VARIATION AMONG MANGROVE FORESTS AS FISH HABITAT: THE ROLE OF PROP-ROOT EPIBIONTS, EDGE EFFECTS AND BEHAVIOR IN NEOTROPICAL MANGROVES

by

JAMES A. MACDONALD

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Written under the direction of

Judith S. Weis, Ph.D.

And approved by

Judith S. Weis, Ph.D.

Rebecca Jordan, Ph.D

Peter Morin, Ph.D.

Joseph Rachlin, Ph.D.

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ABSTRACT OF THE DISSERTATION

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Mangrove forests are an important nursery habitat for many species of reef fish, as well as a key component of the interlinked mangrove-seagrass-reef system. However, understanding how juvenile fish utilize the mangrove habitats is hampered by variation between mangrove habitats. This study sought to examine some reasons for variation between mangroves, focusing on physical characteristics, particularly the influence of sessile epibiont organisms.

Using visual census, fish and sessile communities were compared in *Rhizophora mangle* roots in Bocas Del Toro, Panama, and Utila, Honduras. The results revealed significant positive correlation between depth, epibiont diversity, and density and fish species diversity and biomass.

In order to determine a causal relationship between epibionts and fish community variation, two field experiments were established. In one, artificial mangrove roots (AMR) with different sets of artificial (AE) or real epibionts were established in five different locations. In the second experiment, fish were surveyed in 12 different mangrove transects, epibionts were reduced in half of those transects, and then surveyed again. In the artificial mangrove plots, treatments with the most heterogeneous structure had the greatest abundance and diversity of fish. When epibionts were reduced, fish

abundance went up and biomass stayed level in controls, but abundance stayed flat and biomass decreased in treatment transects. The data indicate that epibionts can enhance fish abundance and diversity in mangroves, although the relationship may depend upon the specific epibionts.

Separately, a series of prop-roots were surveyed and placed inside predator exclusion cages. After three months, the cages were removed. The results suggested that grazing mostly does not impact prop-root epibiont coverage.

In a separate study, fish and epibiont communities were measured along a gradient within the mangroves away from boundaries of the mangrove forest. Both fish diversity and abundance showed a significant linear decrease away from the edge. Average size decreased as well, but epibionts showed no significant changes along the gradient.

Last, juvenile reef fishes were captured by in mangroves and seagrass, tagged, and monitored for three months. All recaptures were within 10 meters of the original capture, but most occurred within a short time.

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CHAPTER I: INTRODUCTION

Mangrove forests are being widely altered or destroyed (Ellison and Farnsworth 1996, Valelia *et al*. 2001, Alongi 2002), due to tourism and other development, and mangroves are considered one of the world's most endangered ecosystems. Greater attention has been paid recently to the protective function of fringing mangroves, in the wake of 2004's devastating Indian Ocean tsunami, although a protective function has also been seen in Caribbean mangroves (Danielsen *et al*. 2005, Kathiresean and Rajendran 2005, Granek and Ruttenberg 2007). Even before the tsunami, it was known that mature mangrove forests were particularly effective in dispersing wave energy (Mazda *et al*. 1997). While the coastal protection mangrove forests offer is being re-examined in many areas, widespread destruction for development, charcoal, and aquaculture still continues unabated in many parts of the world, despite evidence that there is greater economic benefit in leaving them alone (Gunawardena and Rowan 2005).

More than just a storm barrier, mangroves are a complex system that links terrestrial and marine ecosystems, supports a diverse array of marine and terrestrial species, and provides a variety of ecological and economic services, any of which can be damaged or destroyed if the mangrove system as a whole is damaged (Ewel *et al*. 1998). The response of many of these organisms to fragmentation or development has received comparatively little attention, as has fish use of developed mangroves (Valelia *et al*. 2001, Manson *et al*. 2005b).

Of the biological functions of mangroves, one that has received particular attention in the literature but surprisingly little consensus is the role of mangrove forest in supporting populations of reef fish. Mangrove forests and seagrass beds are habitats for many

species of fish (Nagelkerken *et al.* 2000b, Nagelkerken *et al.* 2000c, Dorenbosch *et al.* 2004a, Mumby *et al.* 2004, Nagelkerken and van der Velde 2004a) e.g. *Lutjanus apodus*. Juveniles of many coral reef fishes utilize the prop roots for shelter, emerging at times to feed in nearby shallow habitats (Nagelkerken and van der Velde 2004b). Populations of some species may feed almost exclusively in mangroves (Nagelkerken and van der Velde 2004c). There is evidence of ontogenetic shifts in diet as fishes utilizing mangroves as nurseries grow and prepare to shift into adult habitat(Cocheret de la Moriniere *et al.* 2003a, Cocheret de la Moriniere *et al.* 2003b).

Recent studies (Dorenbosch *et al.* 2004a, Mumby *et al.* 2004), have established that mangrove stands enhance biomass of fishes in nearby reefs in both Caribbean and Pacific mangroves although effects may vary between species and locations and are likely facultative, not obligate (Dorenbosch *et al.* 2004a, Chittaro *et al.* 2005b, Dorenbosch *et al.* 2005a). There is a question too as to whether more individuals (particularly juveniles) of reef species simply remain on the reef, rather than spending part of the juvenile life cycle in mangroves or seagrass (Chittaro *et al.* 2005b). Other research has examined why reef fish that do utilize the mangrove prop root habitat actually do so, focusing on its value as a structurally heterogeneous shelter habitat, shade, feeding habitat, or combination of those attributes (Laegdsgaard and Johnson 2001, Cocheret de la Moriniere *et al.* 2004). The intensive structural heterogeneity of the prop-root environment may also impede or deter pursuit by predators (Meager *et al.* 2005). Recent evidence suggests that the manner in which juvenile fishes take advantage of mangrove habitats is heavily dependent on the species, guild, or size class of the fish in question (Verweij *et al.* 2006a).

Adjacent habitats and other landscape factors have an effect on fish communities in mangroves have an impact on mangroves and vice versa. For instance, naturally patchy mangrove areas, interspersed with seagrass, seem to support a more diverse fish community than spatially contiguous mangroves under some circumstances in the Pacific (Pittman *et al*. 2004). Fish communities in seagrass are quite different in seagrass beds near mangroves than those farther away (Jelbart *et al*. 2007). Within mangrove areas, the proximity to the nearest adult habitat may also impact the fish community; samples increasingly differed along a gradient away from a bay mouth in the Caribbean (Nagelkerken and Faunce 2007).

There has been some effort to examine mangroves as part of a larger landscape (e. g. Mumby *et al*. 2002). Comparisons of fish species on larger scales, between mangrove, seagrass, salt-marsh, and other estuarine near-shore habitats have found comparatively few species that seem to be unique to mangroves, with the highest diversity occurring in seagrass (Bloomfield and Gillanders 2005). Comparing mangroves to reefs has found similarities between mangrove fishes and back-reef species assemblages, although lower diversity in mangroves compared to other habitats(Aguilar-Perera and Appeldoorn 2008). Other work has established that some species take shelter in mangroves or seagrass at certain times of day and emerge to feed in other areas (Nagelkerken and van der Velde 2002), so most species found in mangroves at some point in their life utilize other habitats as well- obligate mangrove species are rare. So while mangroves integrated with other habitats, even patchy mangroves, may be beneficial to fish, anthropogenic fragmentation of previously contiguous areas has not been examined, nor have most landscape-scale studies included sessile species.

Of the studies that have been done on the response of mangrove dwellers to development, the majority have been done in the Indo-Pacific Region, particularly Australia (Manson *et al*. 2005b). Studies have examined habitat modification of mangroves such as boardwalks (Skilleter and Warren 2000), and examined abiotic factors affecting fish and invertebrate communities (Singkran and Sudara 2005, Hoq *et al*. 2006). These studies found significant changes in benthic invertebrate community structure in response to boardwalks and environmental gradients, particularly sunlight and salinity. However, while the latter two studies examined environmental gradients, neither addressed development or anthropogenic modification, and all three took place in the western Pacific. No studies have examined highly developed mangroves, and data on this subject is virtually non-existent from the Caribbean, where sessile epifaunal communities are especially diverse and abundant.

What little research there is on the effect of mangrove habitat modification on fish is not completely conclusive, although it does suggest that restored mangroves are capable of supporting a diverse array of fish even in a heavily impacted, urban area (Jaafar *et al.* 2004). A comparison of cleared and forested areas in Kenya yielded mixed results; different species were found in each type of habitat, but overall abundance was not higher in mangroves (Huxham *et al*. 2004). Huxham *et al.* only compared site types, and did not look at results over a larger scale. Evidence from seagrass indicates that clearing results in widespread reduction in biomass and invertebrate diversity loss (Daby 2003). There is also evidence that certain species are particularly sensitive to overall changes in mangrove area (Manson *et al.* 2005a), suggesting that habitat loss or fragmentation may be important in mangrove systems, but no conclusions can be drawn yet. The small

number of such studies leaves the possibility that effects of fragmentation may vary in different areas and are not fully understood anywhere.

The conventional wisdom regarding fish utilization of mangrove habitats is that mangroves serve as a nursery area for juveniles of some species [to avoid predation] before moving to the reef or other areas as mature adults (Beck *et al*. 2001) define nursery habitat as one with greater densities of young fishes, lower predation rates, higher growth rates and more successful migration to subsequent habitats. Indeed, many of the species observed in mangrove forests are juveniles, although presence/absence is not enough to define nursery habitat (Sheridan and Hays 2003). The most compelling evidence for the nursery habitat, in addition to surveys of juvenile fish in mangroves and neighboring habitat, are those, noted above, that demonstrate that reefs have much higher fish biomass in areas with nearby mangroves than in areas without mangroves (Mumby *et al*. 2004). Other studies (Acosta 1999, Nagelkerken and van der Velde 2004c, Pittman *et al*. 2004) have shown that linked habitats, e.g. reefs, seagrass, and mangrove habitats, are more productive than any one habitat alone. None of these studies, however, confirm that mangroves' value is primarily as a nursery habitat, merely that they benefit reef fish populations in some way. For instance, mangroves are proven to trap sediment from terrestrial runoff, thereby mitigating damage to the reef from reduction in water clarity- this function can also benefit fish populations. So far, it has been impossible to tie individuals on a particular reef to individuals from a particular mangrove stand- otolith microchemistry studies have only established that some fish species do go back and forth between reef and mangrove, but haven't been able to tie it together more specifically than that (Chittaro *et al*. 2005a).

A recurring theme is that mangroves, nurseries or not, do not uniformly function as fish habitat. Different workers have also obtained different results under different circumstances (Nagelkerken and van der Velde 2004a, Chittaro *et al.* 2005b), so there is no true consensus on fish use of mangroves. Temporal variation, in particular, is commonly noted. It may be based on season (Stoner 1986, Barletta *et al.* 2003, Lugendo *et al.* 2007), time of day (Rooker and Dennis 1991) and can change quite abruptly (Laroche *et al.* 1997). Species differences are also commonly observed; for instance herbivorous species seem more inclined to feed among the prop-roots then others (Verweij *et al.* 2006a). Fisheries effects also vary substantially between species, depending on how associated a given species is with mangrove habitats (Manson *et al.* 2005a). It has been established, however, that there are few motile species of either fish or invertebrates exclusively dependent on mangroves (Manson *et al.* 2005b). Many tropical species do not seem terribly particular about what constitutes suitable shelter; in at least one instance, an artificial sea wall was more heavily utilized than mangrove habitats by mangrove-associated fish (Weis and Weis 2004).

No study yet explains, however, why stands of mangroves that are in all apparent respects similar to one another may have radically variable density or diversity of fish or invertebrates. Sampling bias may be responsible for weak trends or variability between mangrove and seagrass areas in some cases (Smith and Hindell 2005). To be sure, consistent, accurate fish samples are very difficult to obtain in heterogeneous environments such as mangroves. The phenomenon of widespread variability between similar mangrove areas has been noted in the literature. In particular, inter-site variation was problematic for Huxham *et al.* (2004) and Chittaro *et al.* (2005b), who cited the

widespread variability between different mangrove sites as foiling the detection of larger scale patterns in fish use. Chittaro *et al*., in particular, believe that variability prevented their study from detecting a clear pattern of reef species using mangroves and seagrass specifically as nursery. Abiotic variables, particularly depth, may also affect communities by affecting the circumstances under which fish utilize the mangroves (Ellis and Bell 2004). Variability between sites may help explain the lack of consistent results on this topic in the literature, and given the confusion surrounding the nursery question and the clear conservation value of mangroves it is important to seek out the factors driving inter-mangrove variability.

While mangroves, reefs, and seagrass are interlinked, subtidal mangrove forests are a thriving system in their own right. In addition to juvenile fish and mobile invertebrates, in many areas there is also a community of epifauna and flora (e.g. algae, sponges, oysters, etc.) living on the prop roots themselves. Several studies have found that root epibionts benefit the trees by protecting growing roots or are otherwise important to the mangrove system (Sutherland 1980, Perry 1988, Ellison and Farnsworth 1990). Believe that any management actions undertaken in mangrove habitats must bear these organisms in mind (Ellison 2007). The nekton in mangroves goes well beyond juveniles of reef species; mature adult fish of several feeding guilds and trophic positions, in addition to many species of motile invertebrates, are also frequently found utilizing mangrove habitats. Such well-structured communities and populations with many age classes implies that there is more to these communities than merely a sheltering ground for some juvenile reef fish species while they mature.

Mangrove forests have received far less attention than other tropical estuarine and marine environments, e.g. coral reefs (Ellison and Farnsworth 2001). A lot more attention has been paid to the decline in coral reefs worldwide and in the Caribbean. Widespread damaging practices have been shown to erode ecosystem health on reefs (Gardner *et al.* 2003), and many of these same processes affect mangroves as well. Abundant evidence exists that mangroves, seagrass, reefs, and other shallow habitats are linked in a variety of ways (Acosta 1999, Dorenbosch *et al.* 2004a, Mumby *et al.* 2004, Nagelkerken and van der Velde 2004c, Manson *et al.* 2005a, Skilleter *et al.* 2005). Damage to any of the major tropical near shore habitats, i.e. reef, seagrass, or mangrove, is likely to have an adverse effect on all the others. Insight into what drives use of this habitat by fish, and to what extent fish impact other communities in mangrove habitats, will be essential to help understand these systems and predict how they will respond to environmental changes such as coastal development, urbanization, or climate change. Since there is considerable variability, it is essential to expand studies beyond any one area. The importance of mangroves to the surrounding ecosystems and human communities may be consistent across areas, but the particulars of communities in any given mangrove stand most likely are not.

Following previous studies in Bocas Del Toro (2004-2005), this project was designed to examine reasons for variability between habitat functions of different Caribbean mangroves, focusing particularly on the connection between fish and epifaunal community structure, and to what extent mangrove forests serve not only as links in the broader shallow-water tropical marine system but to what extent they are self-contained communities. Few studies have examined connections between the mangrove epibiont

community, fish habitat use, and community structure, and how the condition of the mangroves affects their quality as habitat, although there has been work on the effects of mangrove destruction (Huxham *et al.* 2004, Jaafar *et al.* 2004) and boardwalk construction (Skilleter and Warren 2000). Most studies of prop root communities have focused on their value to coral reefs; few have examined sub tidal mangroves as systems in their own right.

Given rapidly growing human populations along tropical coastlines and widespread destruction of mangrove forests, an understanding of nekton use of this system is vital in order to understand better what the implications are of such modification. The results of this study may be used to steer development carefully to avoid areas vital for fisheries, thus preserving marine and near-shore biodiversity, ecosystem health, and a potential source of livelihood for future generations. This information is important to conservation and fisheries management programs, particularly for the establishment of successful Marine Protected Areas (MPAs) in the tropics; managers are attempting to apply an ecosystem-wide approach to MPAs, and incorporating supporting habitats such as mangrove forests into MPA network design.

I.1 Hypotheses

The ultimate goal of this research was to ascertain why some mangroves, equal in many ways, support larger populations and more diverse community structures than others. The study examined numerous hypotheses:

1.) Diversity and community structure of fish populations in mangrove stands is partially dependent on the epibiont community in each stand, and in turn the fish community regulates the epibiont community structure;

2.) That additional spatial heterogeneity caused by the epibionts is responsible for this phenomenon;

3.) Given habitat connectivity between mangroves and nearby habitats, whatever they happen to be, edge effects and distance from adjacent habitats is another contributor to inter-mangrove variability;

4.) Many fish species in the mangroves exhibit very local site fidelity, so populations in one mangrove area are distinct from each other; and

5.) These patterns are consistent across a wide area, and not just local.

In the following chapters I outline the ways in which these hypotheses have been tested, along with the outcome. The first part of hypothesis one is addressed in chapters two through four, while the second part, regulation of epibionts by fish, is addressed in chapter five. Chapter two describes analyses based on observational data taken in both Panama and Honduras, demonstrating that there is in fact a pattern between sessile root organisms and fish communities, in actual neotropical mangroves. Chapters three and four detail experiments undertaken to demonstrate a causal link between the epibiont and the fish communities; chapter three shows how additional structure such as that created by the bodies of epibionts attracts fish under controlled field conditions, while chapter four demonstrates that the fish community can be influenced by the removal of epibiont organisms from the roots. The performance of some of these studies in two widely separated locations, Panama and Honduras, addresses hypothesis number five as well.

Chapter five takes a different approach. In this study, prop-root epibionts were isolated from fish by means of cages in order to test whether or not grazing by fish, of

different sizes, had any influence on the structure or abundance of the epibionts growing on the roots. These cages, all controlled, also addressed other possible influences on epibiont growth, especially the effect of light. This experiment, in conjunction with the experiments in chapters three and four, helps determine which direction controls the pattern between fish and epibionts; from the fish downward or the epibionts upwards.

The last two chapters tackle different issues entirely. These chapters examine possible reasons unrelated to epibionts for differences from one mangrove to another. As discussed above, nearby habitats have an influence on mangroves; to examine these as a factor, chapter six examines large mangrove stands on a gradient away from a boundary with another habitat, considering edge effects as well. Chapter seven takes yet another approach, looking at the role of fish movements and behavior in mangroves; if fish move a lot, or very little, within mangroves, this will have an effect, based somewhat on sampling effort and technique, in how fish are distributed throughout the mangroves. This chapter demonstrates the movements of tagged individuals in a small area in Panamanian mangroves, primarily one common species, the schoolmaster snapper, *Lutjanus apodus*.

Taken together, these chapters represent separate, yet connected approaches to the problem of inter-mangrove variability. While the subject of mangroves as fish habitat is a contentious one, none of the particular approaches outlined above have yet been tried. Studies have utilized artificial mangroves, and examined fish movements, but this is the first study to apply these approaches specifically to examining differences between mangroves themselves. This is also the first study to link epibionts to fish communties. Mangroves are such a complicated system that no single dissertation can possibly resolve

all of the unanswered questions, but hopefully these avenues of research will make a start.

CHAPTER II: REAL-WORLD CORRELATIONS OF EPIBIONTS WITH DIVERSITY, BIOMASS, AND COMMUNITY STRUCTURE OF FISHES

INTRODUCTION

Mangrove forests and seagrass, especially in the Caribbean, are important juvenile habitat for some species of reef fish and influence fish communities on associated reefs (Parrish 1989, Nagelkerken *et al*. 2000c, Nagelkerken *et al*. 2002, Dorenbosch *et al.* 2004a, Halpern 2004, Mumby *et al.* 2004). Dependence on mangrove habitat seems to be mostly facultative rather than obligate and varies by species (Nagelkerken *et al*. 2001).

Mangroves have many ecological and hydrological functions, all of which can benefit fish populations with or without a direct nursery function. In some areas there is no direct evidence that juvenile fish move directly from mangroves to reefs; in such a situation mangroves and related habitats would function as an alternative fish habitat and not as a feeder habitat for the reef (Beck *et al*. 2001). There are several benefits mangroves may offer to juvenile fish, particularly their role as predator refuges, recruitment areas for larvae, feeding grounds, shade providers, or resting places in the structural heterogeneity provided by the prop roots. To date many factors seem to be at work, and are often species-, size class-, or life-history-specific (Nagelkerken *et al*. 2000b, Manson *et al*. 2005b, Verweij *et al.* 2006a). It remains difficult to draw any widespread general conclusions about links between mangroves, related shallow habitats, and reefs (Faunce and Serafy 2006).

One confounding factor is that not all mangroves are equally valuable as nursery habitat; even within one geographic area, not all mangroves have the same density of

juvenile fish relative to surrounding habitats and relative to each other (Huxham *et al.* 2004, Chittaro *et al.* 2005b), although not all studies have observed this (Sheridan 1992). Other habitat attributes important to mangroves' nursery function, specifically predation pressure, can vary between equivalent mangrove plots and times (Chittaro *et al.* 2005b).

