in the immediate study area.

Depth and sea grass shoot density were quite consistent throughout the study area; the depth was between 0.73 and 0.9 m, and sea grass density varied from 743 to 762 shoots per square meter at the densest. Sea grass canopy height ranged from 11.5 cm at the shortest to 13 cm at the tallest. Tidal range in the Bahia Almirante is small, between two and 15 cm under most conditions (Guzman et al. 2005).

All replicates of the study were performed during the wet season; fish abundance in inshore habitats usually peaks on a seasonal basis (Stoner 1986; Barletta et al. 2003; Lugendo et al. 2007).

Artificial Mangrove Roots and Epibionts

Artificial mangrove roots (AMRs) were constructed from wooden stakes, 5×2.5×100 cm sharpened and driven into the *Thalassia* beds to a depth of 25 cm, leaving 75 cm exposed. AMRs were arranged into square 1-m² plots, 25 stakes/plot. The stakes were deliberately arranged in a disordered manner with different orientations of the long and short axes to better mimic real mangroves. This density of stakes was slightly under the average root density in the area of 30.1 roots per square meter, but the stakes are considerably broader than the typical mangrove prop-root, giving each plot approximate surface area and space between roots to local conditions.

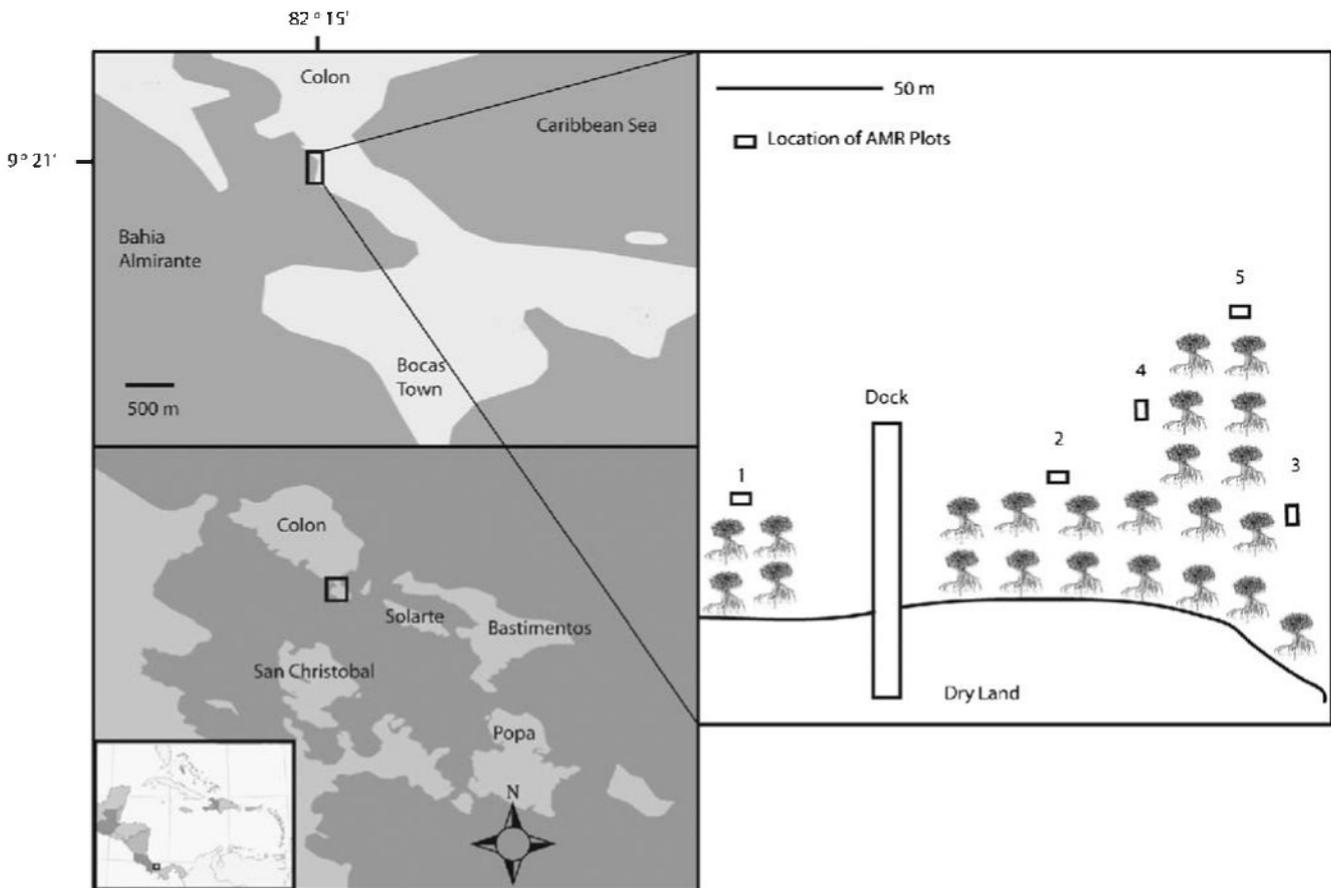


Fig. 1 Map of Panama (*inset*) with the entire Bocas del Toro archipelago and the immediate study area indicated. A close-up diagram of the area surrounding each group of replicate treatments is shown at *right*

Each group of plots had structures attached perpendicular to the stakes according to the following system (Fig. 2a): (a) one plot with blank stakes without attachments, the control (“blank”); (b) one plot with $5 \times 5 \times 10$ cm wooden blocks attached at random heights and directions perpendicularly (long axis) to the side of each stake (“blocks”), one block to each AMR, simulating very bulky root epibionts such as massive sponges or oyster clumps; (c) one plot with blocks attached to 12 of the stakes, and three wooden dowels, 1.5 cm diameter by 5 cm long, attached perpendicularly to each of the remaining 13 stakes in the plot (referred to as the “mixed” plot). As with the blocks, the orientation and height of each dowel was random. (d) The new treatment added in 2006 consisted of three dowels 1.5 cm diameter by 5 cm long attached perpendicularly to all 25 stakes in the 1-m^2 plot (“dowels”). The height above the sea grass and orientation of the dowels was random for each stake. (e) A 1-m^2 plot of *Thalassia* without any AMRs, marked at the corners. In each location the order of the treatment and control plots was rearranged. All AEs were attached to their stakes with a strong waterproof marine epoxy, cured on dry land prior to immersion.