In order to better understand the role mangroves play as fish habitat, it is necessary to understand what influences the relative value of some mangroves compared to others. Experiments have determined that increased structure in the form of increased root density or shade can positively influence the use of mangroves by fishes, although the impact is species or depth-specific (Cocheret de la Moriniere *et al.* 2004, Ellis and Bell 2004). Pre-and post settlement factors for larval fish, e.g. larval supply, currents, or the ability of larval or newly settled fishes to actively select habitats may also play a role in determining nursery habitat (Adams and Ebersole 2002).

Mangroves are a biologically complicated environment, consisting of much more than just prop-roots; in addition to numerous species of fish and motile invertebrates, many mangroves contain a diverse collection of sessile epibiont organisms living on the prop roots, including algae, sponges, and oysters. Some of these organisms play a vital role in protecting the prop roots from damage and encourage the health of the mangrove trees themselves (Ellison and Farnsworth 1990).

The importance of these organisms to fish habitat has rarely been addressed. Epibionts themselves are prey for several mangrove-utilizing species (e.g. *Holocanthus* spp.), and some types are prey habitat for other s(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.

This study examined the hypothesis that the community of sessile organisms on the prop-roots influences fish communities in mangroves by examining a wide variety of mangrove transects across an archipelago in Caribbean Panama and separately in Caribbean Honduras. Specifically, it was hypothesized that within contiguous mangrove areas, those sections with a more diverse community of prop-root epibionts would hold the most diverse community of reef fish compared to similar areas with fewer epibionts. It was also predicted that a more robust community of epibionts would also be associated with a greater abundance of reef fish.

MATERIALS AND METHODS

II.1 Study areas

The first study area was conducted in the Bahia Almirante, Bocas Del Toro Archipelago, Bocas Del Toro Province, Panama (Fig. 1a). This area is sparsely populated outside of Isla Colon and the mainland port of Almirante. Sites were established on 5 islands: Colon, Bastimentos, San Christobal, Pastor, and Cayo Solarte, as well as on the mainland at Punta Gallinazo (Fig. 1). Of these islands, Cayo Solarte and Bastimentos are mostly covered with secondary rain forest. Near the other sites, most land cover is agricultural or pasture. All sites were exclusively red mangroves, *Rhizophora mangle* L, although there were scattered white mangroves (*Laguncularia racemosa* L) behind the *R. mangle* in Isla

Colon and Cayo Solarte, and extensive *L. racemosa* forest behind the Bastimentos sites. On Bastimentos, the total thickness of the mangrove fringe was nearly 500 m, while the site with the thinnest fringe (on Isla San Christobal) had only 7 m of *R. mangle.*

All sites were permanently submerged. The tidal range in the Bahia Almirante is small, ranging between 2 cm and 15 cm under standard conditions (Guzman *et al*. 2005). The shallowest site averaged 33.16 cm deep at low tide, while the deepest was 72.6 cm; the mean was 52.15 cm. Salinity in the Bahia Almirante varies mostly by time of year; within any seasonal type it has been fairly consistent, with a mean of 30.14 (D'Croz *et al.* 2005). In most cases, coral reefs were close to the mangrove fringe, from a minimum of 2 m to a maximum of 1.867 km, averaging 199.65 m. Seagrass was directly adjacent to the mangroves in some sites, but varied up to 7.6 m from the mangrove edge. Intervening areas were muddy bottoms with scattered weeds. Underwater secchi visibility ranged from a low of 3.4 m to a high of 6.2 m, with a mean of 4.6 m.

Figure II.1: Study sites. Transect locations are indicated by dots; bulls eye symbols indicate population centres.

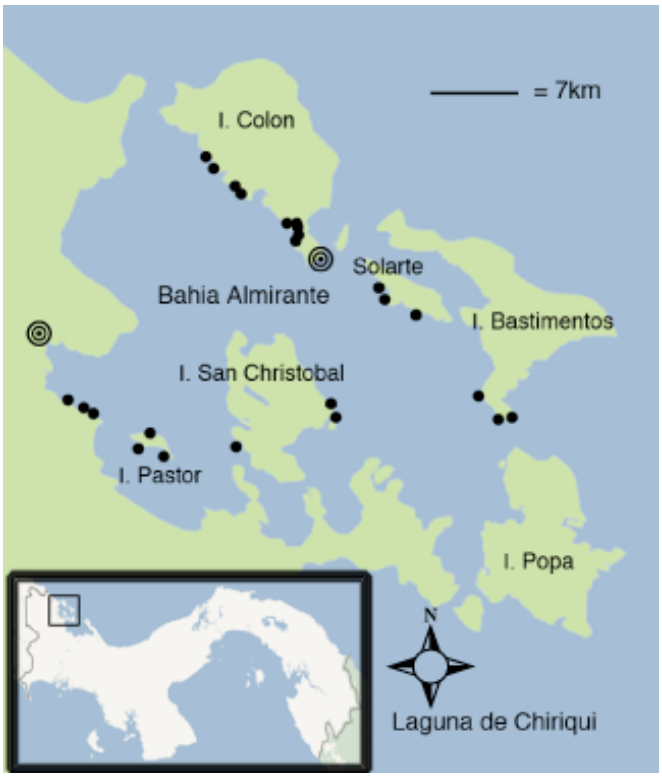


Figure 1a: Map of Panama (inset) with Bahia Grande, Bocas del Toro, Panama, enlarged.

Figure 1b: Map of Honduras (inset) with Isla Utila enlarged.

The second study area was on Isla Utila, Honduras, a small island consisting primarily of mangrove-fringed lagoons, lowland flooded forest, and tropical savannah (Fig. 1b). Settlement on the island is mostly restricted to the island's southeastern corner, with the exception of a few resorts on the western end. The mangrove fringe has been essentially eradicated by human settlement outside the lagoons on the island's southern half. The north side is dominated by natural beach and volcanic shoreline, but some inlets retain an extensive mangrove fringe. The mangrove forests surrounding the lagoons are very extensive, showing the complete gradient of Caribbean mangrove growth with *R. mangle* on the water, backed by black mangrove, *Avicennia germinans* and white mangrove (*Laguncularia racemosa* L) farthest inland. Abundant rainfall allows some *R. mangle* to reach extraordinary size (Fig. 2). The interior and northern sides of the island are uninhabited, but some areas are in the process of being graded for potential future settlement. For the moment, the north side is only utilized by artisanal fishermen, gatherers, as well as crab or iguana hunters.

In the lagoon sites, there were underwater weeds, but no complete seagrass beds;

Fig. II.2: A huge (~50) m *R. mangle* from Utila, Honduras. This species was found farther upland here than in most places, allowing for more freshwater input and larger size.

in fringing transects, *Thallassia testudinum* beds were immediately adjacent to the mangrove fringe, with no intervening mudflat. Offshore reefs were present immediately outside the lagoons and within 100 meters from the fringe. Underwater secchi visibility ranged from 3m to 5.3m, with a mean of 4.3 m. As in Panama, all sites were permanently submerged, although the tidal range was considerably higher in Utila, near to 30cm. Detailed studies of salinity have not been conducted in Utila.

II.2 Fish Surveys

In Panama, twenty-four 2 x 50 m belt transects were measured and marked along the edge of the mangroves, and the markings left in place for the duration of the study. An additional five lagoon and six fringing transects (2 X 40 m) were established in Utila. Fish were surveyed by means of underwater visual census (UVC) similar to that of (Nagelkerken *et al*. 2000c). Each transect in Panama was surveyed 11 times on non-consecutive days between 5 June and 1 September, with 12 transects surveyed in 2005 and another 12 in 2006. In Honduras, all transects were surveyed 11 times between 1 July 1 and 26 August, 2007. Each UVC lasted 10 minutes. A single highly trained observer counted every fish observed inside each transect, identified each individual to species, and estimated total length using a reference ruler attached to a slate. The observer was the same throughout the study to keep observational bias consistent. A second observer accompanied the main observer and kept a separate count. The two counts were compared at the end of every survey and in the event of large discrepancies the count could be repeated on another day, although that situation never arose. The exceptions were species of the genus *Haemulon*; in the mangroves, juvenile *Haemulon* frequently

formed large mixed aggregations, and given the sometimes poor visibility, observers could not be absolutely certain of the identification of every individual. This genus was treated as one taxon. Large aggregations were counted three times and the average number used. In order to avoid double counting, any fish that approached from behind was not included. Neither cryptic species (e.g. Syngnathidae spp., Gobiosocidae spp.) nor the ubiquitous schools of Atherinidae and Clupeidae were included in the census.

II.3 Epibiont surveys

In each transect, sessile organisms on the prop roots were surveyed on one root per meter of transect. A 50m logging tape was laid down the length of each transect, and the root closest to each meter mark (50 roots total in Panama, 40 in Honduras) was selected. In Panama, where epibiont diversity was considerably higher; an additional 5 random roots were surveyed, for a total of 55 roots per transect in Panama; this number was chosen based on species area curves generated from pilot data taken in 2004 (unpublished). The epibiont survey was always conducted after the fish census had been completed.

Root organisms were tentatively identified to the lowest taxon possible using keys provided by the Smithsonian Tropical Research Institute (STRI) and assistance from local experts. Species that could not be identified with confidence were classified as unknowns. Cyanobacteria were not identified to species and were considered as one taxon. Likewise, species confirmation of hydroids was not possible in all sites, so hydroids were treated as one taxon. The percent area covered by each species per root was measured using a framed grid of 5x5 cm squares (75 cm long x 10 cm wide). Each

25 cm^2 square was the base unit of measurement, and any measurements smaller than approximately 0.25 of a square were considered trace amounts.

II.4 Abiotic Factors

In every site, depth, distance from the nearest reef, seagrass bed, and entrance to open ocean were measured, along with total thickness of the mangrove fringe (beyond the 2m width of the transect), and underwater secchi distance. Sites were chosen to keep root density as constant as possible; in Panama the prop root density varied from 25 to 29 roots m^{-2}. Honduran mangroves had considerably denser prop roots, ranging from 33 to 54 roots m^{-2}.

II.5 Statistical Analysis

Panama and Honduras data were analyzed separately due to large differences in the two study sites. For each data set, multiple linear regression was used to examine relationships between aggregate features of the fish community, the epibiont community, and habitat variables. Community features examined were Species Richness (SR), Shannon Wiener Diversity Index (H'), epibiont density (measured both by % area covered per root and total epibiont area per root), and total numbers of individual fish per 100 m^2 transect. Fish biomass was estimated based on established length-weight (L-W) relationships published on fishbase.org (Fraese and Pauly 2007). For the genus *Haemulon*, the L-W relationship for the bluestriped grunt, *Haemulon sciurus* (Shaw), the most common Haemulonid at both sites, were used. Any fish species observed during only one of the 11 surveys was not included in analysis, and any epibiont species present in less than 0.25 of a grid square was likewise eliminated. The feature of the fish community in question (e.g. SR) was then analysed by all root and habitat variables in

multiple regression. The multiple regression results were compared to individual regression results to insure that multiple regression explained more variance than individual variables alone. Each independent variable was examined for significance, and collinearity was examined by comparing tolerance and eigenvalues. Only variables that explained variance in the dependent variable to the 0.05 level and for which the variance explained was not also explained by another variable were included in the final model.

In multivariate space, the ratio of epibiont species present to sample size was too high for most analyses, and no particular components explained much variance. Therefore, community analysis was performed at a suprageneric level for epibionts (e.g. poriferans, corals). Canonical Correspondence Analysis (CCA) was used to correlate the epibiotic and fish communities. Fish species (both numbers and biomass) were ordinated by CCA using total epibionts (measured by area). In the analysis of biomass, an uncommon but high mass species, the Southern stingray *Dasyatis americana* (Hildebrand and Schroeder), was excluded from analysis after a trial showed that its removal did not change the orientation of the other species. No other transformations were used. Multivariate analysis was not applied to the Honduran data given the smaller number of observations.

All of the above tests were performed a second time after dividing fish into adult and juvenile size classes following (Nagelkerken and van der Velde 2002). In this analysis, any individual was classified as a juvenile if its total length was less than one-third of the total published length for the species.

RESULTS

II.6 General

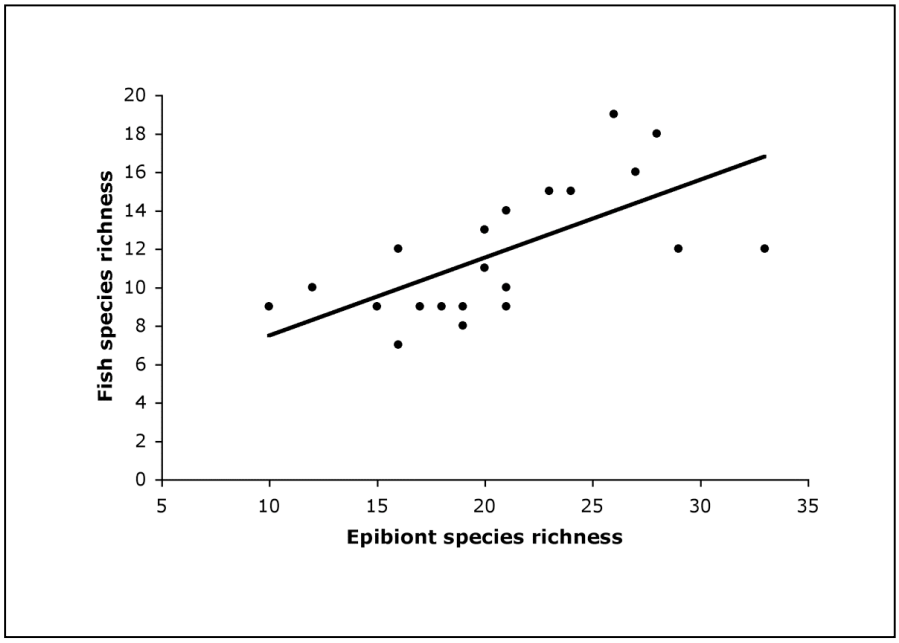
In Panama a total of 9622 individual fish, representing 30 different species and 18 families, were observed in sufficient abundance to include in the analysis. Total fish biomass was estimated to be 372.7 kg, for a mean of 1.41 kg biomass per survey. When separated into size classes, adult fish made up an average of 19.5% of all fish observed, and 41.2% of total fish biomass. At least 59 species of root epibionts, were observed, including four species of green algae, three sessile molluscs, 10 tunicates, nine cnidarians (including seven corals, one hydroid, and one anemone), 27 sponges, two rhodophytes, two phaeophytes, two annelids, cyanobacteria, and one crustacean. The annelids consisted primarily of calcareous tubes created by colonial worms.

In Honduras, a total of 4560 individuals from 28 species representing 13 families were observed in sufficient abundance. Nearly 23 % of observed individuals belonged to one particular species, the mangrove rivulus, *Rivulus marmoratus*. Overall fish biomass was estimated at 134.4 kg total, or 1.11 kg/survey, very similar to Panama on a per survey basis. Root epibiont diversity was lower in Honduras; only 37 species of epibionts were observed, including 14 sponges, 4 sessile molluscs, 8 species of green algae, 4 rhodophytes and 2 tunicates, in addition to cyanobacteria, hydroids, feather duster worms, and barnacles. Unlike Panama, the only tunicates observed in the transects were colonial rather than solitary (one solitary tunicate was observed but not within a transect).

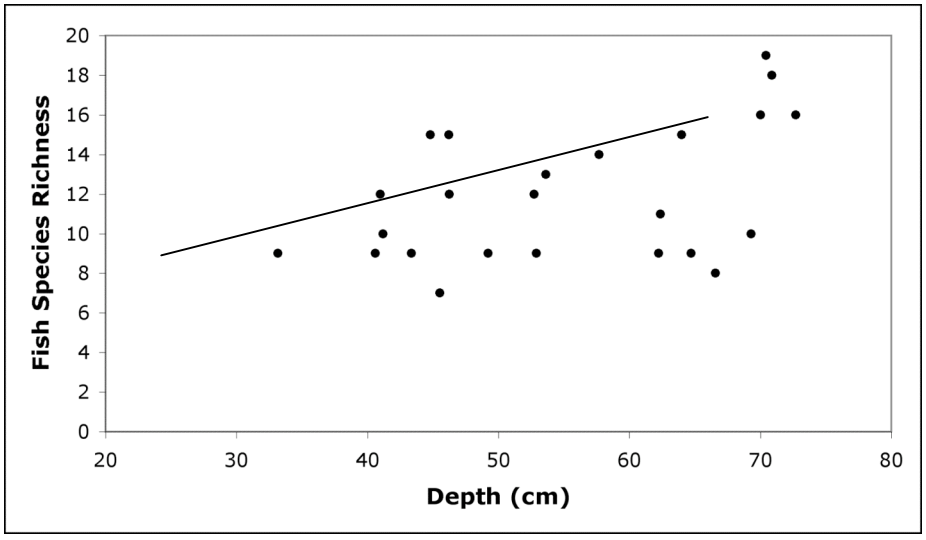
II.7 Diversity and abundance of fishes

In Panama, after adjusting for collinearity, only two variables, SR of epibionts and depth, correlated significantly with fish SR, and of those two factors, epibiont SR explained a greater proportion of the variance in fish SR than depth did. Together, depth and epibiont SR explained nearly 60% of the variance in fish SR (Linear regression,

adjusted R^2= 0.572, ß=0.638 epibiont SR; ß = 0.401, p ≤ 0.0001) (Fig. 3a,b). Epibiont diversity (H') was the only significant predictor for fish H' (Linear regression, R^2=0.440, ß=0.663, p ≤ 0.0001 Fig. 4).



3a: Epibiont species richness v. fish species richness. R^2 = 0.449, y = 0.406x + 3.42



3b: Depth v. fish species richness R^2=0.204, y=0.128x +4.86

Figure II.3: Partial correlation plots of epibiont species richness (a) and depth (b) v. fish species richness from Bocas Del Toro, Panama. Combined R^2= 0.572.

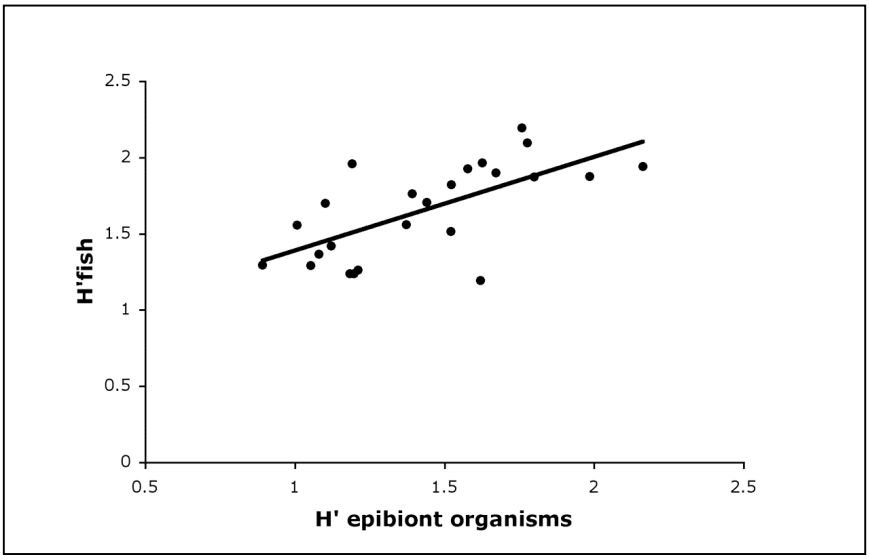


Figure II.4: Epibiont Shannon Diversity Index (H') versus Fish H' in Panama. R^2 = 0.440, y = 0.614x + 0.770

No factor explained significant variance in numbers of individual fish in the mangroves, but an increase in the total area of epibionts/root significantly correlated with an increase in biomass of fishes, the only variable to do so (Linear Regression- R^2=0.182, ß= 0.427, $p \leq 0.037$, Fig. 5). However, two sites, both adjacent to one another on the northwest edge of San Christobal were outliers responsible for nearly 36% of the variance in biomass; with these sites excluded from analysis, the relationship is much stronger (Linear Regression- R^2=0.542, ß=0.736, $p \leq 0.0001$, Fig. 5). Both of these sites have exceptionally lush growth of algae and cyanobacteria, a result of their location near a farm, in an area that has registered elevated levels of inorganic nutrients (D'Croz *et al.* 2005). These characteristics distort epibiont coverage data, creating outliers.