For each AE treatment type, a “Structure Score” consisting of the total surface area of AE/plot (in meters) multiplied by the total number of individual AEs present in the plot and divided. The “mixed” treatment scored highest (187.91), followed by the “blocks” treatment (140.625), and finally the “dowel” treatment (132.53). These structures were designed to mimic existing epibiotic organisms common in the study area. The size of the blocks approximately mimics the large sponges found on many of the local prop-roots. The dowels are a fair approximation of many of the species of solitary tunicates found on the mangroves. Mature epibiont communities in the Bocas del Toro region are more spatially complex than the set-up described here, but aside from the difficulty of duplicating such complicated structures this arrangement provided structure without severely impeding the ability of the observer to count every fish in each plot.

Experimental Design

The experiment was performed three times: August 2005, late May/early June 2006, and again in late June–August 2006.

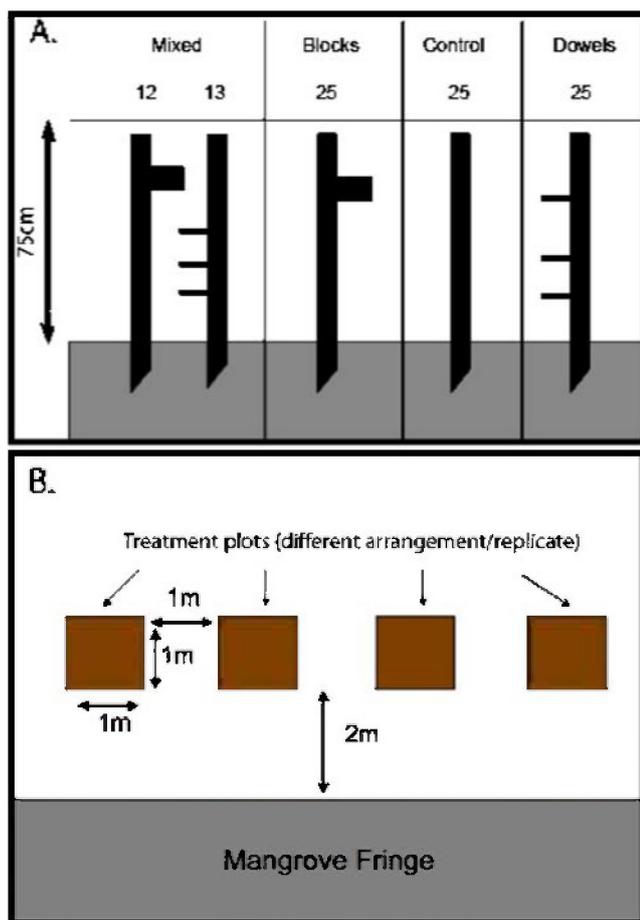


Fig. 2 (A, bottom) Artificial Epibiont (AE) treatment types. A 1-m² sea grass plot (not depicted) was also included in each replicate of the experiment. (B, top) Diagram of a replicate (site). Each square represents a different treatment. The configuration of each set of treatments was different at each replicate. Treatments varied slightly depending on the study period (see text)

During each study period, the 1-m² treatment and control plots were arranged into groups of three (or four; see below). Each AMR treatment plot or sea grass control was separated from adjacent plots by a 1-m² patch of sea grass. Each complete group of plots (75–100 stakes total and sea grass plot) was separated by at least 25–40 m from the other groups; there were three complete groups, each referred to as a “site”. Each site was exactly 2 m from the nearest mangrove fringe, and each was in the shade of the trees at all times except midday (Fig. 2b). All sites were located very close to a Smithsonian Tropical Research Institute (STRI) facility to discourage vandalism (Fig. 1).

After establishment, each treatment was left in place for 15 days to recruit fish, and scrubbed clean of algae or other settling organisms every other day during this period. After 15 days, every site was then surveyed by means of visual

census by a very experienced observer twice a day for 16 days, always in full daylight between the hours of 8:00 and 9:00 A.M. and again between 3:30 and 4:30 P.M. The observer entered the water at least 20 m from each site to avoid startling any fish inside. The census was conducted by swimming slowly around the edges of each treatment plot, looking left and right in the slots between them, surveying edges of two separate treatments simultaneously, which allowed the observer to count fish in one that were startled by the census of an adjacent treatment. Each treatment within a site was surveyed along each of its four edges, beginning from a different direction and at a different treatment and a different site each time. The structures were still cleaned every other day during this period, but only well outside of census periods.

The observer identified, counted, and estimated the size of each fish observed using a ruler attached to a clipboard for reference. Biomass was estimated using size estimates and published length–weight relationships available at www.fishbase.org (Froese and Pauly 2007). A fish was included if any part of its body was inside the treatment plot. Fish were counted as belonging only to the first treatment where they were observed; no fish could be counted as belonging to more than one treatment per location per survey. Fish were chased completely out of the sites in between counts; individuals that moved from one treatment plot to another within a site were chased completely out of the entire group of plots in order to reduce double counting of individuals between morning and afternoon counts.