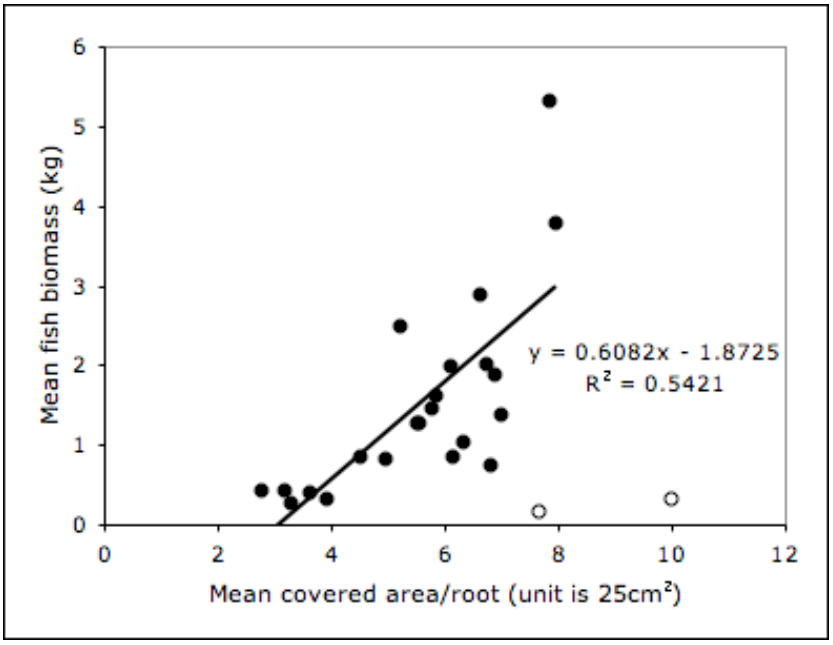


Figure II.5: Mean fish biomass v. Mean total area of epibionts per root in Panama. For all sites, $R^2 = 0.1816$. Slope: y = .3042x - .367. The open circles represent 2 sites adjacent to one another on the Northwest edge of Isla San Christobal, which were both outliers (see results, and R^2, slope on graph above).

In Honduras, results for diversity and biomass were similar, but not identical. As in Panama, epibiont species richness was the best predictor for fish species richness, (Linear Regression- R^2=0.403, ß=0.635, $p \leq 0.036$, Fig. 6) although depth did not have a significant effect on fish species richness. Regression of epibiont H' with fish H' was not significant in Honduras either (R^2=0.02, $p \leq .65$).

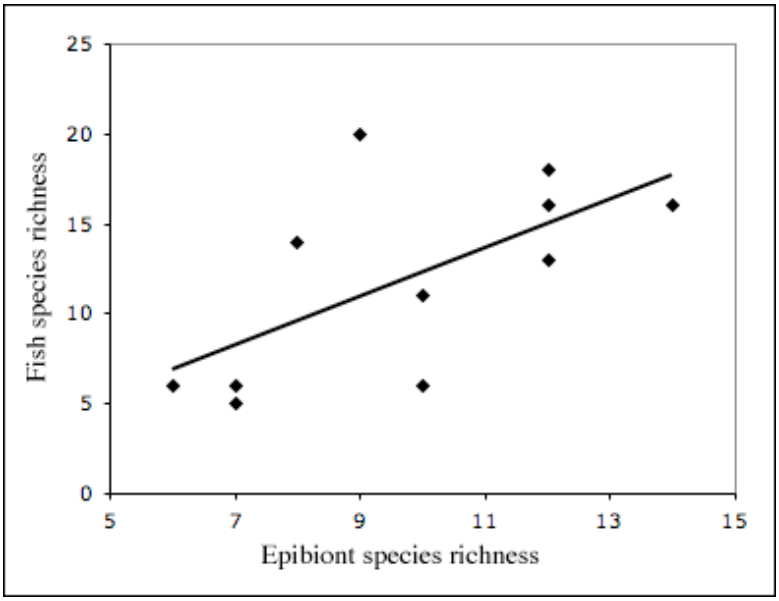


Figure II.6: Epibiont species richness v. fish species richness from Utila, Honduras. R^2 = 0.403, y = 1.34x - 1.13.

The relationship of fish biomass to epibiont coverage was similar to that seen in Panama. The total area of epibionts/root did correlate with increases in fish biomass (Linear Regression- R^2=0.38, ß=0.660, $p \leq 0.04$, Fig. 7), although the slope was considerably steeper and the correlation not quite as strong.

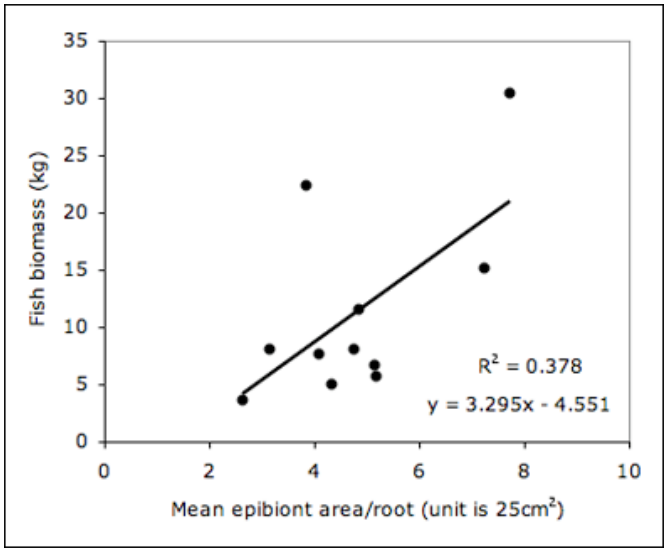


Figure II.7: Mean fish biomass v. Mean total area of epibionts per root from Utila, Honduras.

II.8 Age Classes

Results were similar when fish age classes were analyzed separately. In Panama, Mean SR, H', and biomass were not significantly different between adults and juveniles (separate Mann- Whitney U-tests, lowest $p \leq 0.20$). The mean number of individual fish was significantly higher for juveniles than adults (Mann-Whitney U test, $p \leq 0.0001$).

Epibiont SR and depth were again the only significant predictors for juvenile fish SR (Linear regression, adjusted $R^2 = 0.527$, $p \leq 0.0001$, ß= 0.631 epibiont SR; ß= 0.364 depth). A smaller percentage of variance in adult fish SR was explained by the same variables, and depth was more important than for juvenile fish (Linear regression, $R^2 = 0.337$, $p \leq 0.005$; ß = 0.487 epibiont SR, ß= 0.359 depth) Adult H' did not significantly correlate with epibiont H' (Linear regression $R^2 = 0.0440$), but juvenile H' did correlate with root organism H', although it only explained about 30% of variance (Linear regression $R^2 = 0.3153$, $p \leq 0.004$). Biomass of adult fish correlated to total epibiont area ($R^2 = 0.1818$, $p \leq 0.04$) while juvenile biomass showed a strong trend but did not quite

correlate significantly with this measure ($R^2 = 0.1513$, $p \leq 0.06$). As with the pooled data, the relationship between epibiont area and fish biomass for each size class was stronger without the San Christobal outlier sites (adults: $R^2 = 0.4962$, $p \leq 0.003$, ß= 0.704; juveniles: $R^2 = 0.4903$, $p \leq 0.0003$, ß= 0.700).

In Honduras, results were slightly different. As in Panama, overall trends were much stronger when age classes were pooled, rather than analyzing adults and juveniles separately. Juvenile SR did not correlate significantly with epibiont SR ($P \leq 0.229$), but adult SR did, explaining about 44% of variance ($R^2 = 0.44$, $p \leq 0.025$, ß= 0.667). The results for biomass were similar to Panama (Linear Regression- Juveniles: R^2=0.719, ß=0.848, $p \leq 0.002$, Adults; R^2=0.547, ß=0.739, $p \leq 0.015$). Fish H' did not correlate with epibiont H' for juveniles or adults, explaining essentially no variance ($R^2 = 0.0008$). There were also significant differences between adults and juveniles in other categories. Juveniles had higher SR (2 sample T-test, $p \leq 0.012$) and higher abundance than adults (2 sample T-test, $P \leq 0.001$), but biomass was not significantly different between the 2 age groups. H' was not compared between the age classes; the major differences in abundance and SR distort the value of the evenness based H' measurement beyond recognition.

II.9 Abiotic Factors

Of the abiotic factors examined, only depth, discussed above, had any significant relationship with fish diversity or biomass. Turbidity and distance to the open Caribbean correlated inversely with epibiont SR and H' (Linear regression SR: $R^2 = 0.527$, ß= 0.491, Bay mouth distance; ß= 0.32 turbidity, $p \leq 0.001$. Linear regression H': $R^2 = 0.585$, ß= 0.652, Bay mouth distance; ß=0.354 turbidity, $p \leq 0.001$.). These relationships did not

exist in Honduras, where the measured abiotic variables did not have a measurable impact on fish or epibiont communities in either lagoon or fringing mangroves.

II.10 Community Level Effects

For the three epibiont taxa that displayed a significant diversity of species (corals, sponges, and tunicates), SR strongly correlated with abundance, so abundance is a proxy for diversity (corals: $R^2 = 0.7844$, $p \leq 0.00001$; sponges: $R^2 = 0.3953$, $p \leq 0.001$; tunicates: $R^2 = 0.5789$, $p \leq 0.0001$).

The first two ordination axes in CCA of either fish biomass or number of individuals explained at least 50% of the variance in the data for juvenile fish as well as pooled data for juveniles and adults (Figs. 8a-d). CCA explained much less variance in adult fish (Figs. 8e, f). Different vectors and distributions appeared in each analysis, depending on age class and whether or not biomass or numbers were analyzed. For total numbers the predatory species tended to cluster together, influenced more by barnacles than any other taxa, while green algae and hydroids influenced a mixed species suite (Fig. 8a). Total fish biomass revealed a similar pattern; many of the predators clustered with barnacles, but additional epibionts had equal influence, particularly sponges, annelids and bare root, which were associated with a collection of smaller species from various feeding guilds (Fig. 8b).

By size class, juvenile biomass and numbers (Figs. 8c, d) revealed a more dispersed distribution along both axes with more vectors, with many of the larger predatory species clustered loosely with sponges, and many herbivorous species associated with bare root and annelids. Adult fish revealed few coherent patterns (Figs.

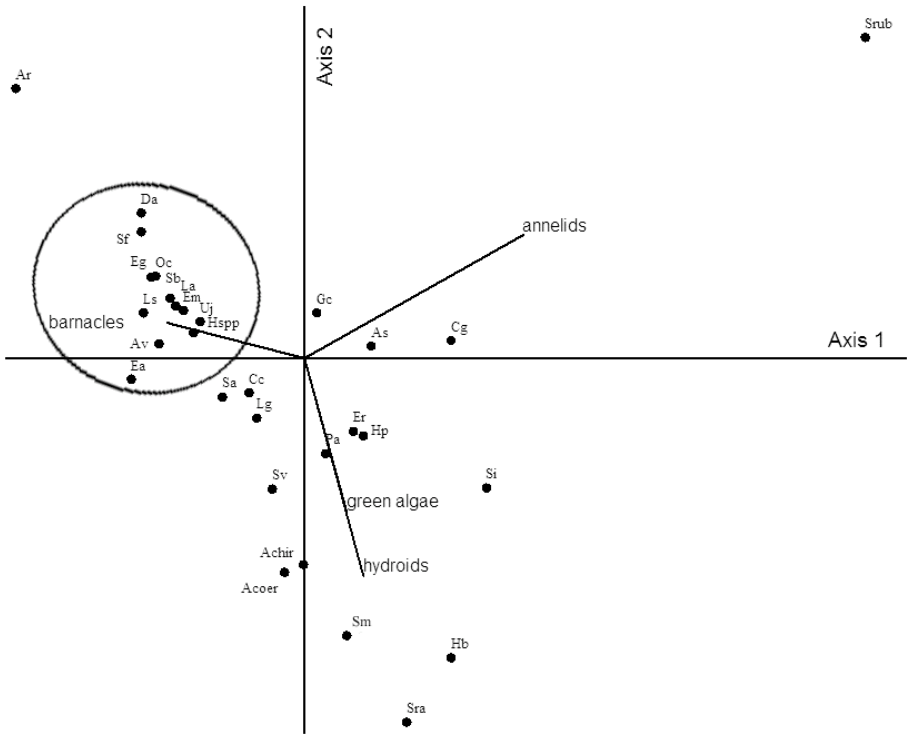
8e, f). Biplots show two rough clusters, one consisting of primarily predatory species influenced by barnacles and Rhodophyta, and a looser cluster of most remaining species.

Figure II. 8: CCA biplots and ordination results for all fish species by sessile taxa abundance

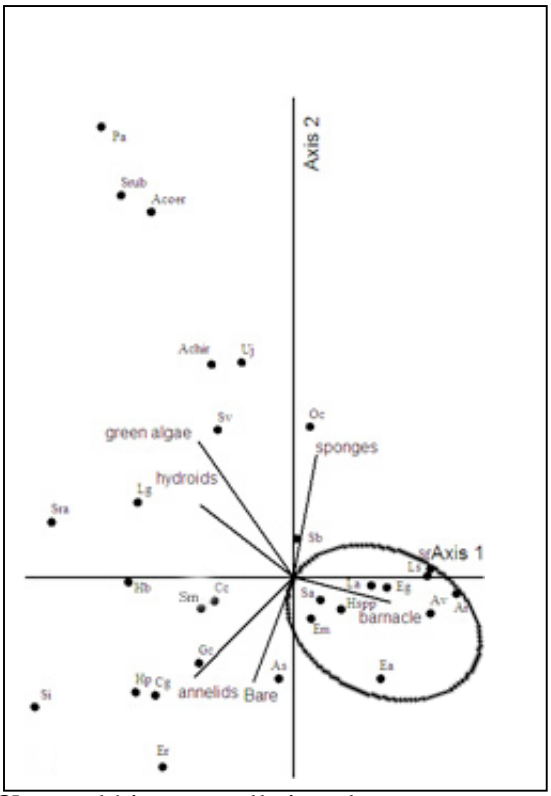
Figure	Analysis	Cumulative Variance (%) Axis 1 + 2	p axis 1	p axis 2
8a	All individuals	56.1	0.01	0.01
8b	All biomass	54.0	0.01	0.05
8c	Juvenile individuals	53.3	0.01	ns - 0.08
8d	Juvenile biomass	56.3	0.01	ns - 0.06
8e	Adult individuals	36.2	0.01	ns
8f	Adult biomass	36.7	0.01	ns

Species abbreviations used in figure 8 are listed below.

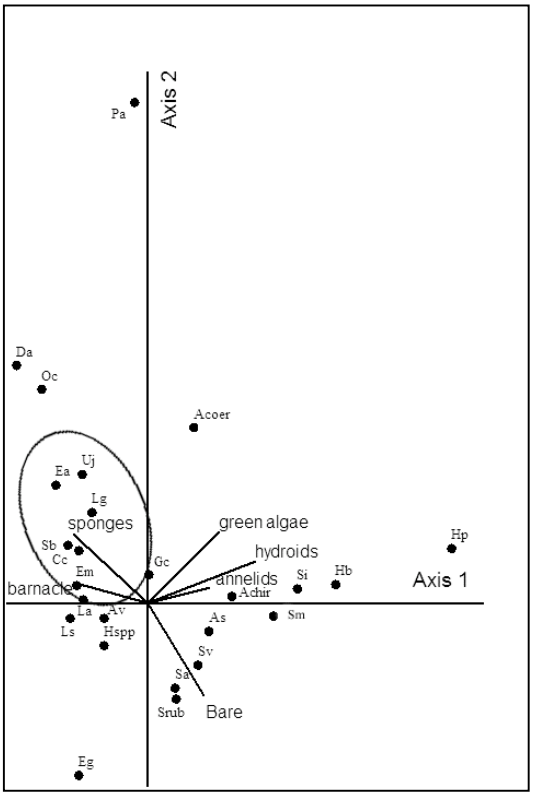
Acoer: *Acanthurus coeruleus*. As: *Abudefduf saxatilis*. Achir: *Acanthurus chirurgus*. Ar: *Archosargus rhomboidalis*. Av: *Anisotremus virginicus*. Cc: *Chaetodon capistratus*. Cg: *Coryphopterus glaucofraenum*. Da: *Dasyatis americana*. Ea: *Epinephelus adscensionis*. Eg: *Eucinostomus gula*. Em: *Eucinostomus melanopterus*. Er: *Elacatinus randalli*. Gc: *Gerres cinereus*. Hb*: Halichoeres bivittatus*. Hp: *Hypoplectrus puella*. La: *Lutjanus apodus*. Lg: *Lutjanus griseus*. Ls: *Lutjanus synagris*. Oc: *Ocyurus chrisurus*. Pa: *Pomacanthus arcuatus*. Sa: *Stegastes adustus*. Sb: *Sphyraena barracuda*. Sf: *Synodus foetens*. Si: *Scarus iseri*. Sm: *Strongylura marina*. Sra: *Sparisoma radians*. Srub: *Sparisoma rubripinne*. Sv: *Sparisoma viride*. Uj: *Urobatis jamaicensis*.



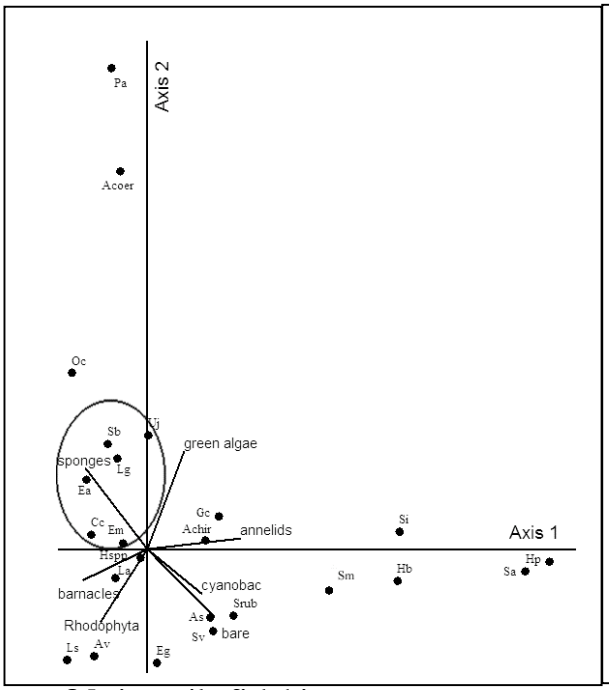
8a: Fish numbers, all size classes



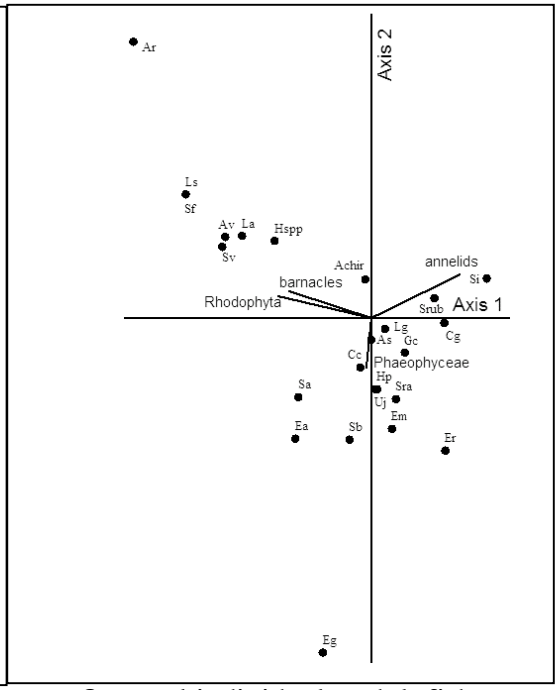
8b: total biomass, all size classes



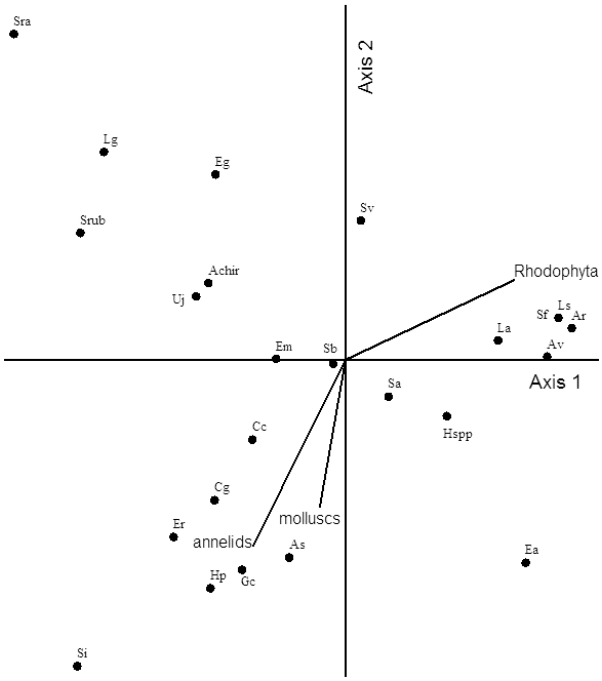
8c: total numbers, juvenile fish



8d: juvenile fish biomass



8e: total individuals, adult fish



8f: adult fish biomass.