Period One: August 11–27, 2005

The first three sites (Fig. 1) were first established during late July of 2005 and surveyed during the days mentioned above. During this period the dowel treatment was not included in the study, although all others were, so for the initial run each site consisted of three treatment plots in addition to the sea grass plot.

Period Two: May 24–June 7, 2006

After the first set of surveys in 2005, the AMRs were left in place for 11 months to allow settlement of sessile organisms. During this period, the marine epoxy binding the AEs to the stakes was dissolved or the AEs were otherwise shaken loose, as none remained attached by the time of the second run of the experiment. In June 2006, the plots of stakes, now fouled with living epibiota, in addition to the same sea grass plots, were once again surveyed twice a day for 15 days (bad weather necessitated shortening the study period by a day) under the same conditions as before, and afterward the settled organisms were identified and the

percent cover estimated using a 10×75 cm (grid squares are 5 cm across) quadrat.

Period Three: June 24– August 16, 2006.

Starting in late June 2006, the original experiment was repeated with all of the treatments, including the newly added dowel treatment, for a total of four treatment plots plus a sea grass plot at each location. After the waiting period and the 15-day census had been repeated at sites 1–3, two additional complete replicate sites of the entire set of five treatments, blank control stakes, blocks, mixed, dowels, and sea grass were established in two additional locations (4 and 5, Fig. 1) and the experiment continued in late July/early August 2006. Periodic bad weather during the study period meant that the observations were not all taken on subsequent days.

Statistical Analysis

Species were grouped into families, and the mean density for the eight most common families in addition to overall abundance and species richness/plot, were compared using three-way multivariate analysis of variance (MANOVA) using treatment, site, and date as factors. Overall biomass between treatments and entire sites was compared using three-way analysis of variance (ANOVA) with treatment, date, and site as factors. This analysis was followed up by an analysis of size classes of fish: less than 10 cm, 10–20 cm, and larger than 20 cm total length (TL). These data were based on an aggregate of all families (there were too few observations to analyze the mean size of each family) and compared using three-way MANOVA (date, site, and treatment). All MANOVA *F* statistics reported below are the Pillai's Trace *F*. Homogeneous groups were determined in each case using Tukey post hoc tests. Given that there were only two groups to compare, time of day was not added to the MANOVA design.

All analyses were performed separately in each phase of the study (July 2005, May 2006, and July 2006) due to differences between them, e.g., month, weather, and additional treatments. Rare species, defined as those observed only once, were discarded from analysis of species richness and aggregate fish density; one sighting was chosen as the cutoff as there was never an instance where only exactly two or three individuals were observed in a given study period. These species tended not to be representative of the local mangrove ichthyofauna. All analyses were performed using SPSS v. 13.0 for Macintosh. Community structure in the AMR plots was compared by non-parametric non-metric multidimensional scaling (NMMDS) using mean results for each treatment plot as individual observations. The NMMDS ordination was performed using PC-ORD 4.0.

Results

Abundance and Diversity

In total, the plots attracted 982 fish from 28 species and 16 families. Of these, 21 species from eight families were present in sufficient abundance to be included in analysis. The plots attracted fishes from all trophic levels ranging from herbivores to the top predator, the barracuda, *Sphyraena barracuda*. The most common species observed was the four-eye butterfly fish, *Chaetodon capistratus*, which accounted for 19.8% of total observed individuals. Schoolmaster snapper, *Lutjanus apodus*, which accounted for 17.8%, and lane snappers *Lutjanus synagris* at 9.1% were the second and third most common species, respectively. Grunts, *Haemulon* spp., made up 19.9%, and parrotfishes (Scaridae) 9%. Overall, the top eight most abundant families—Lutjanidae, Scaridae, Chaetodontidae, Sphyraenidae, Gerreidae, Serranidae, Acanthuridae, and Haemulidae—accounted for almost 99% of individuals observed.

Mid July/Early August 2005 Results

The mixed treatment had the highest density for seven of the eight families compared (the exception was Lutjanidae, which had highest abundance in the block treatment); this difference was significant in six of these (Fig. 3a). In most cases, block and mixed treatments were not significantly different from one another. Control treatments had significantly lower densities than the mixed treatments for three families, but did not generally differ significantly from the block treatments (Fig. 3a). Sea grass treatments had significantly lower densities than all AMR treatments (Fig. 3a). The mixed treatment did have significantly higher total fish abundance and species richness than all other treatments (Fig. 3a). Site was also a factor as there were significant differences between locations and site–treatment interactions, although the trend was similar in every site. There were significant day-to-day differences, but the date did not significantly impact treatment or site. MANOVA *F* values are listed in Table 1.

May–Early June 2006

The following spring, the AEs had all worn off the stakes, and these were replaced with a low-relief covering of living epibionts. Under these conditions, there were significant differences between treatments only in the Lutjanidae, which were still most abundant in block and mixed treatments (Fig. 3b, Table 1). All other families, as well as total abundance and species richness, did not vary significantly between AMR treatments in the absence of the

Fig. 3 Variation in fish density/treatment type for the eight most common families observed. *Letters* indicate significant differences between groups (within each family). *Error bars* represent ± 1 SE. **a** (*top*) shows results from the first study period, July–August 2005. **b** (*middle*) shows the same plots fouled with living epibiota but no artificial epibiota in June 2006. **c** (*bottom*) depicts the final study period, July 2006, when an all-dowel treatment was added and additional replicates were installed