DISCUSSION

The results in this study are consistent with the hypotheses that: (1) a greater diversity of prop-root epibionts in mangroves will make those mangroves more attractive as habitat to a more diverse community of fishes and (2) more abundant epibionts correspond to more abundant fish, although diverse epibionts do not necessarily lead to higher fish biomass. The influence of the epibionts is exerted by several different taxa.

Diversity and Abundance of Fishes

Of the habitat variables examined, epibiont community density and diversity were the best predictors for fish diversity and biomass. Not surprisingly, depth was also associated with increasing fish diversity; it is obvious that a wider variety of fishes are physically capable of using deeper habitats. (Ellis and Bell 2004) found that smaller fish

began to prefer shadier environments in water deeper than 75cm, while preferring unshaded foraging areas at shallower depths. This study did not examine unshaded habitats, but those findings may help explain the relationship between depth and fish diversity. Nevertheless, epibiont coverage and diversity were still the best predictors for fish biomass and diversity. As depth was not related to epibiont diversity or abundance, the epibiont- fish relationship exists independently of depth.

Distance between the mangroves and neighbouring habitats also did not influence epibiont or fish communities. This was surprising, as connectivity in mangrove-seagrass-reef habitats is important (Dorenbosch *et al*. 2004a, Sheaves 2005, Verweij *et al*. 2006b, Dorenbosch *et al*. 2007, Jelbart *et al.* 2007). The lack of differences in this study probably reflects the short distances between habitats; the largest mangrove-reef distance in this study was 1.9 km, and most were less. Reef-mangrove trends may be evident at an island scale rather than for individual reefs (Dorenbosch *et al*. 2006). It was also surprising that turbidity had no direct impact on fish communities; it was expected that reduced visibility would limit UVC effectiveness.

One distance variable, the distance to the nearest bay entrance, was significant in Panama; as distance from the bay entrance increased, epibiont diversity increased. This distance had a greater apparent influence on epibiont diversity than turbidity did. There are ample sources of larvae or spores within the bay to found new epibiont colonies; it seems more likely that this pattern has to do with currents, which are wind driven and unpredictable in the Bahia Almirante (Guzman *et al*. 2005). Fish do settle faster closest to a bay mouth (Nagelkerken and Faunce 2007); the presence of extensive reefs inside the bay probably confounds that effect.

The lack of influence of abiotic variables in Honduras, while the same general relationship between fish and epibionts remains, further suggests a more basic role for epibionts over abiotic factors. Epibionts influenced fish communities despite differences in geography, epibiont and fish community composition, and habitat type (e.g. lagoon v. fringing mangroves), while similar physical factors did not. The pattern persisted despite very important differences like the much higher tidal range in Honduras, which is likely responsible for the far less diverse epibiont community, suggesting a role for epibionts that applies to many Caribbean areas.

Given the more limited impact of the abiotic variables, the relationship between fish and epibionts appears to be more direct, although the mechanism is not certain. However, fish are not known to have a strong influence on benthic communities as predators; competition between organisms is a larger influence in mangrove habitats than predation (Wulff 2005). Therefore, the fish community is more likely to be influenced by the epibionts rather than vice-versa. . Epibiont diversity also increased with decreased turbidity, a result of increased primary productivity rather than fish activity; more photosynthesis in clearer water allows for greater growth of algae and photosynthetic symbiotes in corals, some sponges, etc. Only certain filter feeders, e.g. duster worms, increase in abundance with higher turbidity.

The effect of epibionts on fish communities may then be related to either feeding or shelter. As a feeding habitat, epibionts have much to offer. Some epibionts, particularly algae and other vegetation, are a habitat for invertebrates and small fishes (Kieckbusch *et al.* 2004). Mats of cyanobacteria also shelter and feed several invertebrate species (Cruz-Rivera and Paul 2006), although the cyanobacteria present in Bocas Del Toro or Utila

have not been examined. Fish may also feed on the epibionts directly. Some of the species observed, e.g. foureye butterflyfish, *Chaetodon capistratus* L, feed directly on certain root epifauna, e.g. sponges. The extent to which fish feed in mangroves, however, may be limited to certain species or populations (Nagelkerken and van der Velde 2004c). Age class also has an impact; for instance, both juvenile and sub-adult French grunts, *Haemulon flavolineatum* (Desmarest) feed opportunistically within mangroves, but juveniles do so more frequently (Verweij *et al*. 2006b).

For some species, any relationship with epibiotic organisms is probably partially related to feeding. The Dusky damselfish, *Stegastes adustus* (Troschel) is a strongly territorial, primarily herbivorous species, although a portion of its diet may consist of zoobenthos (Randall 1967). Likewise, the bridled goby *Coryphopterus glaucofraenum* (Gill), a small, burrow-associated species, feeds primarily on benthic algae as well as invertebrates including bivalve molluscs. For both species, a prime food source within their home ranges is on the prop roots.

The other possibility is that these organisms (e.g. corals, massive or branching sponges, some algaes) increase habitat complexity and shelter enough to attract more fish than less settled sites. There is abundant evidence that many fish species utilize mangroves during the day for shelter (Laegdsgaard and Johnson 2001, Cocheret de la Moriniere *et al.* 2004, Verweij *et al.* 2006a). The greater heterogeneity of mangrove detritus has also been shown to attract the most prawns (Meager *et al*. 2005).

The epibionts make an already heterogeneous environment even more so. Encrusting growths and algal mats increase available areas in which to hide, rest, or ambush prey. Large growths can also create shade which helps hide smaller fish from

predators under some conditions (Cocheret de la Moriniere *et al.* 2004, Ellis and Bell 2004). Too much structure and shade may impede foraging (Crowder and Cooper 1982, Duffy-Anderson and Able 2001) but this is not an issue for fishes that primarily feed elsewhere.

Increasing habitat complexity increases reef fish SR due to the increased diversity of available shelter (Luckhurst and Luckhurst 1978a). Rugosity correlates best with SR, while hard cover and small refuge holes are the most important characteristics across several habitat types (Gratwicke and Speight 2005b, a).

As diversity of epibionts increases, a diversity of shapes and forms are also available for fishes to use. Many of the commonly observed sponge species, e.g. *Spongia tubulifera* (Hyatt), *Clathria schoenus* (de Laubenfels), or *Desidea etheria* (de Laubenfels), typically exhibit a complicated or massive body shape (or both), and the presence of any one of these species can increase rugosity substantially. Structural shape may have a greater effect on predator efficiency than density (Warfe and Barmuta 2004). Sponges, the taxa with the greatest diversity of shape and form, were more closely associated with more species of juvenile fish than any other epibiont taxa. Many of the other taxa observed on the roots, e.g. corals, coralline algae and tubes of colonial annelids, also specifically increase not only rugosity but also the specific attributes acknowledged to increase reef fish diversity; hard substrate cover, shelter holes, or a combination.

The taxa providing the hardest substrates, especially barnacles, correlated with more fish species than softer types such as algae. Hard substrate itself is attractive to fish because it provides attachment points for periphyton, enhancing available resources

(Gratwicke and Speight 2005b). Barnacles in particular, especially empty shells of dead individuals, are utilized by many prey organisms, including isopods, crustaceans, small mollusks and fish (Barnes 2000, Garcia-Guerrero and Hendrickx 2004). Larval and adult barnacles themselves are also food for many fish species (Barnes 2000), although fish are most likely drawn by the prey items hiding among the shells or within empty shells. Barnacles are a smaller version of the entire fish-epibiont relationship, providing food, shelter, and nest sites for an entire network of organisms, and a superior habitat to algae alone. Softer substrates, especially green algae and hydroids, were more closely associated with benthivores and herbivorous species, the groups most likely to utilize mangroves for feeding (Verweij *et al.* 2006a). In addition, some herbivores, e.g. striped parrotfish *Scarus iseri* (Bloch) or Acanthurus spp., were observed feeding directly on the roots, presumably on epibionts.

The same arguments that apply to the relationship between epibiont and fish diversity are also applicable to the epibiont cover/fish biomass relationship. Greater density of epibionts can harbour greater abundance of small prey, particularly small invertebrates, or, alternatively, can provide more structure and shelter than bare prop roots alone as previously discussed.

Age Classes

The connection between epibionts and fish was for the most part much weaker for adult fish than for juveniles. A possible explanation is that many adult fish diurnally present in mangroves are there due to temporary, short-range migration (Dorenbosch *et al.* 2007). Among juveniles, where more species have similar needs and spend more time

among the prop roots, a more diverse assemblage was influenced by a broader diversity of epibiont taxa, and epibionts explained more variance. The more transient adults are less influenced by specific conditions within the mangroves. The exception was adult SR in Utila, which related more strongly to epibiont SR than juvenile SR did. As it turns out, however, these results are not inconsistent. Most of the adult species observed in Honduras were small species, e.g. *S. adustus* or *Chaetodon* spp. These species have very limited range (especially the Pomacentridae) and are most likely residents in the mangroves.

Within each size class for certain species there is wide variation in biomass. For instance, a 50 cm barracuda *Sphyraena barracuda* (Edwards) is still technically a juvenile, as is a 10 cm conspecific individual. These ranges may result in differences when individuals or biomass are used as the base data. Biomass is mostly an indicator of larger, as opposed to more numerous, individuals, and larger individuals apparently have different relationships to the epibionts. In all the CCAs, there were more, and often different, epibionts affecting biomass than affecting numbers of individuals. Barracuda biomass, for instance, was more closely associated with sponges, while barracuda numbers were more closely associated with barnacles. One possibility is that epibionts are used as ambush sites by larger individuals, while greater densities of smaller individuals are drawn to the hard substrate barnacle areas. The presence of disparate sizes is itself a form of diversity, irrespective of species; biomass is sometimes more indicative of actual diversity of niche and trophic level than numbers of individuals.

CONCLUSIONS

The results of this study are consistent with the hypothesis that epibionts enhance mangrove habitats for use by fishes, and both feeding and shelter play a role. Epibionts have the capability to improve both the quality and diversity of feeding and shelter in mangroves, making mangroves more attractive to a broader community of fishes. Since the trends were strongest when all size classes were pooled, it appears that epibionts enhance mangroves as habitat for fishes more generally than just as a nursery habitat.

The generally similar results in two completely different, widely separated locations imply that the relationship between epibionts and mangrove fish exists beyond just the Bocas del Toro archipelago. Nevertheless, there were differences between the two sites, e.g. no relationship in H' in Honduras and no effect of depth. These differences imply that even though basic trends may be consistent, there is still considerable local scale variation. These subtle differences between locations increase the difficulty of drawing general conclusions about mangroves as fish habitat. These results and those of previous studies confirm that not all mangrove habitats function equivalently. Moreover, other elements of the subtidal mangrove community as well as the difficulty of generalizing about multiple species may contribute to the inequality. A lot of variation remains unexplained, so there are clearly other factors affecting such a complex situation as fish community differences in mangroves.

Chapter III: Artificial roots and epifauna

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 (Parrish 1989, Nagelkerken *et al.* 2001, Nagelkerken *et al.* 2002, Lindeman and DeMaria 2005). The presence of mangroves increases abundance or biomass and enhances fish communities on nearby reefs and fisheries (Dorenbosch *et al.* 2004a, Mumby *et al.* 2004, Dorenbosch *et al.* 2005a, Manson *et al.* 2005a).

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 (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 fish communities (Luckhurst and Luckhurst 1978b, Luckhurst and Luckhurst 1978a, 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, Crowder and Cooper 1982, Ellison and Farnsworth 1990). Their loss potentially has severe ecological or economic implications (Ellison 2007).

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 by 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 hypothesized that the most abundant and complex AEs would attract the most and most diverse fish, and that habitat heterogeneity would be more important to fish than the feeding potential provided by epibionts.

MATERIALS AND METHODS

III.1 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 meters away. The majority of the human population is found in Bocas del Toro town on I. Colon, 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.

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).

Figure III.1:
Map of Central America and the Caribbean (inset) with the entire Bocas del Toro archipelago and the immediate study area indicated.

III.2 Artificial Mangrove Roots

Artificial mangrove roots (AMRs) were constructed from wooden stakes, 5 cm X 2.5 cm X 100cm sharpened and driven into the *Thalassia* beds to a depth of 25 cm, leaving 75 cm exposed. AMRs were arranged into square one-m^2 plots, 25 stakes/plot. The experiment was performed twice, in July/August 2005, and again in June-August 2006.

In 2005, the one-m^2 plots were arranged into groups of three along with a one-m^2 plot of seagrass without stakes. Each AMR plot or seagrass control was separated from adjacent plots by a one-m^2 patch of seagrass. Each complete group of four plots (75 stakes total and seagrass plot) was separated by at least 25-40 meters from the other groups; there were three complete groups, each referred to as a "site". Each site was exactly two m

from the nearest mangrove fringe, and each was in the shade of the trees at all times except mid-day. All sites were located very close to a Smithsonian Tropical Research Institute (STRI) facility to discourage vandalism (Fig. 1). Depth and seagrass shoot density were quite consistent between sites; the depth was between 0.73 and 0.9 m, and seagrass density varied from 743 to 762 shoots m^{-2} at the densest, with equivalently sized leaves. Tidal range in the Bahia Almirante is small, between two and 15 cm under most conditions (Guzman *et al.* 2005).

Each group of three plots had structures attached perpendicular to the stakes according to the following system (Fig. 2): a.) One plot with blank stakes without attachments, the control ("blank"); b.) One plot with 5 X 5 X 10cm blocks attached randomly 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 dowels, 1.5 cm diameter by 5 cm long, attached to each of the remaining 13 stakes in the plot (referred to as the "mixed" plot). d.) A one-m^2 plot of *Thalassia* without any *AMRs,* marked at the corners. In each location the order of the treatment and control plots was re-arranged.

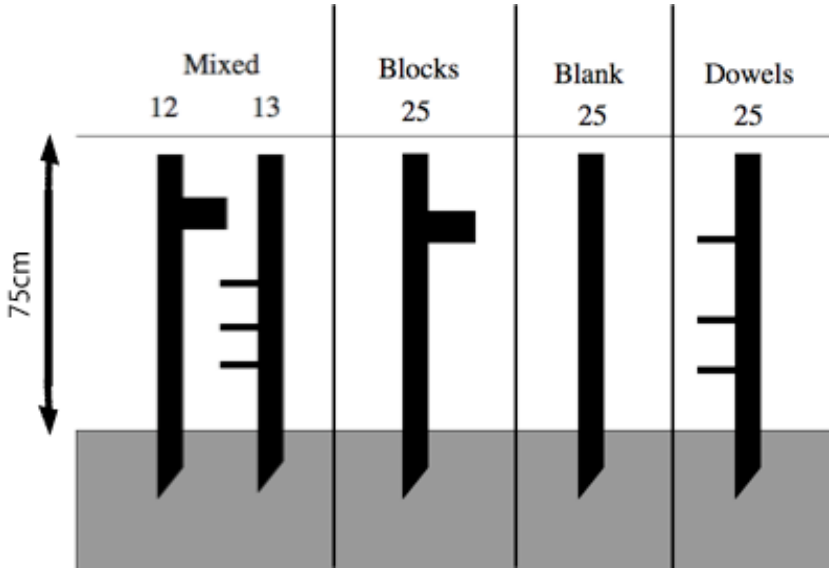


Figure III.2: Diagram of AMR treatment types.
1 replicate location consisted of all types, plus a $1m^2$ seagrass plot (not depicted) separated by 1 meter of seagrass. The mixed, blocks, and blank (control) were included in 2005; all types, including dowels, were included in 2006.

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. After 15 days, every site was 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- 9:00 AM and 3:30-4:30 PM. 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 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 (Fraese and Pauly 2007). A fish was included if any part of its body was inside the treatment. 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/location/survey. Fish were chased out of the sites in between counts to reduce double counting of individuals.

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 all of the AEs were completely eroded away by natural processes. In June 2006 these plots, now with only natural epibionts, were surveyed twice a day for 15 days under the same conditions as before, and afterwards the settled organisms were identified and the percent cover estimated using a 5 X 5 X 75 cm quadrat.

Starting in late June 2006, the original experiment was repeated with an additional treatment plot added at each location. The new treatment consisted of three dowels attached to all 25 stakes in the one m^2 plot ("dowels", Fig. 2). After the waiting period and 15 day census had been repeated, two additional complete replicate sites of the entire set of three treatments, blank control stakes, and seagrass were established in two additional locations and the experiment continued in late July/early August 2006.

III. 3 Statistical Analysis

Mean fish abundance, species richness and biomass between treatments and entire sites were compared using two- way Analysis of Variance (ANOVA) after confirmation of normality and equivalence of variance. Where variance was highly unequal, Kruskal-Wallis Non-Parametric ANOVA was employed. Abundances were pooled rather than analyzed on a per species basis due to the relatively low numbers of any given species. The low abundance in some sites also prevented comparison of evenness measurements such as H'. Rare species, defined as those observed only once, were discarded from analysis. The July/August 2006 results could not be directly compared to the 2005 results due to different treatments (the addition of the "dowels") and the presence of significant site/treatment interactions. 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. The NMDS ordination was performed using PC-ORD 4.0.

RESULTS

III. 4 Abundance and diversity

In total, the plots attracted 941 fish from 28 species and 16 families. Of these, 21 species 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 foureye 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.

Grunts, *Haemulon spp.,* made up 19.9%, and parrotfishes (Sparidae) 9%. The remaining 35% were fairly evenly distributed among 10 less common taxa.

III.4.1: 2005 Results

The mixed treatment had significantly higher fish abundance than all other treatments, followed by the block and control treatments, while the lowest abundance was in seagrass (Fig. 3). Compared with the same plots after ten months in situ, by which time the AEs had been replaced by live epibionts, the plots with AEs still had the highest mean fish abundance, and seagrass still had the least. There were also differences in overall abundance by site, in that some sites (complete groupings of treatments and controls) attracted more fish, but these differences were not significant. The sites did have some effect on treatment results, as there were significant site*treatment interactions. (2 way ANOVA, site by treatment. Treatment: $F_{96,6}$=17.611, $p \leq 0.0001$. Site: $F_{128,4}$= 1.880, $p \leq 0.112$. Site*treatment: $F_{96,12}$=2.710, $p \leq .001$).

Similar results were observed for species richness, (2 way ANOVA, site by treatment; Treatment: $F_{96,6}$= 17.656, $p \leq 0.0001$ Site: $F_{128,4}$= 1.339, $p \leq 0.254$; Site*Treatment: $F_{96,12}$= 2.173, $p \leq .011$, Fig. 4).

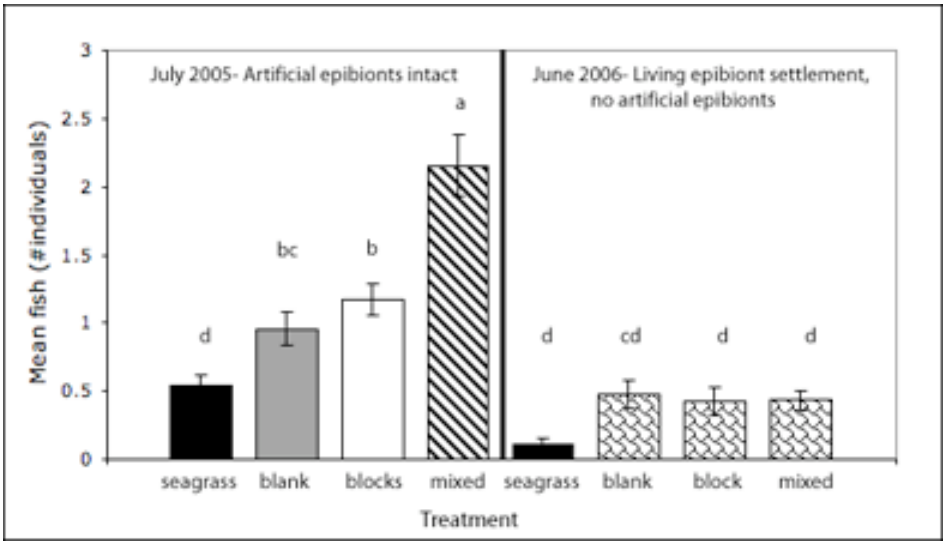


Figure III.3: Mean fish abundance/observation by treatment in July 2005, before epibiont settlement, and June 2006, after epibiont settlement and after natural processes had destroyed the artificial epifauna. Letters indicate significant differences between groups. Error bars indicate +/- one SE.