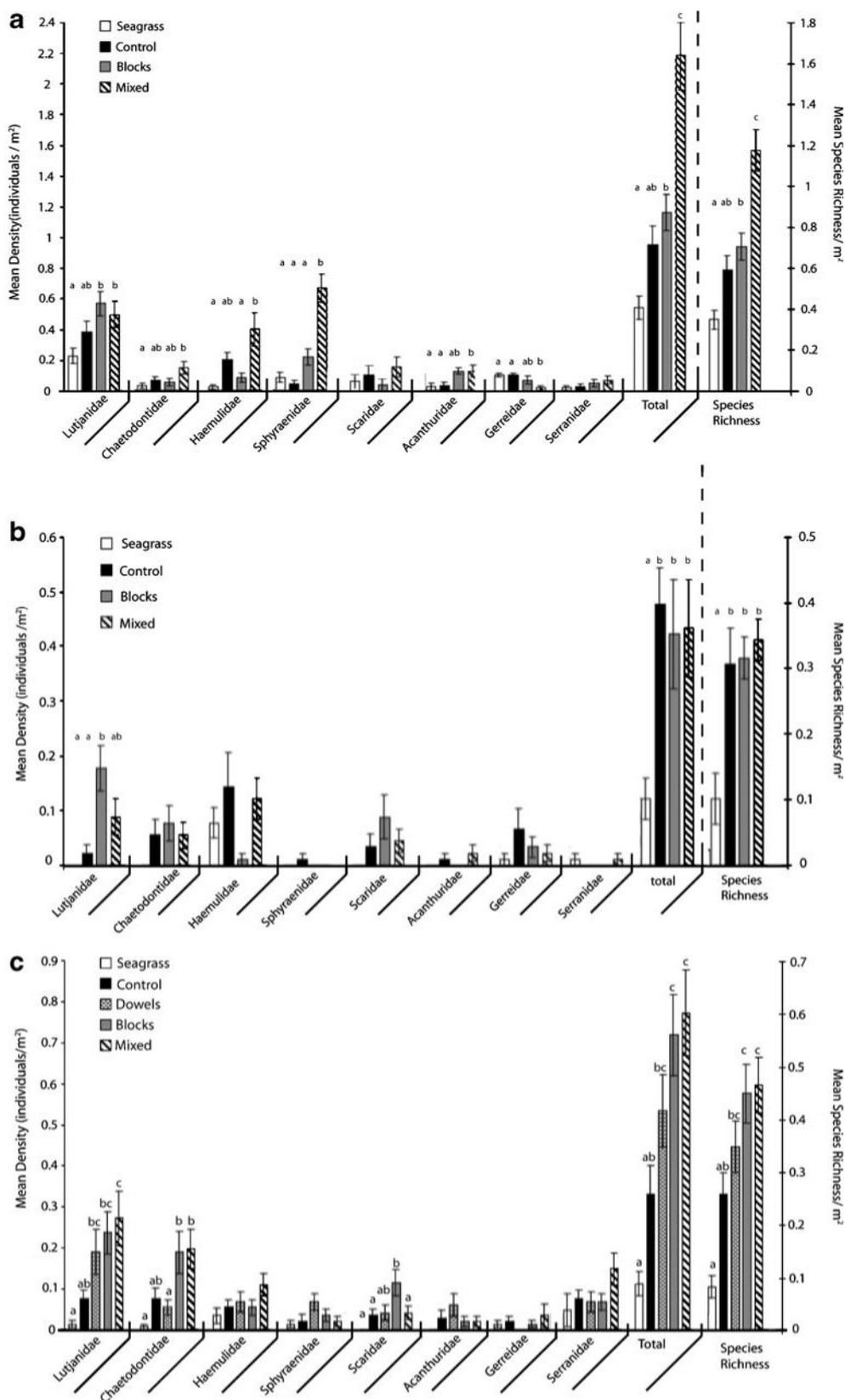


Table 1 MANOVA *F* values and significance levels for comparison of fish density among treatments, sites, and time periods

Effect/Family	<i>F</i>	<i>p</i> ≤	<i>df</i>
July 2005 (AEs, but no dowels)			
Site	1.466	0.212	2
Treatment	10.709	0.001	3
Date	1.026	0.432	15
Site × treatment	1.739	0.057	6
Site × date	0.998	0.491	45
Treatment × date	0.909	0.667	30
Site × Treatment × Date	1.075	0.279	90
Between subjects—site			
Lutjanidae	5.478	0.005	2
Scaridae	3.198	0.043	2
Sphyrenidae	3.090	0.048	2
Chaetodontidae	0.875	0.419	2
Acanthuridae	6.391	0.002	2
Haemulonidae	6.426	0.002	2
Gerreidae	1.444	0.238	2
Serranidae	3.588	0.030	2
Total abundance	1.798	0.168	2
Total Species Richness	0.903	0.407	2
Between subjects—treatment			
Lutjanidae	4.652	0.004	3
Scaridae	1.165	0.324	3
Sphyrenidae	27.204	0.001	3
Chaetodontidae	2.917	0.035	3
Acanthuridae	3.638	0.014	3
Haemulonidae	8.704	0.000	3
Gerreidae	3.667	0.013	3
Serranidae	1.157	0.328	3
Total abundance	24.071	0.001	3
Total Species Richness	23.184	0.001	3
May 2006 (No AEs, fouled)			
Site	2.511	0.001	2
Treatment	2.588	0.001	3
Date	1.153	0.126	15
Site × treatment	2.212	0.001	6
Site × date	0.945	0.715	45
Treatment × date	1.077	0.173	30
Site × Treatment × Date	1.032	0.314	90
Between subjects—site			
Lutjanidae	12.35	0.001	2
Scaridae	0.391	0.677	2
Sphyrenidae	1.632	0.199	2
Chaetodontidae	1.00	0.370	2
Acanthuridae	3	0.052	2
Haemulonidae	0.333	0.717	2
Gerreidae	0.667	0.515	2
Serranidae	2.000	0.138	2
Total abundance	1.440	.240	2
Total Species Richness	1.972	0.142	2
Between subjects—treatment			
Lutjanidae	10.33	0.001	3
Scaridae	1.889	0.131	3
Sphyrenidae	1.00	0.394	3
Chaetodontidae	1.87	0.135	3
Acanthuridae	1.222	0.303	3