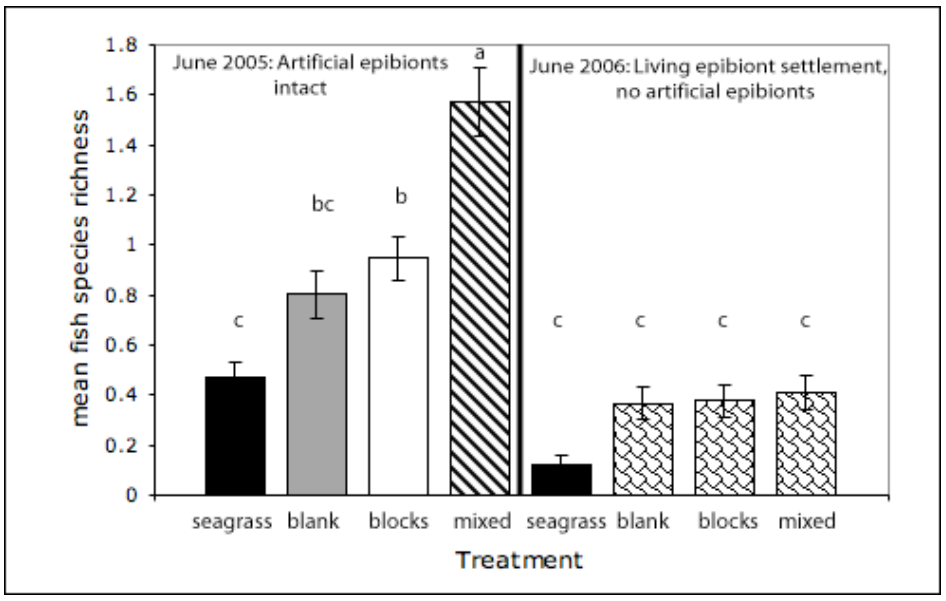


Figure III.4: Mean fish species richness/observation by treatment in July 2005, before epibiont settlement, and June 2006, after epibiont settlement and after natural processes

had destroyed the artificial epifauna. Letters indicate significant differences between groups. Error bars indicate +/- one SE.

III.4.2: 2006 Results

After the addition of the dowel-only treatment, the mixed treatment still had the highest fish abundance. Mixed, block and dowel treatments were not significantly different from each other, but all had higher abundance and richness than the blank control stakes. (2 way ANOVA, site by treatment. Treatment: $F_{150,6}$=11.513, $p \leq 0.0001$. Site: $F_{150,4}$ = 9.763, $p \leq 0.0001$. Site*Treatment: $F_{150,16}$=3.804, $p \leq 0.0001$, Fig. 5).

The pattern for species richness followed that for abundance exactly; the mixed treatment had the highest richness, and all AE plots had higher richness than blank stakes or seagrass. (2 way ANOVA, site by treatment; Treatment: $F_{150,4}$= 12.470, $p \leq 0.0001$. Site: $F_{150,4}$= 10.618, $p \leq .0001$. Site*Treatment: $F_{150,16}$=3.268, $p \leq 0.0001$, Fig. 6).

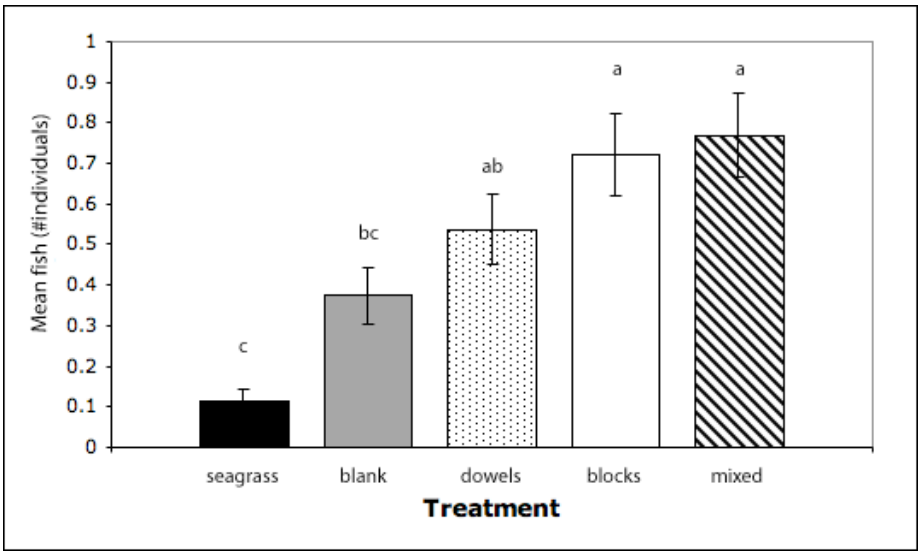


Figure III.5: Mean fish abundance by treatment in July-August 2006, when a dowel treatment had been added, settled epifauna removed, and 2 additional replicate sites were

established and surveyed. Letters indicate significant differences between groups. Error bars indicate +/- one SE

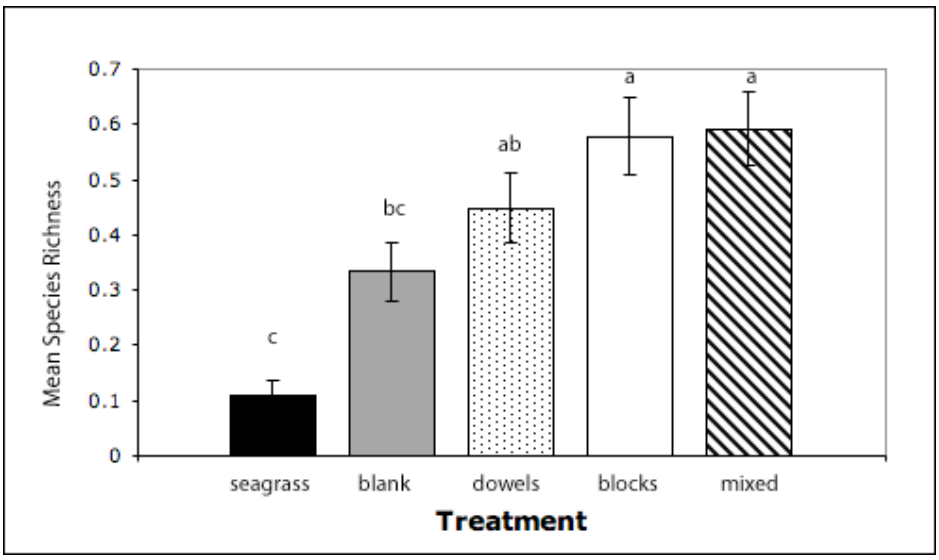


Figure III.6: Mean fish species richness by treatment in July-August 2006, when a dowel treatment had been added, settled epifauna removed, and 2 additional replicate sites were established and surveyed. Letters indicate significant differences between groups. Error bars indicate +/- one SE

III.5 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; larger fish than other sites visited some sites. There were also significant site/treatment interactions in both years (July 2005- June 2006: Treatment: $F_{96,6}$= 1.519, p ≤ 0.195. Site: $F_{128,4}$=3.751, p ≤ 0.005. Site*Treatment: $F_{96,12}$=0.699, p ≤ 0.693. July-August 2006: 2 way ANOVA, Treatment $F_{150,4}$= 1.775, p ≤ 0.132. Site: $F_{150,4}$= 7.886, p ≤ 0.0001. Site*treatment: $F_{150,16}$=1.936, p ≤ 0.015).

III.6 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 were no coherent groupings by either site or treatment in ordination space (NMS ordination, 3 axes, stress= 26.32). Herbivores (Scaridae and Acanthuridae) made up a slightly higher percentage of individuals in plots fouled with living epibiota, 20% instead of 14%.

III.7 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 substantial horizontal relief on the AMRs.

There were significant differences in fish abundance within this subset of plots (the least abundant plots were significantly different from the highest abundant plots – Kruskal Wallis NP ANOVA, $X^2= 18.181$, $p \leq 0.02$) 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 such as that provided by epifauna enhances both the abundance and diversity of fish utilizing mangrove prop root habitats. This effect persists despite spatial variation in fish assemblage. The pattern furthermore remained essentially consistent from year to year despite some 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 evidence from the AMR plots suggests that, over-all, shelter is the most important factor attracting fish. Comparing the identical plots from 2005, when they had artificial epifauna but no living growth, and June 2006, when they had a thin layer of epibionts, but no blocks or dowels, the plots with the artificial structure had significantly higher abundance and SR than the plots with live epibiota. 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 responsible for the differences.

This indicates that the low-relief stakes with live epibionts were inferior habitat to the highly heterogeneous AEs. This is consistent with evidence that some species, particularly as juveniles, utilize mangroves primarily for shelter while feeding opportunistically (Verweij *et al.* 2006b). These results differ from (Laegdsgaard and Johnson 2001), who noted that cleaned artificial roots attracted fewer fish than when they were fouled with epibiota. However, in our case only the initial AMRs had the AEs. There was a higher percentage of herbivores in the fouled plots, and herbivores are most inclined to feed in mangroves (Verweij *et al.* 2006a). However, these species were

encountered in the AE treatments as well. Other species, particularly Lutjanidae and Haemulidae spp., were present in equal percentages in both fouled and unfouled sites, but were nevertheless more abundant in the unfouled AE sites. Epibionts may well enhance feeding for some species where they are present, but more heterogeneous structure still attracts more juvenile fish.

There were some fluctuations in fish abundance between years, accounting for the higher abundance and richness of cleaned blank control stakes in 2005 than fouled blank stakes in June 2006. In 2006 the overall abundance was lower and the fouled stakes provided equivalent shelter to the scrubbed control stakes, but were surveyed during a period of reduced abundance**.** It is also likely that the presence of the dowel treatment in 2006 further diluted the available pool of fish into a greater number of plots.

The actual pattern of abundance and diversity observed in the AMR plots shows that shape and configuration of epibionts are important. The mixed treatment, which had the greatest abundance and diversity of independent pieces of shelter, had significantly higher fish abundance and diversity; this was the only treatment to have significantly higher abundance than control blocks 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. These results suggest that a certain critical amount of structure is necessary for epibiota to impact fish communities. When epibionts do not grow to sufficient size, they contribute little to available shelter. The roots themselves, with or without epibionts, still provide more structure than seagrass alone, and demonstrated consistently higher fish abundance.

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 density in decreasing predator pursuit and effectiveness (Meager *et al.* 2005, Warfe and Barmuta 2004). Prop root epibionts, given their irregular shapes and haphazard arrangement, are analogous more to complicated vegetation shape than to denser stems. 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).

The pattern observed in species richness mirrors that observed for 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 suggest 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.

The lack of significant differences in biomass among treatments suggests that the sizes of fish utilizing each treatment type were fairly consistent. The low numbers and the

fact that the majority of individuals were fairly small, as demonstrated by the low mean biomass, means that the addition of only a few larger fish can seriously affect biomass. The only significant differences in biomass were observed between experimental locations, not treatments; larger fish were present in certain locations, but within each location did not preferentially utilize any particular treatment type. The differences in abundance among treatments, then, were caused by smaller fish, which were better able to utilize the available structure than larger individuals would be.

Aside from treatment differences, there were still significant spatial differences between virtually identical replicate AMR sites, some only 25 meters 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 seagrass (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. However, at least one common species, *L. apodus*, exhibits site fidelity and might not move great distances very often (Verweij *et al.* 2007).

CONCLUSIONS

In accordance with the hypotheses, the type and amount of prop-root epibionts contribute to the density and diversity of fish assemblages in mangroves, enhancing the habitat primarily by increasing heterogeneity. 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 sub tidal mangrove ecosystems.

Chapter IV: Effect of epibiont removal on fish communities

INTRODUCTION

Mangroves and other shallow water tropical habitats are believed to function as nursery habitats for reef fish, sheltering large numbers of juveniles and other fish among the prop roots(Parrish 1989, Nagelkerken *et al.* 2001, Nagelkerken *et al.* 2002). The presence of mangroves increases abundance or biomass and impacts fish communities on nearby reefs and fisheries (Mumby *et al.* 2004, Dorenbosch *et al.* 2005a, Manson *et al.* 2005b, Dorenbosch *et al.* 2007).

However, all mangroves are not equally beneficial to fish communities. Not all mangroves function equivalently as fish habitat, even within the same geographical area (Huxham *et al.* 2004, Chittaro *et al.* 2005b). Seasonal or temporal variation in fish usage of mangrove habitats has been widely reported, with abundance typically, but not always, peaking during the rainy season (Stoner 1986, Barletta *et al.* 2003, Lugendo *et al.* 2007).

A question remaining to be addressed is what sets mangrove habitats apart from one another. In reefs and beach habitats, variation in the complexity or composition of the habitat has an important impact on the fish community, specifically that rugose or diverse habitat increases diversity and abundance in fish communities, (Luckhurst and Luckhurst 1978a, Gratwicke and Speight 2005b, a). In addition to habitat complexity, the availability of shelter in the form of holes or other hiding places has also been shown to influence the abundance and community structure of coral reef fish, especially given the impact of numerous resident and transient predators in tropical systems (Caley and St. John 1996, Eggleston *et al.* 1997). Removing or manipulating the availability of shelter has been shown to have a corresponding effect on juvenile fish; removing shelter reduces

fish abundance, while adding shelter increases abundance (Piko and Szedlmayer 2007, Finstad *et al*. 2007).

Mangrove habitats may contain similar variation in habitat complexity. (Cocheret de la Moriniere *et al*. 2004) noted that increasing the density of prop roots and shade increased use of the habitat by some species. Ellis and Bell (2004) found that shade, an important characteristic of virtually all mangrove habitats, interacts with depth, predation, and the preferred foraging habitats of fish; at greater depths fish are more inclined to seek out shade as protection from predators. Examining the effect of structure beyond root density, Meager *et al*. (2005) found that the most complex aspect of the mangrove system, the litter and detritus, was a better shelter from predation for prawns then the roots alone.

Another source of variation in mangrove habitat stems from the community of organisms growing directly on the prop-roots themselves. In many areas, particularly in the Caribbean, a diverse community of epibiotic organisms, e.g. algae, sponges, etc., colonize subtidal and intertidal mangrove roots, and these organisms may directly influence fish. Kieckbusch *et al.* (2004), for instance, noted the role of algae as a base of the food web in these areas. Nagelkerken *et al*. (2000a) found that some preferred invertebrate prey species of mangrove fish are sometimes found on and around these epibiotic organisms. However, the diversity of body shape and function of the epibiotic organisms leads to the possibility that their role may extend well beyond primary food webs or as a physical protective barrier for the trees. Many of these organisms, e.g. sponges, are large enough to increase substantially the amount of shelter available to fish in the mangroves.

In this study existing epifauna were reduced in replicate mangrove environments in order to examine experimentally the importance of epibionts to mangroves as fish habitat. We hypothesized that reducing the density and diversity of these organisms would reduce the abundance of fish in existing habitats.

MATERIALS AND METHODS

IV.1 Site description

All experiments were established in a maze of mangrove islands just South of Isla Bastimentos and east of Cayo Solarte, Bocas Del Toro, Panama (fig 1). The shorelines in the area facing the bay are almost exclusively fringing red mangroves *Rhizophora mangle*, with occasional stands of white mangroves *Laguncularia racemosa* behind them. In shallow areas the *R. mangle* abut extensive beds of the marine grass *Thalassia testudinum,* frequently interspersed with *Porites porites* and other species of shallow-water corals. Coral reefs tend to be found in shallow water quite close to the mangrove fringe. Non-lagoonal mudflats are small and typically found either beneath the prop roots of the *R. mangle* or in a narrow band between the roots and the *Thalassia*. The Eastern half of I. Bastimentos, including associated marine areas, is a marine National Park, with fishing restricted to hand capture exclusively by indigenous residents of the area. This area is dotted with shallow reefs and thousands of mangrove cays. The majority of the area's population is found in Bocas del Toro town on I. Colon, or the port of Almirante on the mainland. The rest of the area is sporadically settled, although there has been extensive clearing of *R. mangle* fringes on many islands and the mainland.

Figure IV.1: Map of Central America and the Caribbean (inset) with the entire Bocas del Toro archipelago and the immediate study area indicated.

IV.2 Surveys

Fish in six small mangrove islands located at the edge of the Bastimentos Marine Park in the gulf between Isla Bastimentos and Cayo Solarte (fig 1) were surveyed on ten separate days between July 15 and July 25, 2006. All of the fish in a 2-m wide belt transect around the circumference of each island were identified to species, counted, and their sizes estimated. The one exception were the grunts (*genus Haemulon*) which were often found in large mixed schools and in poor light observers could not be absolutely certain of the identity of every single individual; these were accordingly identified only to genus. Each island was divided in half, and a coin toss determined which side would be the experimental treatment and which side the control. A summary of characteristics of each island is shown in Table 1.

Table IV.1: Site characteristics of locations of field removal of epibionts

Island	Circumference (m)	Depth (m)	Total Density of Epibionts reduced	% species reduced	Epibiont SR before/ after reduction
1	32	.55	~30%	30	23/16
2	22.4	.55	~33%	28.5	21/15
3	18.9	.8	~31%	30	20/14
4	20	.55	50%	n/a	n/a
5	34.5	.55	50%	n/a	n/a
6	42	.7	50%	n/a	n/a

IV.3 Treatments

The treatments were of two types, “diversity”, and “density.” Three of the six islands were used for diversity treatments, and three were used for the density treatments (and associated controls for each type).

The diversity treatment consisted of the selective removal of particular species of epibionts. First each island was surveyed for epibionts by trained observers, and total species richness/island estimated. In each diversity replicate every single individual of a given species was removed from a given treatment transect. Target epibiont species were removed from every root in a given treatment transect where the species occurred until it had been completely extirpated from the transect. Controls were left completely undisturbed. Additional species were removed in the same manner until a.) Between 20 and 30% of available species had been removed and b.) Epibiont density, measured by total percentage of coverage, was reduced by an estimated 30-35%. Since not every

replicate had the exact same starting assemblage of epibionts, it was impossible to remove the identical suite of species from each replicate. Species were selected for removal based on four criteria; 1.) The species was common and not endangered or threatened in any way; 2.) Whether it was possible to effectively scrub, transplant, or otherwise completely remove the species from the transect; 3.) If the organism's abundance was such that its removal would keep final density relatively constant between sites; and 3.) To make sure that the amount of structure provided by the removed epibionts was reasonably consistent between sites. Species were also selected to prevent overbalanced removal of trophic groups, e.g. a carnivore (hydroids, anemones) was removed from each site. A full list of species that were initially present and which were removed is available in appendix 2.

The "density" treatments consisted of the across the board removal of a fixed percentages of epibiont cover. In the treatment half of each replicate island, every root was divided in half (upper and lower) and all epibionts growing on one of the halves were completely removed with a wire brush or dive knife. The result was that 50% of epibiont coverage, measured in terms of area covered, was removed from every root, regardless of species. Which half was scrubbed off (e.g. upper or lower) was alternated. No particularly dense clusters of any given species were present, ensuring that removal was relatively even across species. As with the diversity replicates, the other side of each island, opposite the treatment side, was left untouched as a control.

The islands were left alone for 21 days to allow disturbance from the clearing process to subside. Each replicate island was then re-surveyed ten times over fifteen days

between August 14 and August 29, 2006; abundance and species richness of fishes were counted and biomass estimated in both control and experimental transects.

IV.4 Statistical Analysis

Fish data were standardized to a 10 m transect by multiplying each variable by 10 and dividing by the actual length of each island transect to account for different transect lengths. Only the 11 most abundant species were used in analysis, as these accounted for 99% of individuals observed Biomass was estimated using length estimates and published length-weight relationships available at www. fishbase.org (Fraese and Pauly 2007); one extremely large species, the nurse shark *Ginglymostoma cirratum* was not included in biomass analysis as one individual can have more biomass than an entire transect combined, severely distorting results. Once standardized, mean fish abundance, species richness, and biomass among sites and treatments were compared using two- way Analysis of Variance (ANOVA). Abundance and biomass data were log-transformed to reduce heteroscedacity.

At the species level, log-transformed abundance data for each species was compared using MANOVA. Finally, fish were also separated into three size classes: <10cm, 10.1-20cm, and >20 cm, and the relative abundance of each class analyzed by MANOVA. (This was not done to species level due to insufficient abundance.) All analyses were performed using SPSS v. 13.0 for Macintosh. Community data were compared using Bray-Curtis ordination with the Sorensen distance measure using PC-ORD v 4.0.

RESULTS

Over the course of the study, 5703 individuals, comprising 23 fish species 17 families were observed in the islands (treatment or control half) either before or after the manipulation; 18 species were observed in sufficient quantity to be used in analysis. 58.5% of those individuals were grunts (*Haemulon spp*). Three additional species, *Lutjanus apodus, Chaetodon capistratus*, and *Scarus iseri*, made up another 32% of observed individuals. In total, 11 species, *C. capistratus, Haemulon spp., Sphyraena barracuda, Stegastes adustus, L. apodus, Gerres cinereous, Scarus iseri, Abudefduf saxatilis, Hypoplectrus puella, Halichoeres bivittatus* and *G. cirratum* accounted for 99% of all individuals observed. The remaining 12 species accounted for the last 1 %.

IV. 5 Abundance and diversity

There were significant differences in fish abundance and species richness among different islands based on location; Species richness varied significantly by location but not by treatment (2 way ANOVA, site by treatment, $F_{30,4}= 0.63$, $p \leq 0.728$ site; $F_{60,6} =28.1$, $p \leq .0001$, treatment; $F_{60,12}=10.38$, $p \leq 0.0001$, site*treatment. These data are summarized in table 2. The groupings are roughly divided by island size.

Table IV.2: Mean fish abundance, biomass, and species richness by site. Letters indicate significant differences (Islands 1-3 are the "diversity" replicates; 4-6 are the "density" replicates.

Island	Mean abundance	Mean Species richness	Total Species Richness	Mean Biomass(kg)
1	30.69 c	2.35 a	11	0.71 b
2	21.59 b	5.71 c	14	0.54 b
3	26.58 b	4.41 b	14	0.93 c
4	21.43 b	3.84 b	10	0.53 b
5	4.69 a	2.30 a	13	0.09 a
6	10.36 a	2.51 a	12	0.64 b

In the treatment transects where the epibionts were removed, fish abundance remained stable; however, in the control transects, abundance increased significantly during the period of the experiment. This pattern was consistent in both the "diversity" and "density" replicates (2 way ANOVA, site by treatment, $F_{30,4}$= 16.23, $p \leq .0001$ site; $F_{60,6}$ =9.691, $p \leq .0001$, treatment; $F_{60,12}$=5.828, $p \leq 0.0001$, site*treatment. Fig. 2a.)

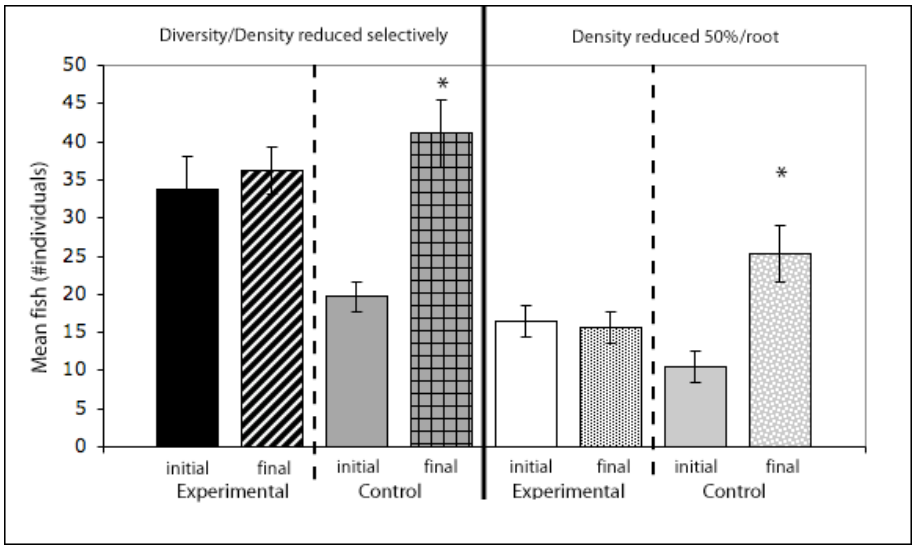


Figure IV.2a: Initial and post-manipulation mean fish abundance for experimental and control transects. The left hand columns display treatments where epibiont diversity was selectively reduced by species (n=6, 3 experimental, 3 control). The right hand displays treatments where epibiont density was reduced 50% across the board (n=6, 3 experimental, 3 control).

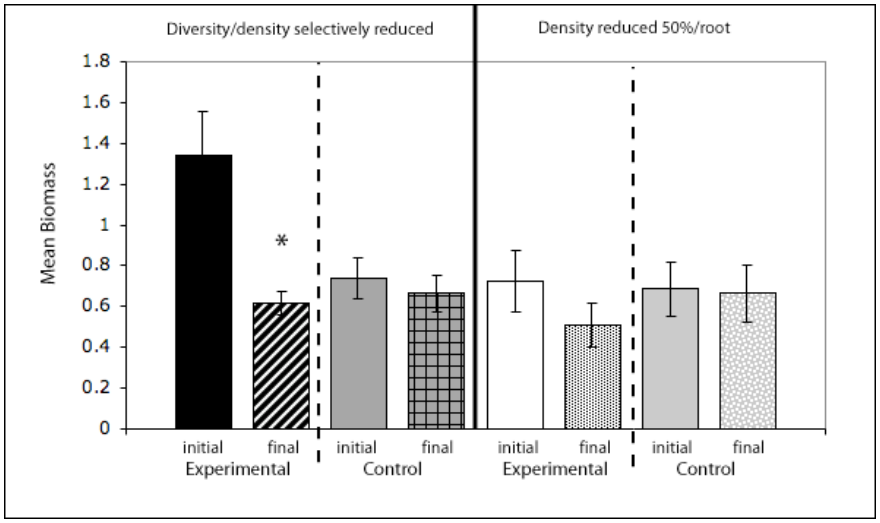


Figure IV.2b: Initial and post-manipulation mean fish biomass for experimental and control transects. The left hand columns display treatments where epibiont diversity was selectively reduced by species (n=6, 3 experimental, 3 control). The right hand displays treatments where epibiont density was reduced 50% across the board (n=6, 3 experimental, 3 control).

Figure IV.2: Experimental reduction of epibiont diversity and density: changes in controls relative to manipulated sites. Asterisks indicate significant pre/post experimental differences; error bars are +/- 1 SE.

Unlike abundance, mean biomass of fish actually decreased in treatments compared to controls, although the reduction was statistically significant only in the "diversity" treatments. (2 way ANOVA, site by treatment, $F_{60,4}$=13.755, $p \leq .0001$, site; $F_{60,6}$=6.202, $p \leq 0.0001$, treatment; $F_{60,12}$=7.661, $p \leq 0.0001$, site*treatment. Fig. 2b). Biomass also varied significantly by site (Table 2).

Species richness was not significantly affected by the experiment; SR varied according to site but not experimental treatment, although site did influence diversity in each treatment. ($F_{60,,4}$= 60.113, p ≤ .0001, site; $F_{60,6}$=1.181, p ≤ 0.318, treatment; $F_{60,12}$=8.065, p ≤ .0001, site*treatment).

When fish were separated into size classes, the significant changes in abundance in controls relative to most treatments was found to apply only to smaller fish. The smallest fish increased in abundance in most replicates, while abundance of intermediate-sized fish decreased in treatments and increased in controls, and large fish were unchanged. There were also significant differences in location for all size classes. The MANOVA results are summarized in Table 3 (Full MANOVA statistics are in appendix 2).

Table IV. 3: Mean fish abundance/treatment by size class of fish, before and after the epibiont reduction. All the individuals in the largest category were from species considered predatory. DIVR= Diversity Reduced, DENR=density reduced, DIVCON=control for diversity reduction, DENCON=control for density reduction.

	Size Class of Fish *= Significant before/after difference, p≤ 0.0001					
Treatment	**0-10 cm**		**10.1-20cm**		**20cm<**	
	Before	**After**	**Before**	**After**	**Before**	**After**
DIVR	5.14	9.51*	7.58	4.12*	.197	.110
DIVCON	5.46	8.93*	1.82	4.79*	.301	.213
DENR	2.63	2.89	2.62	2.05	.141	.101
DENCON	1.02	5.89*	2.49	2.85	.113	.170

IV.6 Community Composition

Reducing density and diversity of epibionts did not affect overall community structure significantly. There were significant differences in the abundance of the top 11 individual species among both sites and treatments (MANOVA, $F_{60,6}$= 3.81, p ≤ .0001 treatment; $F_{60,4}$= 16.78, p ≤ .0001 site; and $F_{60,12}$= 3.004, p ≤ .0001 treatment*site - F statistics shown are Pillai's trace). For the most part the pattern of abundance/species followed the pattern for overall fish abundance (increased in controls, stayed flat in experimental treatments) with the exception of *H. bivittatus* (slippery dick), which increased in experimental treatments. Other species, e.g. *G. cinereous* (yellowfin mojarra), followed a geographic pattern, decreasing between surveys in some islands, regardless of treatment, but not in others. The species data are summarized in Table 4 (full MANOVA statistics are in appendix 3).

In ordination space, site had the greatest influence on species composition. Transects clustered together mainly by island rather than by treatment. In Bray-Curtis ordination, the first two axes explained 54.9% of variance (Fig. 3).

Table IV.4: Species by species response to epibiont reduction. Significant increases/decreases are marked by an asterisk.

Species	**Diversity reduced**		**Diversity control**		**Density reduced**		**Density control**		
	before	after	before	after	before	after	before	after	P ≤
Chaetodon capistratus	1.23	1.83	1.37	**2.70***	0.71	1.08	0.46	**1.17***	0.03
Haemulon spp.	24.87	25.90	10.47	**27.33***	7.21	3.96	4.42	**11.83***	0.001
Sphyraena barracuda	0.10	0.20	0.10	0.03	0.54	0.54	0.38	0.79	ns
Stegastes Adustus	0.47	0.10	0.20	0.03	0.79	0.83	0.50	**1.29***	0.002
Lutjanus Apodus	2.30	3.03	2.87	**4.80***	5.25	7.46	4.50	**8.88***	0.001
Gerres	0.40	**0.60***	0.20	**0.87***	0.21	**0.00**	0.17	**0.04***	0.001

cinereous						*			
Scarus iseri	2.10	2.43	2.80	3.87	0.58	0.00	2.00	0.00	ns
Abudefduf saxatilis	0.97	0.40	0.87	0.53	0.13	0.46	0.38	0.21	ns
Hypoplectrus puella	0.20	0.43	0.13	0.33	0.50	0.50	0.25	0.42	ns
Halichoeres bivittatus	0.03	**0.63***	0.13	0.23	0.17	**0.75***	0.38	0.46	0.001
Ginglymostoma cirratum	0.33	0.37	0.33	**0.10***	0.29	**0.08***	0.33	**0.00***	0.001

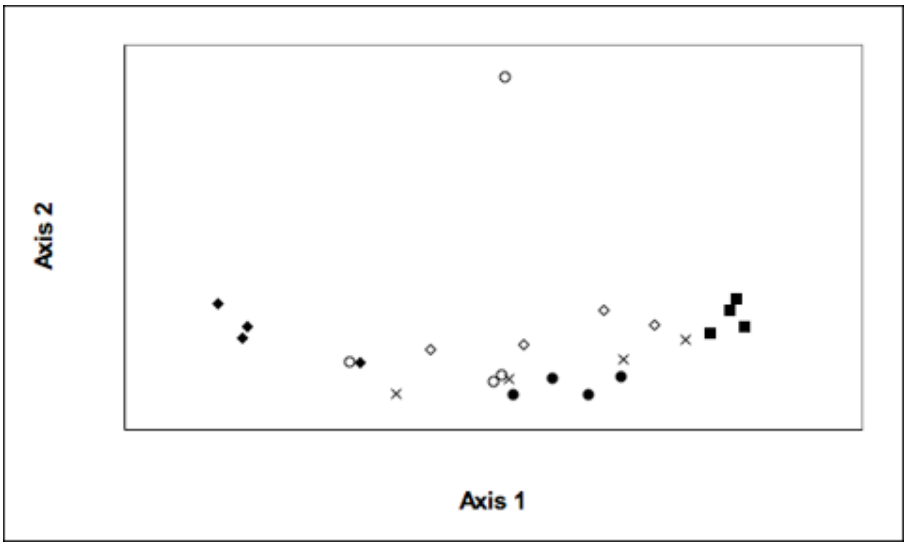


Figure IV.3: Bray-Curtis ordination of fish assemblages in treatment and control transects; each different symbol corresponds to a different island (6 in total). As the groupings indicate, samples cluster mostly by island. Treatment did not seem to have a significant effect on community structure.

DISCUSSION

The results of manipulating epibiont density and diversity are not straightforward. Contrary to expectations, overall fish abundance actually increased over the course of the experiment. However, it increased significantly only in the untouched control plots, while

at the same time, biomass in most transects decreased. The probable explanation is that a large pulse of new, smaller fish moved into the study area during the second half of the experiment, and preferentially settled in the control transects. These results are consistent with field observations taken in the area, where biomass increased in proportion to total area of epibionts in a mangrove area (MacDonald 2007). Likewise, Gratwicke and Speight (2005b) found that the best predictor for fish abundance was height of structure; these results are consistent, as removing epibionts reduces overall habitat height; abundance was higher where height was unaffected.

Some of the most dramatic results came from transects in which particular species were removed completely rather than those with across-the-board reductions. In these transects, in which primarily blocky sponges and bivalves were removed, fish biomass decreased significantly, while the numbers of the smallest fish increased significantly. The changes in biomass, therefore, were driven by the sharp reduction in intermediate-sized fish, since the numbers of larger fish remained unchanged.

Furthermore, the changes made in the epibionts did not impact the smallest fish. Many of the epibiont species removed tended to be blocky, massive organisms, e.g. bivalves or the massive sponge *Cliona delitrix*. These organisms do not apparently provide sufficient shelter to affect habitat choice in the smallest fish, and while younger juveniles are more inclined to feed opportunistically in mangroves than their intermediate sized counterparts (Verweij *et al*. 2006b), it is not likely that such sporadic removal of epibionts would significantly affect feeding habitat relative to controls.

Where epibiont density was reduced evenly, the most common organism removed was coralline algae, which provides little additional heterogeneity to the mangrove

habitat. In these transects, fish biomass did decrease, but not quite significantly. However, in these transects, the numbers of the smallest fish increased dramatically in controls relative to those in which epibiont density was reduced. In these transects, a far larger proportion of potential habitat complexity was removed, even if the specific structures were removed were individually not as dramatic. The smallest fish are potentially able to utilize these lower relief structures as shelter, or feed more easily on small invertebrates in the crevices of the coralline algae; coralline algae is not dissimilar to barnacles, which are known to provide feeding and shelter opportunity to small fish in the tropics (Barnes 2000). In this case, the intermediate-sized fishes were not significantly affected, as they are less able to utilize the lower relief structures for shelter and less inclined to feed within mangroves.

The results suggest that not only the amount of structure but the quality or type of structure makes a big difference to fish habitats; if fish are using the epibionts as shelter from predation, the nature of the structure, the predators, and the existence of competing species may all impact the effectiveness of shelter structures (Almany 2004). At the depths present in this experiment, the shade provided by the epibiota may be valuable to conceal smaller prey species from predators (Ellis and Bell 2004); a few larger organisms provide a lot more shade than a larger coat of low-relief epibionts.

Warfe and Barmuta (2004) observed that the shape of vegetation cover mattered more than the density, and that more complex shapes not only impeded predation, but set up negative interactions between predators, impeding multiple predators at once. Because of the complex fish communities in mangroves, prey species will almost always face threats from multiple predators simultaneously. Moreover, the structure provided by

epibionts may be used as ambush sites by smaller predators. The results do not rule out a threshold of epibiont density in which smaller fish are best able to utilize the structure provided by these organisms, but the relatively small scale of the experiment may not have exceeded the threshold. There does seem to be such a threshold level density beyond which the greatest reductions in predator foraging efficiency are achieved in vegetated habitats (Gotceitas and Colgan 1989).

Adult fish, for their part, were relatively unaffected by the change in epibionts. A possible explanation is that many adult fish diurnally present in mangroves are there due to temporary, short-range migration, rather than residency (Dorenbosch *et al*. 2007). Furthermore, the majority of the adult fish observed during the experiment (e.g. *L. apodus*) are primarily piscivorous as adults (Rooker 1995); these most likely are not feeding on tiny isopods or crabs between the cracks of bivalve clusters. Likewise, the largest species, e.g. the nurse shark *G. cirratum,* or the great barracuda *S. barracuda*, while they do enter the mangroves to feed or rest are not likely to benefit from the shelter of a massive sponge. However, the presence of these large, transient species in all transects may encourage smaller fishes to seek out habitats with better opportunities for shelter.

The results suggest that different sizes of fishes may interact with the epibionts in different ways. A likely explanation for these differences is the effect of predation pressure. Eggleston *et al*. (1997) found that on small patch reefs (the shelter equivalent of a mangrove island) predator (Nassau grouper, *Epinephlus striatus*) removal significantly increased the density of prey fish (>4cm), but did not do so when the smallest fish were included. Those results, and the patterns observed in this study, suggest that slightly

larger fish may be more dependent on available shelter than the smallest fish. Evidence from patch reefs suggests that transient predators have enough impact to shape populations of newly settled recruits (Carr *et al*. 2002); the positive impact of prop-root epibionts previously observed does not appear to take effect until fishes have grown past this stage.

It was a little bit surprising that overall community structure did not change in response to treatments; all of the most common species, particularly *Haemulon spp*., *L. apodus*, and *C. capistratus*, followed the overall pattern of increase in control transects. It was likewise surprising that fish species richness was unaffected by epibiont removal. More heterogeneous or rugose habitats correlate to higher fish species richness (Luckhurst and Luckhurst 1978a, Gratwicke and Speight 2005b). The removal of a significant portion of that complexity should have an impact on fish species richness. Part of the explanation may be the generally similar nature of the removals across replicates; no species removed were preferred food items or part of an obligate mutualism. The relatively small scale or even nature of the removals may not have reduced habitat complexity in such a way to disproportionately affect certain species. Plenty of rugosity and habitat heterogeneity remained, supporting fewer fish relative to controls but not crowding out particular species.

Nevertheless, there were species that diverged from the main pattern. It is not surprising that abundance of larger species, particularly transient predators, varied independently of experimental factors; as discussed above, these are unlikely to be affected by epibionts. The herbivores showed divergent patterns; one, the striped parrotfish *S. iseri*, did not increase or decrease significantly, likely because its preferred

food source, algae were not removed, nor was there sufficient time for significant new growth to occur. Only one species, H. *bivittatus* responded more positively in the experimental transects than the controls. It is possible that the disturbance to the area reduced shelter for the diverse variety of small motile prey favored by this species; the reduction in shelter made foraging easier, although it is not clear why only this species would be affected in such a way.

For most species, however, it seems that the reduction in epibionts affected the habitat in a very basic, universal way, e.g. shade or general structure that did not impact one particular niche more than another. Many juvenile fish in the mangroves utilize a similar niche as well, so a relatively consistent alteration in habitat affected the overall community, reflected by abundance, but for the most part not its individual members.

There was one other pattern in the relative abundances of certain species, and it applied to general trends in fish abundance as well. For every species, there were spatial differences among sites, which persisted even after adjusting for differences in transect size. In this study, in addition to species differences there were differences in biomass, abundance, and diversity among mangrove islands that were only 100 meters apart. Community structure as a whole was dependent on specific islands but not on treatment. The size of the island had some effect; the smallest islands were fairly similar in abundance, but the larger islands varied considerably, and did not always have higher abundance, diversity, or biomass contrary to what biogeographic theory would predict.

Planes *et al*. (1993) and Stoner (1986) both found spatial variation in abundance, the former in a mangrove lagoon, the latter on reef and related habitat. Both of these studies suggested that significant differences in habitat were responsible for variation in

fish abundance. In this case, each replicate was very similar, with no obvious biotic or abiotic differences among them to account for the differences. However, fish communities in mangroves are affected more by the overall landscape composition of the area and neighboring habitats, rather than within-patch influences (Pittman *et al.* 2004). Connectivity between fishes in mangrove and adjacent habitats has been widely reported (Dorenbosch *et al*. 2007, Jelbart *et al*. 2007, Saintilan *et al*. 2007).

In the Bastimentos area, the numerous mangrove cays where this experiment was conducted are part of a very diverse shallow water environment including reef, *Thalassia* beds and a rare habitat known as coral garden. The nature and abundance of piscivorous predators varied as well; some areas had abundant piscivorous avifauna, while large sharks (*Negaprion brevirostris*) were observed in others. The influx of smaller fish over the course of the experiment presumably came from the surrounding habitat. As such, the variability of the landscape is a probable contributor of short-scale fish variation among cays. It also contributes to the difficulty of drawing widespread conclusions about fish communities in mangroves.

Conclusions

The results of this experiment confirm a link between epibionts and fish, and suggest an important contribution of fish size, but it remains difficult to draw overarching conclusions about this link. However, the fact that numbers did not for the most part decrease significantly in treatment transects suggests that this interaction is not obligate. Fish are still able to utilize habitats in which epibionts have been removed, even if undisturbed habitats were preferred. There may be influences of shape and degree of relief in which this relationship is more important. It is possible that the removal

experiment did not go far enough, and that a larger reduction of epibionts would have shown greater effects; in short the removal may not have met a threshold level in which the effects become apparent. Location also clearly exerts a very key role in mangrove fish assemblages, as these differences persisted despite differences caused by experimental treatment, and these differences manifest themselves at small scales.