Table 1 (continued)

Effect/Family	<i>F</i>	<i>p</i> ≤	<i>df</i>
Haemulonidae	2.333	0.076	3
Gerreidae	1.037	0.377	3
Serranidae	0.667	0.574	3
Total abundance	4.113	0.007	3
Total Species Richness	5.343	0.002	3
July–August 2006 (with dowel treatment)			
Site	20.122	0.001	4
Treatment	2.360	0.001	4
Date	1.296	0.016	15
Site × treatment	1.500	0.001	16
Site × date	1.033	0.308	60
Treatment × date	0.891	0.952	60
Site × Treatment × Date	0.900	0.995	240
Between subjects—site			
Lutjanidae	2.569	0.038	4
Scaridae	4.812	0.001	4
Sphyrenidae	1.555	0.186	4
Chaetodontidae	32.104	0.001	4
Acanthuridae	2.599	0.036	4
Haemulonidae	6.891	0.001	4
Gerreidae	0.433	0.784	4
Serranidae	3.886	0.004	4
Total abundance	8.752	0.001	4
Total Species Richness	8.565	0.001	4
Between subjects—treatment			
Lutjanidae	5.808	0.001	4
Scaridae	4.036	0.003	4
Sphyrenidae	1.754	0.138	4
Chaetodontidae	7.072	0.001	4
Acanthuridae	1.496	0.203	4
Haemulonidae	1.520	0.196	4
Gerreidae	0.635	0.638	4
Serranidae	2.034	0.09	4
Total abundance	10.973	0.001	4
Total Species Richness	11.082	0.001	4

Please refer to text for details of the model.

AEs, although sea grass still had significantly lower aggregate abundance and richness (Fig. 3b, Table 1).

July–Early August, 2006 Results

After the addition of the dowel-only treatment, the mixed treatment still had the highest fish abundance. Similar to the 2005 results, mixed and block treatments as well as the new treatment, dowel, had significantly higher abundance and species richness than control and sea grass treatments (Fig. 3c, Table 1). Most families again had the highest mean abundance in the mixed or block treatments; the differences were significant in three of the eight families (Fig. 3c, Table 1). Dowel treatments had higher means than control treatments for five of eight families, but these differences were not significant. Despite site-treatment

interactions (Table 1), the basic trend was similar in every replicate site, but the magnitude varied.

Biomass

There were no significant differences in biomass among treatments or controls in either 2005 or 2006, but there were significant differences between different sites when the AEs were present, but not during May 2006 when AEs had fallen off. There were significant interactions between site and treatment only in July–August 2006. July 2005—three-way ANOVA (date and site random), treatment: $F_{96, 3} = 1.585$, $p \leq 0.335$; site: $F_{128, 2} = 9.291$, $p \leq 0.001$; date, all interaction effects not significant (NS). May 2006—three-way ANOVA (date and site random), treatment: $F_{90, 3} = 3.116$, $p \leq 0.16$; site: $F_{120, 2} = 2.786$, $p \leq 0.24$; date: all interaction effects NS. July to August 2006—three-way ANOVA (date and site random), treatment: $F_{150, 4} = 0.928$, $p \leq 0.474$; site: $F_{150, 4} = 3.379$, $p \leq 0.03$; date \times treatment \times date NS; site \times treatment: $F_{150, 16} = 2.158$, $p \leq 0.007$. site \times date: $F_{150, 4} = 1.51$, $p \leq 0.019$.

Fish Size:

July–August 2005

When broken into size categories and aggregated, for all individuals under 20 cm TL, the mixed treatment had the highest mean abundance, while there was no difference between either sites or treatments for the largest individuals (Fig. 4a). Date did not have a significant effect on treatment, although there were some site–treatment interactions; one site (4) had a higher density of larger individuals in the “dowel” treatment, different from the overall trend of no treatment difference for the largest individuals. MANOVA results are shown in Table 2.

May 2006

In May 2006, the highest mean density of individuals under 10 cm TL was observed in the block treatments, although abundance was only significantly higher than sea grass treatments, with significant site–treatment interactions. Individuals larger than 10 cm did not vary between sites or treatments (Fig. 4a, Table 2). Date did not have a significant effect.

July–August 2006

In July 2006, for size classes under 20 cm TL, the highest mean density again was seen in the mixed treatment. The largest individuals, over 20 cm TL, were significantly higher in the newly added dowel treatment, although there was a particularly strong site–treatment interaction, with