Chapter V: Grazing by fish or other motile organisms does not have a meaningful impact on prop-root epibiont communities

INTRODUCTION

As previous chapters have indicated, there is convincing evidence for a link between epibiont and fish communities in mangroves, especially in terms of biomass and diversity (See chapters 1-3 for a complete discussion). While most evidence to date suggests that habitat influences the fish community rather than the other way round, the possibility of fish predation structuring the epibiont community has yet to be ruled out (MacDonald and Weis 2007). Such a top-down effect on the epibionts would mean that epibionts are connected to fish in mangroves primarily through feeding rather than as a habitat component, and might imply that differences in fish communities in mangroves are a result of variability in food availability.

There are many possible contributors to epibiont community structure without any influence by fish. Competition, particularly for space, but also, to a lesser extent, food is a common mechanism contributing to benthic organism distribution (Lohse 2002). In mangroves, however, the discontinuous environment formed by multiple, non-connected prop-roots can prevent any particular competitor from gaining dominance over other organisms beyond any particular root, at least for sponges (Sutherland 1980). Other research has suggested, however, that abiotic factors may be the most important driver of benthic invertebrate distribution and abundance in mangroves (Pawlik *et al*. 2007).

Fish or invertebrate predation, particularly grazing, does have a role in structuring some benthic communities on reefs (Mumby *et al.* 2006). Top-down effects of fishes

have been observed in Caribbean corals and sponges (Dunlap and Pawlik 1998, Pawlik 1998, Mumby *et al*. 2007); in the former study, regulation of smaller grazers by large predatory fishes was found to be very important to the structure of Caribbean coral communities; fishes do not need to eat benthic organisms directly to impact their distribution. Sponges have also been observed among the stomach contents of some *Sparisoma spp*. in mangroves, although not a species present in Bocas del Toro (Dunlap and Pawlik 1998).

Many species of fishes do feed, at least opportunistically, on the surface of the prop-roots, although not automatically on the epibionts themselves (Verweij *et al*. 2006b). Diurnal benthivores and herbivores were most likely to use the mangroves for feeding on epiphytic species, while most other species found in mangroves utilize the roots for shade and shelter (Verweij *et al*. 2006a). Likewise, over the course of this study, more than one herbivore species (*Scarus iseri, Acanthurus spp*.) was observed feeding directly on epibionts on the mangrove roots, sometimes in schools (Figure 1). Non herbivores, especially *Lutjanus apodus*, were also observed biting at the surface of the prop-roots, although it was not possible to determine exactly what the target was. Furthermore, quantitive analysis of the behavior of common mangrove species in Honduras suggests that feeding is quite infrequent (Shahrastani, pers. comm.).

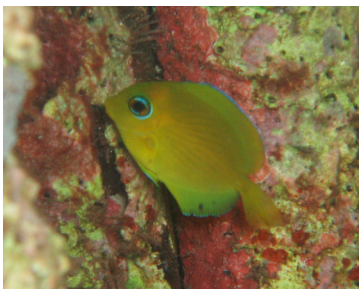


Figure V.1: A juvenile Blue tang, *Acanthurus coelurius,* takes a bite off a prop root.

This study tested the influence of grazing or predation on epibiont abundance, diversity, and community structure by excluding fishes of all or select size classes from

the surfaces of the prop-roots. By restricting all fishes, the cages also exclude the effect of indirect grazing, e.g. a predatory fish attacking small fauna among the epibionts, inadvertently damaging the sessile organisms in the process. Based on the relative infrequency of observed feeding events and the importance of abiotic factors to sessile communities in mangroves, the hypothesis for the experiment was that restricting grazing would not have a significant effect on epibiont communities.

MATERIALS AND METHODS

V.1 Site description

The experiment was established during the rainy season 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 to the study area is 75 meters away. The majority of the human population is found in Bocas del Toro town (about 4 km from the study site) on I. Colon, 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. The construction of a resort and marina was taking place during the study across an inlet from the location of the cages; the result was considerable input of sediment and other terrestrial contributions into the local water. These inputs were not measured in the immediate study site, but

were quantified and found to be substantial in areas closer to the construction (D. Carlon pers. comm.).

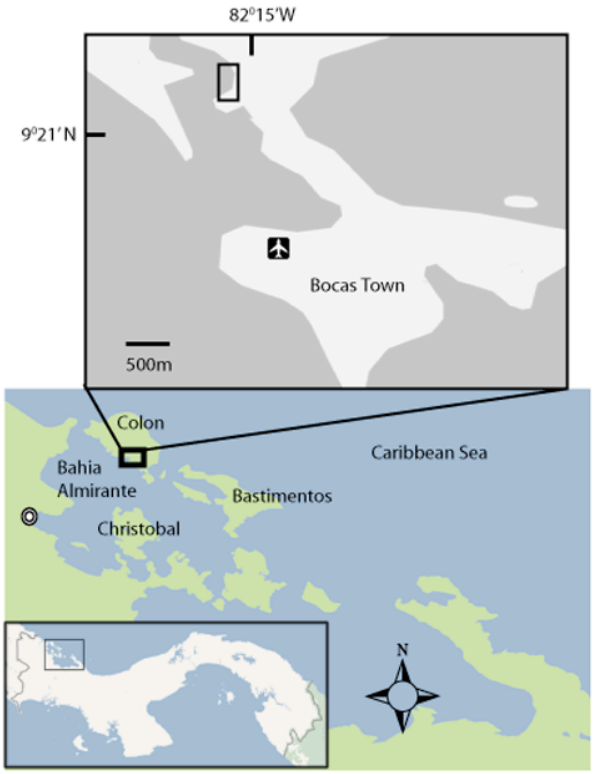


Figure V.2: Map of Bocas Del Toro with site of cages enlarged

V.2 Cages

Between May 15 and August 17th, 2006, 40 individual *R. mangle* prop roots were monitored for changes in epibiont community composition in response to a variety of exclusion cages designed to keep out small or large fishes, and equivalent controls (Table 1). Cages were composed of a 50 cm wide section of screening material (1 cm grid size) or chicken wire (6cm octagonal grid) attached to a prop root at the top and bottom edge of the material by means of plastic cable ties threaded through the material and tightened around the root. The effect was that a 50cm tall section of each root was covered by the

appropriate mesh cage to exclude fish or any other motile fauna from the caged section of root. All effort was made to cage off sections on each root of equivalent diameter, but this was not always possible. Likewise, all effort was made to choose roots with a similar initial configuration of epibionts, but this was not always possible, either. Motile fauna (e.g. Ophiuridae) were removed from the section to be caged prior to the completion of the enclosures. Controls for the various treatments consisted of the same caging type with large holes cut into the side to allow access of any sized fish. On control roots that had no cages at all, 50 cm sections of each root were marked by cable ties above and below in the area a cage would be attached, but there was no cage. Cages were inspected and scrubbed clean every 14 days during the study.

The initial census was conducted between May 10-15, 2006, and repeated from August 15-18, 2006, after the cages had been in place for 3 months. Root organisms inside the caged or control areas on each root in the study were identified to the lowest taxon possible using keys provided by the Smithsonian Tropical Research Institute (STRI) and assistance from local experts. Species that could not be identified with confidence were classified as unknowns. Cyanobacteria were not identified to species and were considered as one taxon. Likewise, species confirmation of hydroids was not possible, so hydroids were also treated as one taxon. Bare root, uncovered by any epibionts, was also treated as a taxon for analytical purposes and measured in the same way. The percent area covered by each species per root was measured using a framed grid of 5x5 cm squares (75 cm long x 10 cm wide). Each 25 cm^2 square was the base unit of measurement, and any measurements smaller than approximately 0.25 of a square were considered trace amounts and rounded to 0.1 for analytical purposes.

Table V.1: Description of cages, both treatment and control types

Treatment name	Material/mesh size	Scrubbed clean of epibionts	Sizes of fish excluded	n
1mm Screen * 1mm	Screen/1mm	N	all	5
Screen Control (1mm-C)	Screen/1mm	N	none	5
Wire	Fencing/6cm	N	Larger than ~15 cm	5
Wire scrubbed (Wire-Scr)	Fencing/6cm	Y	Larger than ~15 cm	5
Wire control (Wire-C)	Fencing/6cm	N	none	5
Wire scrubbed Control (Wire Scr-C)	Fencing/6cm	Y	none	5
No cage (NC)	n/a	N	none	5
No cage scrubbed (NCScr)	n/a	Y	none	5

* No 1mm or 1mm-C roots were scrubbed- the small mesh size is a substantial barrier to new colonization

In some treatments (Table 1) all epibionts were removed by means of vigorous scrubbing with a wire brush or dive knife in the caged (or control) area prior to the study; care was taken not to damage the bark of the root. The area of these treatments was determined using the same mechanism used to measure percent area of epibionts described above, although these sections were clear of fouling organisms.

V.3 Statistical Analysis

The occurrence of any given epibiont species was typically very low; as a result before/after epibiont coverage was calculated exclusively at the suprageneric level (e.g. hydroid, rhodophyte, tunicate, etc.). Overall community characteristics- Species Richness, Shannon Weiner Diversity Index (H') and overall epibiont coverage were compared among treatments using one way ANOVA (treatment was the only factor). The responses of individual taxa (and bare root) to the treatment was examined using MANOVA. Data were log (n+1) transformed to reduce heteroscedasticity. Community composition was examined using Non-Parametric Non Metric Multidimensional Scaling Ordination (NMDS) in Pc-Ord v 4.0. All other tests were conducted using SPSS v. 13.0.

RESULTS

There were statistically significant differences among taxa assemblages in the different treatment types (MANOVA: $F_{80,15}=1.870$, $p \leq 0.0001$ -Pillai's trace, 3 other F statistics significant as well). However, only a few coverage types (algae, sponges, and bare root) showed significant changes (Table 2, figure 3). Of those taxa which did change in coverage over the experiment, post-hoc tests revealed significant among-group differences in only algae and bare root (Figure 3). The significant differences in the overall model are likely the result of subtle, compound changes in most or all of the taxa, but there are not sizeable among group differences. The largest differences, in turn, are seen on those roots that were initially scrubbed of all epibionts prior to the experiment.

Table V.2: MANOVA statistics by epibiont taxa (cover type in the case of bare root). Values shown are from log(n+1) transformed data.

Taxa	df	F	P≤
Bare	15	3.1	.001
Algae (all Rhodophyta)	15	7.97	.0001
Hydroid	15	1.73	.068
Sponges	15	2.13	.019
Tunicates	15	.84	.631
Bivalves	15	.833	.638
barnacles	15	1.2	.240

Similarly, overall epibiont coverage was also significant between scrubbed roots before and after the experiment, but no other treatments (ANOVA, $F_{80,15} = 7.271$, $p \leq 0.001$) showed a similar effect. Similar results were observed for both overall species richness/root and H' (ANOVA $F_{80,15} = 7.066$, $p \leq 0.0001$ Species richness; $F_{80,15} = 4.55$, $p \leq 0.001$, H'). Note: n= 80 comes from 8 treatments X 5 replicates, before and after.

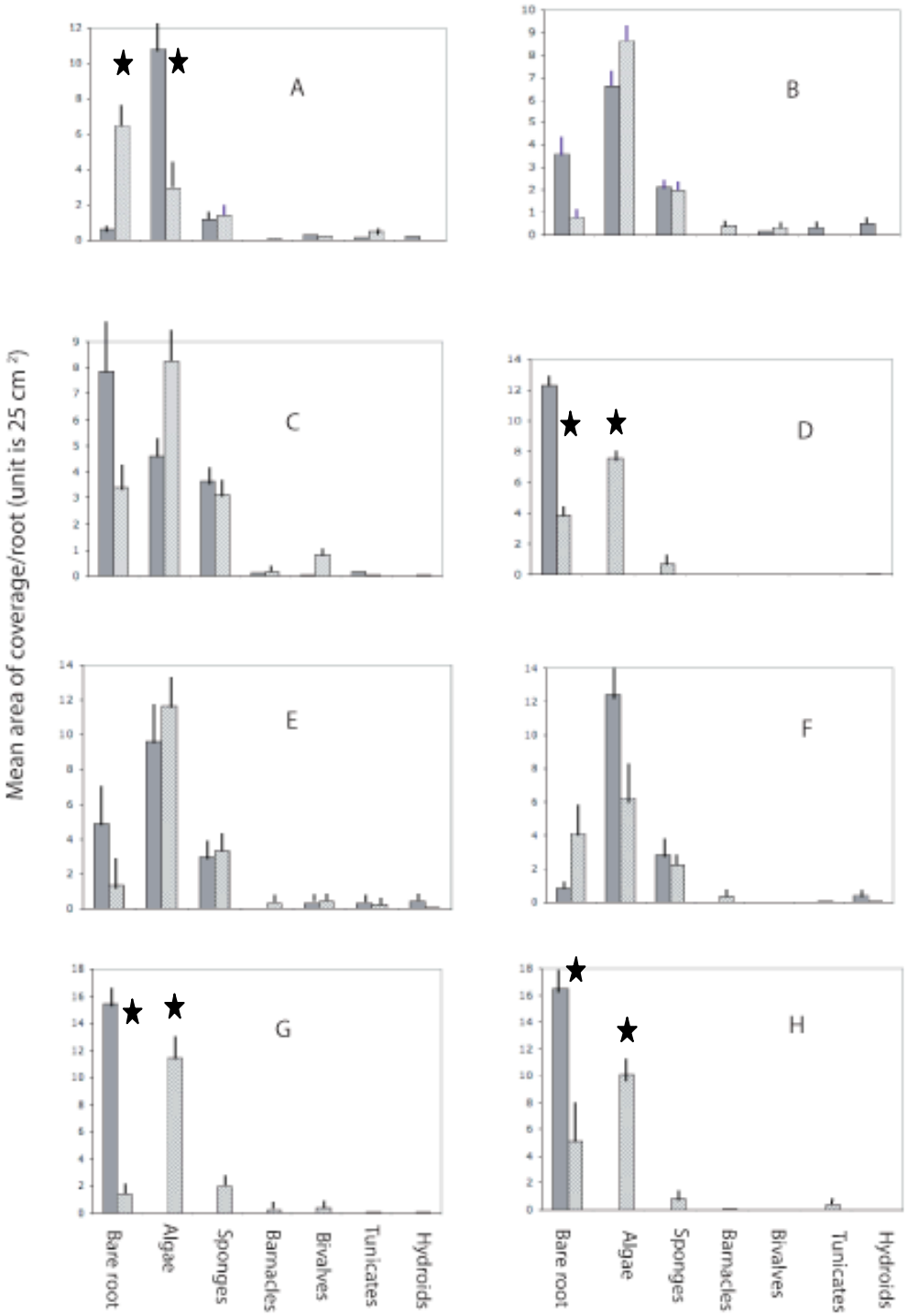


Figure V.3: Changes in epibiont cover/ treatment. A= closed screens, B=closed screen control, C= no cage, D= no cage-scrubbed, E=Wire, F= Wire-control, G=Wire-scrubbed, H= Wire-scrubbed, control. Dark bars indicate surveys before cage installation; light bars

indicate surveys after. Stars indicate significant differences in before/after groups for that taxa, and error bars are +/- 1 SE.

Discussion

The results of the caging experiment show that grazing by fishes or other motile fauna (As the cages excluded all sessile fauna, grazing by not only fishes but invertebrates such as echinoderms was limited as well) is not a significant factor in epibiont community structure on mangrove prop roots. This is in contrast to coral reef environments, where grazing exerts a large influence on algal cover (Mumby *et al.* 2006). In this experiment, for almost all epibiont taxa, there was no significant change in coverage after the installation of the cage. For those taxa where there were changes, the nature of those changes suggests that reduction in predation was not the cause. The results do show, however, that roots are colonized quickly when space is available, and that the epibiont community is somewhat fluid over time.

It is not surprising that predator exclusion cages had little effect on mangrove epibiont communities. In reef environments predation by fishes does seem to influence sponge diversity and distribution on reefs (Dunlap and Pawlik 1996, Wulff 1997, 2005). Mangroves in the study area did harbor known spongivores, including one specifically cited by Wulff, *Pomacanthus arcuatus*. However, Wulff (2005) also determined that mangroves in Belize are a refuge from predation for sponges, with competition between organisms a larger influence on benthic communities than predation.

For the most diverse epibiont group, sponges, there were no significant differences between communities before and after the introduction of the cage. Likewise,

while the epibiont community in Bocas Del Toro is extremely diverse and does vary extensively from one place to another (see chapter 2), there were not significant differences in the responses of uncaged roots to the time period of the study compared to caged roots. The overall difference in the MANOVA results, in fact, was driven by differences between roots that were scrubbed clean of epibionts at the start of the experiment, compared to all of those other roots in the experiment which were not. Sponges begin settlement and growth of colonies in less than three months, but excluding fish does nothing to encourage or discourage settlement and growth.

Algae, the most common epibiotic organism, showed a more distinct pattern of change as a result of the cages than sponges did. Like sponges, and unsurprisingly, algal coverage increased over the course of the experiment on roots which had been scrubbed clean. As the most common organism, it was not much time before algae began to grow on scrubbed roots. In fact, while the changes were not always significant, algae increased across the board, increasing substantially on uncaged roots as well as caged roots. Algae increased in all cases except for those roots enclosed by the fine mesh screen designed to keep out all fish. In those cages, algal cover decreased substantially, which was not the case in the controls for those cages, which had large holes cut in them. In those cases where algal cover decreased, it was replaced with bare root, not with another organism.

The lack of a replacement organism suggests that the algal die-off observed in the most intensively caged roots is the result of a reduction in the light level rather than evidence of a predation-induced effect. In previous cases where grazing by small grazers on algae (most fish in the study area are small) was a major factor, restrictions on those grazers should have led to an increase in algae (Power *et al.* 1985). The opposite occurred

here. Another possibility, that fish are a keystone predator on root organisms, is likewise ruled out; in that case another competitor already present on the roots should have taken over space from the algae (Paine 1969). Instead, the algae under the closed screens simply died, and increased when the screens had holes in them; greater access for grazers should not increase cover of algae if they are an important factor. (The small mesh would also have presented a strong barrier to further settlement of other organisms.) The screens with holes most likely allowed sufficient light for algal growth, while the closed screens did not, resulting in death of the algae. Epibiont diversity in general also increases with decreased turbidity, probably the result of increased light and primary productivity (Wulff 2005).

The last coverage type to change significantly over the course of the experiment, bare root, follows basically the opposite pattern observed in algae. Where algae increased, bare root decreased, and vice-versa. Scrubbed roots, which were completely bare at the beginning of the experiment, all showed a significant decrease in bare root after the experiment, with a corresponding significant increase in algae, and usually a small increase in other taxa, e.g. sponges. The increase in cover of other organisms comes at the expense of bare root, suggesting that epibionts tend mostly to expand into unoccupied space rather than crowding out other organisms. A similar pattern has been observed in corals (Muko *et al*. 2001). Hard substrate availability is the biggest limitation on coral reef algae and some other organisms (Dahl 1973).

Overall community measures-species richness, H', and overall epibiont abundance, only showed significant differences among roots that had been scrubbed clean before and after the experiment. As with the individual taxa, grazing does not seem

to have a major impact on diversity on individual roots. Furthermore, while differences in epibiont diversity do exist among individual roots, the differences are not noticeable except at larger scales, perhaps 50 roots instead of five (see chapter one). Again, as with individual taxa, there were some changes on the same roots over the course of the experiment, suggesting that epibiont communities are variable temporally as well as spatially. New species may settle on a root while others are lost over the course of months. Long-term stability of these communities is unknown; only longer term monitoring can determine if epibiont communities fluctuate around an equilibrium point or are genuinely constantly undergoing changes.

Conclusion

Overall, the results suggest that despite some predation on epibionts by fishes, such predation does not make a significant contribution to the structure of the epibiont community. Changes were observed over the course of the experiment in some taxa even on uncaged roots, suggesting that the prop-roots are fluid, frequently changing environment, at least over short temporal scales. These changes may have some relationship with the other organisms living among the prop-roots, but are probably not caused by motile grazing organisms. The experiments confirm that the relationship between fish and epibiont biomass and diversity is probably an effect on the fish community exerted by the epibionts rather than the other way round.

Chapter VI: Edge effects and influence of neighboring habitats

Introduction

Mangrove forests are one of the world's most endangered tropical habitats, cleared for development, agriculture, or aquaculture, or sometimes burned for firewood or charcoal (Ellison and Farnsworth 1996, Farnsworth and Ellison 1997, Valelia *et al.* 2001, Alongi 2002). The subsequent reduction of coastal protection can exacerbate natural disasters large and small, as in the Asian tsunami of 2004 (Danielsen *et al.* 2005, Kathiresean and Rajendran 2005, Granek and Ruttenberg 2007). The reduction of mangrove forest also reduces the area available as nursery grounds for several species of reef fish, potentially reducing populations of some species, including endangered and fishery species (Lindeman and DeMaria 2005, Dorenbosch *et al.* 2006, Barbier 2003, Dorenbosch *et al.* 2004a, Mumby *et al.* 2004).