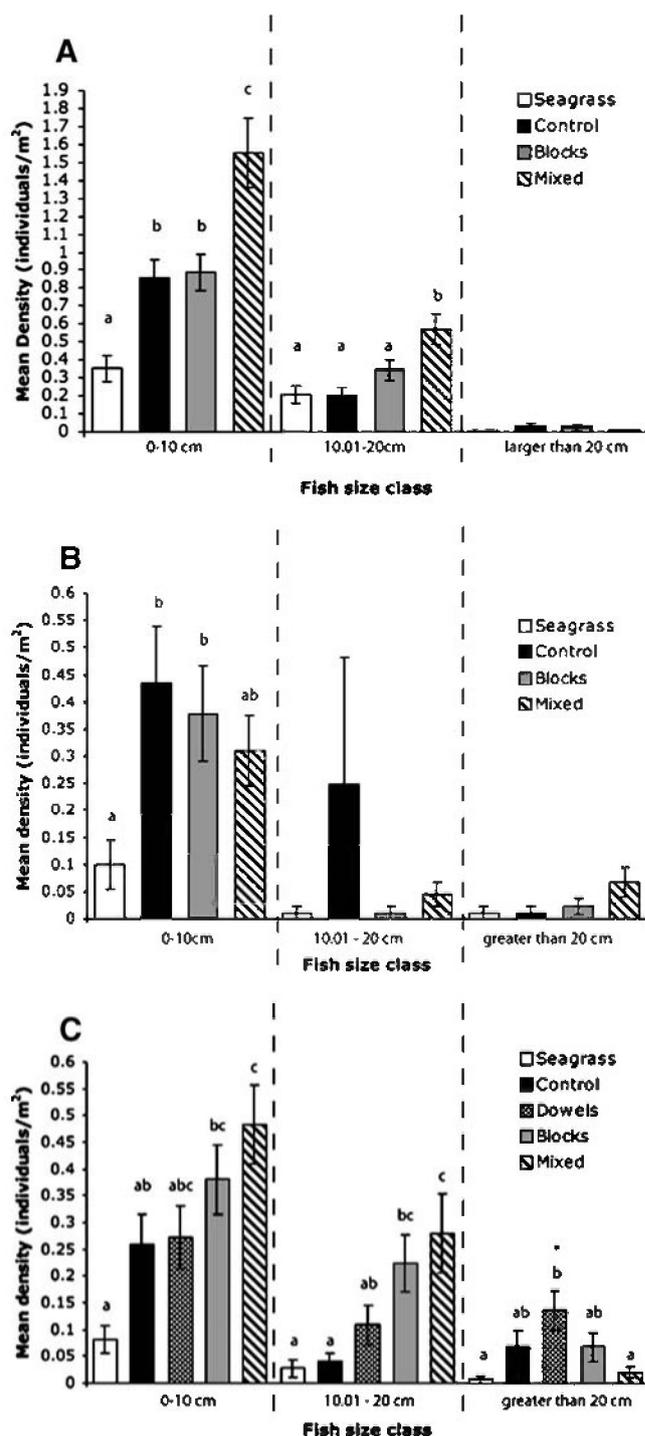


Fig. 4 Variation in fish density/treatment type for total individual densities according to three size classes: <10 cm, 10.01–20 cm, and >20 cm. Letters indicate significant differences between groups. Error bars represent ± 1 SE. **a** (top) shows results from the first study period, July–August 2005. **b** (middle) shows the same plots fouled with living epibiota but no artificial epibionts in June 2006. **c** (bottom) depicts the final study period, July 2006, when an all-dowel treatment was added and additional replicates were installed. The asterisk in **c** indicates the significant difference indicated occurred in only one replicate

Table 2 MANOVA *F* values and significance levels for comparison of fish size classes among treatments, sites, and time periods

Effect/Family	<i>F</i>	<i>P</i> ≤	<i>df</i>
July 2005 (AEs, but no dowels)			
Site	3.378	0.003	2
Treatment	7.470	0.001	3
Date	1.116	0.218	15
Site × treatment	1.566	0.064	6
Site × date	0.366	0.744	45
Treatment × date	0.957	0.616	30
Site × Treatment × Date	1.148	0.09	90
Between subjects—site			
0–10 cm	1.518	0.222	2
10.01–20 cm	7.822	0.001	2
>20 cm	1.300	0.275	2
Between subjects—treatment			
0–10 cm	15.851	0.001	3
10.01–20 cm	8.711	0.001	3
>20 cm	2.267	0.08	3
May 2006 (No AEs, fouled)			
Site	1.878	0.084	2
Treatment	2.235	0.019	3
Date	1.037	0.411	15
Site × treatment	2.017	0.008	6
Site × date	0.963	0.571	45
Treatment × date	1.013	0.451	30
Site × Treatment × Date	0.987	0.545	90
Between subjects—site			
0–10 cm	0.622	0.538	2
10.01–20 cm	3.273	0.04	2
>20 cm	1.900	0.153	2
Between subjects—treatment			
0–10 cm	3.830	0.011	3
10.01–20 cm	0.818	0.485	3
>20 cm	2.267	0.08	3
July–August 2006 (with dowel treatment)			
Site	8.353	0.001	4
Treatment	5.366	0.001	4
Date	1.057	0.374	15
Site × treatment	2.733	0.001	16
Site × date	1.314	0.007	60
Treatment × date	0.733	0.994	60
Site × Treatment × Date	0.836	0.995	240
Between subjects—site			
0–10 cm	11.911	0.001	4
10.01–20 cm	2.904	0.022	4
> 20 cm	10.212	0.001	4
Between subjects—treatment			
0–10 cm	6.667	0.001	4
10.01–20 cm	6.209	0.001	4
>20 cm	4.285	0.002	4

Please refer to the text for details of the model.

one site driving the mean individual size up across dowel replicates (Fig. 4c, Table 2). As in previous years, date was not a significant factor, although there was a site–date interaction.

Community Structure:

Overall, fish community structure was fairly consistent between treatments and sites in both years of the study. There were no significant community level differences between treatments or sites in either year. There was a weak segregation along axis 2 between the fouled plots in May 2006 (no AEs) and the cleaned, fully intact plots from July 2005 and 2006, but this may be the result simply of lower numbers in May. There were no coherent groupings by either site or treatment in ordination space (NMS ordination, three axes, stress=26.32, Fig. 5). Herbivores (Scaridae and Acanthuridae) did make up a slightly higher percentage of individuals in plots fouled with living epibiota, 20% instead of 14%.

Epibiont Growth:

The nine plots where epibiota were allowed to settle accumulated an average of 16.5 species/plot, for an average of 86.5% coverage/AMR. Algae of the genus *Bostrychia* were dominant, making up 92% of the total epibiont cover, followed by 2.5% cover by sponges. Barnacles made up 1.8% of total cover, followed by 0.8% tunicates, and the remaining epibionts were green algae, corals, annelid worms, and hydroids. The percentage cover by each organism was very consistent between plots. Only the tunicate *Phallusia negra* and certain bivalves (particularly the scallop *Chlamys* sp. and the oyster *Isognomon alatus*) created any horizontal relief on the AMRs greater than a few centimeters.

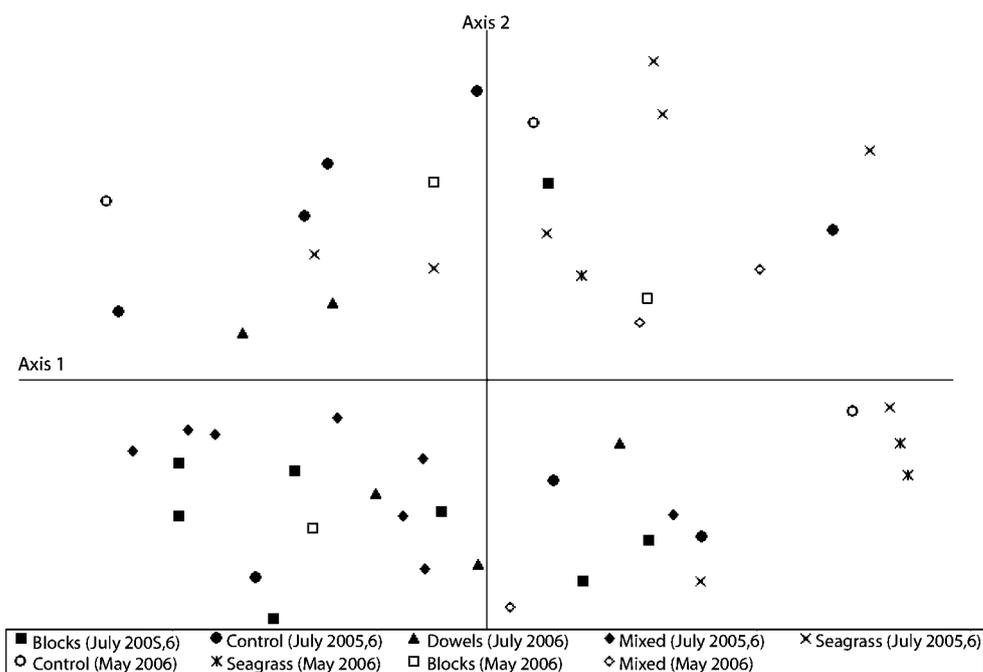
There were significant differences in fish abundance among the fouled plots (results listed under Fish Density above) but these differences did not correlate with density, diversity, percentage of any particular organism, or any other evident characteristic of epibiont coverage (linear regression—average $p \leq 0.532$).

Discussion

Increasing horizontal relief increased both the abundance and diversity of fish utilizing artificial mangrove prop-root habitats. This effect persists despite spatial variation in fish assemblage. The pattern furthermore remained essentially consistent from year to year despite variation in overall fish communities. While the degree of difference changed, the treatments with the most heterogeneity attracted significantly more abundant and diverse fish in both years. The treatment with both the highest surface area and number of individual structural objects attracted the greatest densities.

The pattern was overall quite consistent across different families of fish. Both nocturnal feeders present, the

Fig. 5 NMMDS ordination of community data for each replicate treatment plot (11 total/treatment across three study periods, including when fouled with living epibiota). Different symbols indicate different treatments and study periods



Haemulidae and Lutjanidae, were most abundant in the higher heterogeneity treatments, consistent with structure contributing to the value of mangroves as a daytime resting habitat. However, diurnally active families, e.g., the Chaetodontidae, were also most abundant in the most heterogeneous habitats. Since the artificial roots were regularly scrubbed in the initial phase of the experiment, direct feeding opportunities were reduced to near zero, so the structure itself is likely responsible for the differences. Aggressive predators, the Sphyraenidae, were also most common in the highly heterogeneous treatments; these may utilize the AEs for shelter or alternatively as ambush sites (Verweij et al. 2006a).

Most surprising was the presence of diurnal herbivores in the experimental plots, despite the lack of feeding potential; herbivorous species have been shown to feed more in mangroves than other groups do (Verweij et al. 2006a). There were two different herbivorous families present, and both the Acanthuridae and the Scaridae were most abundant in the high-structure plots in at least one study period, suggesting that structure may have a value for these groups as well. The benefits may be less pronounced for herbivores, however, given the inconsistency of results for these families.

The different study periods also support the overall pattern. In July 2006, there was lower overall abundance than during the first study period, although abundance was higher than during May 2006 when the AEs were absent. During this period, and to a lesser extent in 2005, effects were frequently cumulative; the mixed treatment had the highest overall abundance and species richness of fish, but

only a few particular families were significantly more abundant in one treatment or another. This effect may be a side effect of the low densities, which make differences harder to detect. These results suggest that higher structural heterogeneity may exert the greatest influence over fish communities in general, but not automatically in any given family or species. It is also likely that the presence of the dowel treatment in July 2006 further diluted the available pool of fish into a greater number of plots.

These results are consistent with evidence that some species, particularly as juveniles, utilize mangroves primarily for shelter while feeding opportunistically (Verweij et al. 2006b). There was a decline in overall abundance and species richness from 2005 to May 2006; these results differ from Laegdsgaard and Johnson (2001), who noted that cleaned artificial roots attracted fewer fish than when they were fouled with epibiota. While in our case only the unfouled AMRs had the AEs, it is not possible to sort out external effects of weather, time of year, temperature, etc. in assessing reasons for the decline between study periods. As a result, it cannot be established from these data that the destruction of the AEs is the cause of the decline in abundance.

What is definitive is that in May–June 2006, the overall densities were lower, but there were also few differences between the treatments. The AMR plots had little variation in heterogeneity from one plot to another during this period—the AEs were gone and had been replaced with an immature, low-relief epibiont community, and only one family, the Lutjanidae, had significant difference in abundance between treatments, compared with seven of eight

families in 2005 and three of eight families in July 2006. The results support the notion that the structural differences are themselves responsible for the differences between treatments, as when the amount of structure was reduced, so were many of the differences in fish density and diversity. The higher abundance of Lutjanidae (primarily *Lutjanus apodus*) in the same treatment plots both with and without variation in structure, however, suggests that other factors related to specific sites may influence small scale habitat use in these species, e.g., site fidelity or some other attribute.

The actual pattern of abundance and diversity observed in the AMR plots shows that the shape of available structures is important. The mixed treatment, which had the greatest abundance and of independent pieces of structure as well as two distinct shapes, had significantly higher fish abundance and diversity; this was the only treatment to have significantly higher abundance than control blocks for most families in both years of the study. The next treatment, blocks, was significantly higher than control stakes only in 2006, and dowels were not significantly different than control stakes, at least in terms of family densities. These results suggest that a certain critical amount of structure is necessary to impact fish communities; in real mangroves, epibionts that do not grow to sufficient size may contribute a little addition beyond the already available shelter. Blank stakes still provide more structure than sea grass alone, and demonstrated consistently higher fish abundance than sea grass alone, although whether that relationship holds true in real mangrove–sea grass areas depends on the species (Aguilar-Perera and Appeldoorn 2008).

Increasing vegetation density of non-woody aquatic plants reduces swimming speed and visibility, leading to reduced prey capture rates in fishes (Manatunge et al. 2000). Similarly, increasing prop-root density increases densities of several common fish species (Cocheret de la Moriniere et al. 2004). However, vegetation shape and structural heterogeneity can be more important than stem density in decreasing predator pursuit and effectiveness, particularly when confronted with multiple predator species (Warfe and Barnuta 2004; Meager et al. 2005). Prop-root epibionts, given their irregular shapes and haphazard arrangement, are more analogous to complicated vegetation shapes than they are to denser arrangements of grass stems or prop roots. The threat of multiple predators is a realistic scenario in a mangrove community; the combination of their shapes and the shade they cast means epibionts contribute to an excellent habitat where smaller fish may avoid multiple predators. At the depth where the experiment took place, shade conceals smaller species from predators (Cocheret de la Moriniere et al. 2004; Ellis and Bell 2004).

Applied to the experimental plots, the likely role of increasing structure as a predation deterrent is bolstered by

seeing the greatest effect among smaller individuals and species. There was little variation in abundance of larger individuals among treatments; these individuals are at less risk of attack from piscivorous predators than their smaller counterparts. Among actual mangrove roots, most real epibionts would be insufficient to conceal a 20 cm or larger individual. The higher mean density of the largest individuals observed in the dowel treatment is entirely the result of effects at one site; it would be premature to conclude that dowels attract large individuals. The overall differences in abundance are driven by the smaller individuals that benefit the most from the presence of structure.

The pattern observed in species richness mirrors that observed for overall abundance: diversity was highest in the most heterogeneous (mixed) plots. Fish diversity increases in response to substrate rugosity (Luckhurst and Luckhurst 1978a; Gratwicke and Speight 2005a). However, as abundance increases, diversity tends to increase proportionally (Caley and St. John 1996). The lack of differences in overall community structure suggests that most species are capable of utilizing most locations, but the most heterogeneous habitats regularly attracted more individuals. This relationship suggests that the heterogeneous treatments may have attracted more diverse fish as a by-product of attracting more fish, an idea supported by the fact that the pattern observed in overall abundance is mirrored by most individual families.

Aside from treatment differences, there were still significant spatial differences between virtually identical replicate AMR sites, some only 25 m apart. Stoner (1986) found spatial variation in abundance in a mangrove lagoon resulting from habitat variation; the replicates in this case were deliberately sited within similar environments. The fish observed in the plots in the present study were too large to be recently settled recruits, so were most likely drawn from surrounding habitats, e.g., real mangroves or sea grass (Nagelkerken and Faunce 2007); variation in these habitats might be responsible for the site-to-site differences. Once settled, juveniles may also potentially move around, resulting in random differences if the survey is conducted while mobile fish are passing through.

Conclusions

In accordance with the hypotheses, the results from this experiment provide a “proof of concept” that the spatial heterogeneity created by mangrove epibionts may influence the nature of mangrove fish communities, although further research will be required to test the idea in living epibionts. Complicated structure is also capable of influencing habitat quality for multiple families of juvenile fish, although the effect varies for certain families and is frequently aggregat-

ed across an entire assemblage rather than on a per-family or per-species basis. Spatial variation unrelated to treatment implies that there are other contributing factors, e.g., depth or fish behavior, to inter-mangrove community variation. It is nevertheless possible, given their abundance in many places, that epibionts play other, undiscovered roles in subtidal mangrove ecosystems.

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