A number of studies have compared communities in mangrove and cleared habitats. Granek and Frasier (2007) found that fish and invertebrate settlement was severely reduced in cleared vs. impact mangrove habitats. Comparison of fish assemblages between cleared and intact mangrove areas found severely reduced abundance and diversity of fishes in cleared areas (Huxham *et al.* 2004, Shinnaka *et al.* 2007). There is also a reduction in bacterial diversity and ecosystem processes in cleared mangroves compared to intact stands (Sjoling *et al.* 2005). The effects of deforestation also extend into nearby habitats, reducing fish biomass on nearby reefs (Mumby *et al.* 2004).

In many case of mangrove deforestation, particularly along the Central American coastline, rather than removing the entire forest, smaller sections of mangrove forest are removed, breaking extensive stands into patches and creating gaps in previously unbroken forest. While the above studies have conclusively demonstrated the deleterious effect of clear cutting mangroves, the impact of these gaps, or, for that matter, of naturally occurring gaps, on the community inhabiting nearby mangroves has not been examined. The impact of anthropogenic forces on surviving mangroves is a significant gap in existing knowledge, particularly as it applies to invertebrates (Ellison and Farnsworth 2001, Manson *et al*. 2005b, Ellison 2007).

One of the most direct consequences of habitat fragmentation is a change in conditions at the edge of the fragmented habitat where it grades into the next habitat, collectively known as edge effects. In many habitats, e.g. forests, conditions near the edge, especially if the adjacent area is open, will often be very different from the interior of a forest stand, due to penetration of sunlight, etc. Ecological edge effects are often deleterious, and can be abiotic, biotic, direct or indirect in nature (Murcia 1995). Edge effects seem to be very diverse, with variation among habitats and geographic areas. To date the vast majority of work that has been done on the topic has been done in terrestrial rather than aquatic or marine environments, and is often focused on birds (Meffe and Carroll 1997).

In marine environments, most of the work on edge effects has been done on seagrass or salt marshes. For instance, nekton densities in coastal wetlands tend to be highest closer to the water's edge rather than the interior of the marsh, a straightforward matter of access (Minello and Rozas 2002). Most of the seagrass studies have focused on

the effect of patch size, and found few consistent results across taxa or areas(Bell *et al.* 2001). Those that have focused on edge effects have focused on motile invertebrates rather than fish or epibionts, and have found either increased abundance of these organisms in edge habitats or tradeoffs between superior growth and predation (Bologna and Heck 1999, Tanner 2005). One study of edge effects and fish in seagrass did find that the strength of edge effects varied with patch size; fish diversity was slightly lower in edge regions of large seagrass patches, but more uniform in smaller patches (Jelbart *et al.* 2006).

In mangroves, naturally occurring fragmentation seems to increase abundance of fish and invertebrates; mangrove islands form a continuous patchwork landscape combined with intervening areas of coral and vegetation to create a better habitat than mangroves alone (Pittman *et al.* 2004). That study did not address edge dynamics within mangrove stands, nor did it address fringing mangroves, only islands. Likewise, conditions in mangroves in different positions relative to the reef have been studied, but edge effects within mangrove forests have not (Nagelkerken and Faunce 2007).

This study examined the effect of gaps and edges in mangrove stands by comparing fish and epibiont communities along a distance gradient along the mangrove fringe away from such gaps. The hypothesis was that there would be greater diversity and abundance of fishes closer to the edges of mangrove stands, and that edge communities would share unique characteristics distinct to edges. Fishes were also expected to be larger closer to edges, which were also closer to the reefs, than in the interior. Given greater light penetration along the edge, it was also hypothesized that prop-root epibiont communities would be dominated by algae to a greater extent in those areas. Given the

presence of both lagoonal and fringing mangroves in the study area, it was also hypothesized that fish and epibiont communities would be distinct, and less diverse in the turbid lagoon waters compared to the clearer waters of the outer fringe.

MATERIALS AND METHODS

VI.1 Study Sites

All edge surveys were conducted on Isla Utila, Honduras, a small island consisting primarily of mangrove-fringed lagoons, lowland flooded forest, and tropical savannah (Fig. 1). Settlement on the island is mostly restricted to the island's south-eastern corner, with the exception of a few resorts on the western end. The mangrove fringe has been essentially eradicated by human settlement outside the lagoons on the island's southern half. The interior and northern sides of the island are uninhabited, but some areas are in the process of being graded for potential future settlement. For the moment, the north side is only utilized by artisanal fishermen, gatherers, and crab or iguana hunters. The north side is dominated by natural beach and volcanic shoreline, but some inlets retain an extensive mangrove fringe. The mangrove forests surrounding the lagoons are very extensive (shaded area, figure 1), showing the complete gradient of Caribbean mangrove growth with *Rhizophora mangle* on the water, backed by black mangrove, *Avicennia germinans* and white mangrove (*Laguncularia racemosa* L) farthest inland.

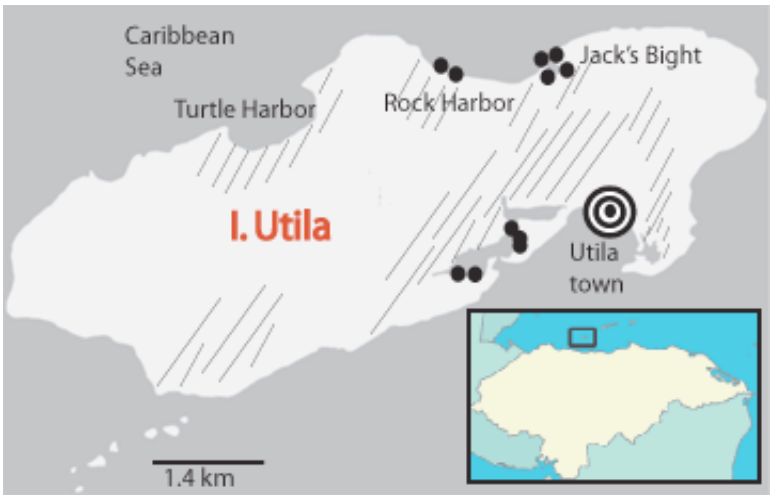


Figure VI.1 Map of Isla Utila, Honduras. Transect locations are indicated by dots; mangroves are indicated by diagonal lines.

In the lagoon sites, there were underwater weeds, but no complete seagrass beds; in fringing transects, *Thallassia testudinum* beds were immediately adjacent to the mangrove fringe, with no intervening mudflat. Offshore reefs were present immediately outside the lagoons and within 100 meters from the fringe. Underwater secchi visibility ranged from 3m to 5.3m, with a mean of 4.3 m. All sites were permanently submerged, although the tidal range was about 30cm. Detailed studies of salinity have not been conducted in Utila.

VI.2 Fish surveys

Five (2 X 85 m) belt transects were established in mangroves; three of these transects were established in fringing mangroves on the North shore; two were established inside the larger, Western lagoon. Each transect began at a break in the mangroves and extended away from the break along the mangrove edge into the middle of the unbroken mangrove stand. An additional shorter (2 X 40m) transect was

established deep in the interior of the western lagoon, away from any edge. Each transect was pre-marked in five meter increments using markers visible above and below the waterline; these markers were left in place for the duration of the study.

Fish were surveyed by means of underwater visual census (UVC) similar to that of (Nagelkerken *et al*. 2000c). All transects were surveyed 8 times on non-consecutive days between 1 July 1 and 26 August, 2007. Each UVC lasted 10 minutes. A single highly trained observer counted every fish observed inside each transect, identified each individual to species, and estimated total length using a reference ruler attached to a slate. The observer was the same throughout the study to keep observational bias consistent. A second observer accompanied the main observer and kept a separate count. The two counts were compared at the end of every survey and in the event of large discrepancies the count could be repeated on another day, although that situation never arose. Large aggregations were counted three times and the average number used. In order to avoid double counting, any fish that approached from behind was not included. Neither cryptic species (e.g. Syngnathidae spp., Gobiosocidae spp.) nor the ubiquitous schools of Atherinidae and Clupeidae were included in the census.

VI.3 Epibiont Surveys

In each transect, sessile organisms on the prop roots were surveyed on one root per meter of transect. A 50m logging tape was laid down the length of each transect (moved when necessary), and the root closest to each meter mark was selected, for a total of 85 roots/transect. The epibiont survey was always conducted after the fish census had been completed.

Root organisms were tentatively identified to the lowest taxon possible using keys provided by the Smithsonian Tropical Research Institute (STRI) and assistance from local experts. Species that could not be identified with confidence were classified as unknowns. Cyanobacteria were not identified to species and were considered as one taxon. Likewise, species confirmation of hydroids was not possible in all sites, so hydroids were treated as one taxon. The percent area covered by each species per root was measured using a framed grid of 5x5 cm squares (75 cm long x 10 cm wide). Each 25 cm^2 square was the base unit of measurement, and any measurements smaller than approximately 0.25 of a square were considered trace amounts.

VI.4 Abiotic Factors

In every site, depth, density of the roots, total thickness of the mangrove fringe (beyond the 2m width of the transect), and underwater secchi distance were measured. Utilan mangroves had high root density, ranging from 33 to 54 roots m^{-2}. Sites were aligned, due to geographic necessity, so that the segment nearest the break in the mangroves was also the segment closest to both reef and open ocean, so these measures were not separately measured. Distance from the mangrove edge to the seagrass was consistent both across and between sites.

VI.5 Statistical analysis

For both fish and root organisms, basic community statistics (Species Richness, total number of fish, fish biomass, Shannon-Weiner diversity index H', total area covered by

root organisms) were calculated for each 10m segment of transect and these statistics compared to one another by way of ANOVA. Average size (for fish) was also compared. Species Richness (SR) for fish was calculated twice; once utilizing all species (SR_{all}), and again excluding rare species (defined as those observed only once/transect over the duration of the study) SR_{comm}. The numbers of these rare species which were observed at each distance from the edge was also compared. These data met criteria for equality of variance and normality. In addition to comparing means for each distance bracket, these same community statistics were examined for linear change along the length of the distance gradient using linear regression. Adults and juveniles were further analyzed separately; juveniles were defined as being 1/3 or less of the total published length for the species (Nagelkerken and van der Velde 2002). Published lengths were acquired from fishbase, www.fishbase.org (Fraese and Pauly 2007).

From these studies it became apparent that there were consistent differences between lagoon and fringing sites; data from these respective areas were combined and each of the above criteria were compared using T-tests and Mann-Whitney U tests, depending on whether the variable was normally distributed or not. For these comparisons, the results of each census/site was the basic unit of comparison rather than results/5 m interval.

Community data were compared separately for fish and root organisms, after multiple CCA and NMMDS tests revealed no significant connection between the groups at this scale. Fish were divided into families and the biomass of each family calculated for each 5 m segment; biomass was used to counter distortion in numbers caused by the mangrove rivulus (Rivulidae), a small fish which collects into huge, unevenly distributed

schools. Root organisms were divided into suprageneric categories (e.g. Rhodophyta, Sponges) due to the preponderance of rare species). Fish and root organism communities along the edge- patch interior gradient were than separately compared by Bray-Curtis ordination using the Sorensen distance measure. These data were log-transformed to reduce stochasticity and ensure multivariate normality.

RESULTS:

VI.6 Species Composition and Abundance

4560 individuals from 40 species representing 19 families were observed over the course of the study. Greater abundance and diversity of fishes were found in the fringing mangroves; 2636 individuals from 37 species, representing 17 families, compared to 1934 total individuals from 22 species and 13 families inside the lagoon. Three species and two families were found exclusively within the lagoon, while 18 species and four families were found exclusively in the fringing mangroves. The fringe communities had a much higher percentage of families typically associated with reefs; the community was nearly 70 % composed of Lutjanidae (Snappers) Haemulidae (Grunts) and Pomacentridae (Damselfishes). The lagoon mangroves harboured a much higher percentage of muddy bottom associated species particularly Rivulidae (Rivulus) and Tetraodontidae (Puffers), although Lutjanidae were still common. Fish community composition is summarized in Table 1.

Table VI.1: Fish families found in both lagoon and fringing mangroves. Only species observed as part of the official census are included; other species were present.

	% of Total		Species Richness/Family	
Family	Fringe	Lagoon	fringe	lagoon
Lutjanidae	35.64	28.13	5	5
Labridae	7.96	0.57	3	2
Pomacentridae	20.41	0.27	4	2
Haemulidae	13.21	0.52	5	2
Sphyrenidae	1.75	2.84	1	1
Acanthuridae	3.24	0	1	0
Gerreidae	8.83	4.65	2	2
Sparidae	7.01	3.31	5	2
Chaetodonidae	1.41	0.05	3	1
Belonidae	0.19	0.05	1	1
Serranidae	0.0	0	1	0
Mureinidae	0.15	0	3	0
Tetraodontidae	0.08	6.05	1	1
Dasyatidae	0.04	0.05	1	1
Rivulidae	0	53.26	0	1
Centropomidae	0	0.31	0	1
Diodontidae	0.04	0	1	0

At the same time, 34 total species of sessile organisms were observed growing on the prop roots, from 10 suprageneric groups, of which 26 species were found exclusively on the fringing prop roots, while 20 were found in the lagoon. Eight of these were observed exclusively within the lagoon, and 14 were only observed on the fringe. The composition of both lagoon and fringing sessile communities is summarized in Table 2.

Table VI.2: Sessile taxa present on prop roots of both lagoon and fringing mangroves. Only species observed as part of the official epibiont census were included; other species were present.

Coverage type	% of total area		Species Richness/Taxa	
	Fringing Mangroves	lagoon	Fringing mangroves	lagoon
Bare	35.90	30.08	n/a	n/a
Green Algae	6.25	7.16	5	4
Rhodophyta	53.41	53.97	4	4
Sponges	2.22	4.16	12	5
Tunicates	0.97	0.00	2	0
Hydroids	1.13	0.79	1	1
Cyanobacteria	0.00	0.21	0	1
Molluscs	0.04	2.82	1	3
Crustaceans (barnacles)	0.00	0.08	0	1
Annelids	0.00	0.74	0	1
Phaeophyta	0.06	0.00	1	0

VI.7 Edge effects

The number of rare species was significantly higher in the 10 m closest to the edge (ANOVA $F_{10,7}$= 2.35, p≤ 0.03, Fig. 2). The identity and location of these species is shown in table 3. There were no significant differences in total fish abundance; fish abundance peaked between 30 and 40m from the edge, but this difference was not quite significant (ANOVA $F_{10,7}$= 2.07, p≤ 0.062). There were no significant or nearly significant differences in H' or biomass at any scale along the gradient. Among sites, there were significant differences (p≤ 0.001) between entire sites in all measures except H'; however in each case the two lagoon sites were much lower than the three fringing

sites, so these measures were compared again in a 2-way manner. In multivariate space, Bray-Curtis ordination extracted 69.28% of variance in 2 axes, and 83.67% in 3; fish communities aligned primarily by overall site and by lagoon or fringe rather than by distance from a gap (Fig. 3).

Figure VI.2: Rare species by distance from the mangrove stand boundary. Error bars represent +/- 1SD.

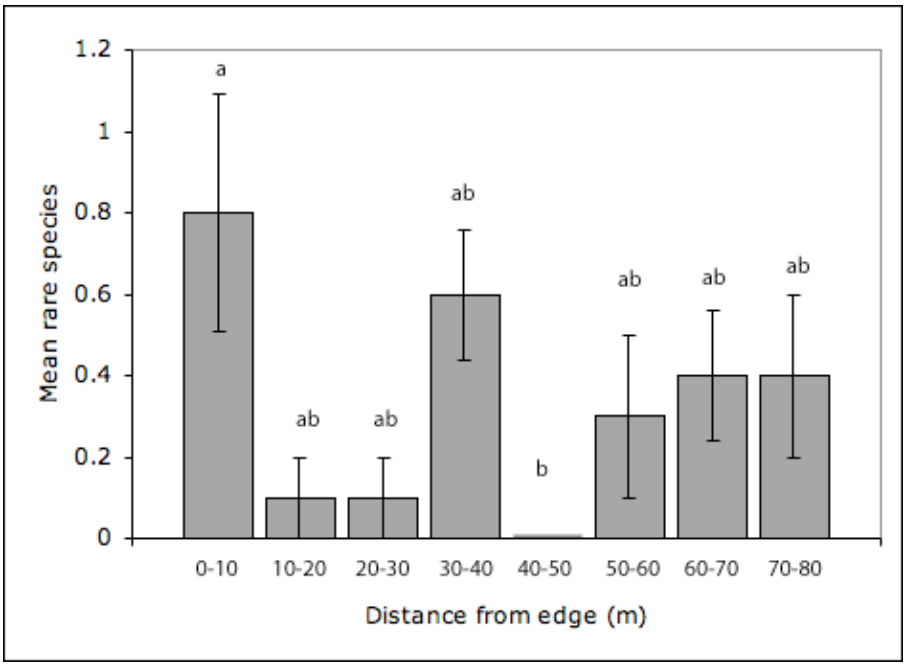


Table VI.3: Rare species. These species were not necessarily uncommon in the study area, and may have been observed in other transects, but were seen exactly once in at least one transect.

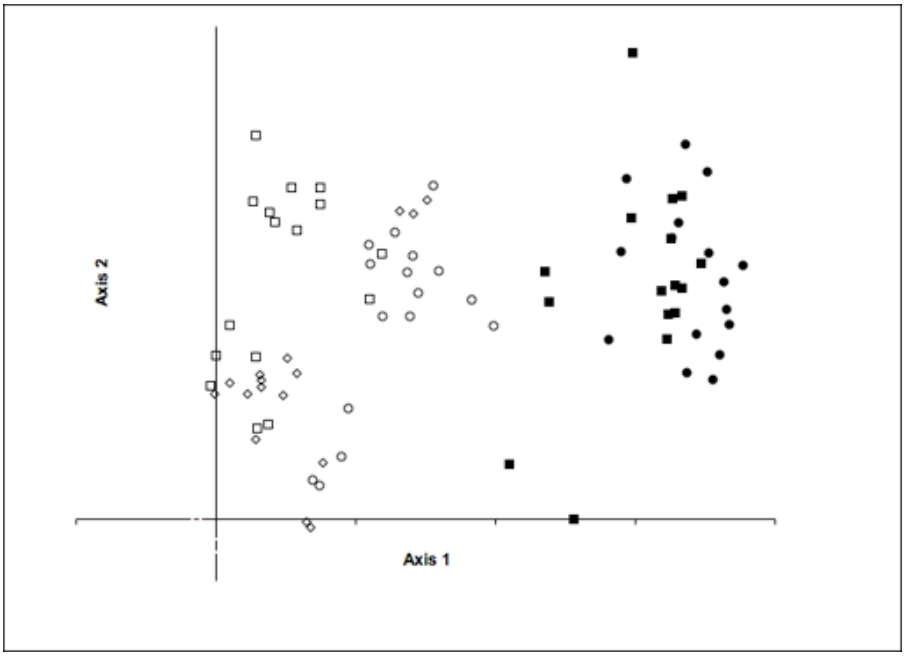
Species Common	Species Latin	Position relative to edge (m)	lagoon/ Fringe	Typical habitat*
Cubera snapper	Lutjanus cyanopterus	10--15	L	mangrove
Yellowtail snapper	Ocyurus chrysurus	30-35	F	seagrass; weeds
Lane snapper	Lutjanus synagris	35-40	F	seagrass
Sailor's grunt	Haemulon parra	0-5	F	seagrass
Bluestripe grunt	Haemulon sciurus	0-5	F	mangrove, seagrass
French grunt	Haemulon flavolineatum	75-80	L	mangrove, seagrass
White grunt	Haemulon plumerii	35-40	F	seagrass
Yellowfin Mojarra	Gerres cinereus	0-5	F	seagrass, mangrove, sand
Flagfin Mojarra	Eucinostomus melanopterus	30-35;50-55	Both	mud,sand
Banded butterflyfish	Chaetodon striatus	0-5	F	reef
Foureye butterflyfish	Chaetodon capistratus	40-45	L	Reef †
Puddingwife	Halichoeres radiatus	0-5	F	reef
Slippery dick	Halichoeres bivitattus	70-75	F	reef, rocky shore, seagrass
Needlefish	Strongylura marina	20-25, 65-70	F	any shallow
Yellowtail parrotfish	Sparisoma rubripenne	30-35	F	Seagrass
Chalk bass	Serranus tortugarum	0-5	F	Seagrass
Mangrove rivulus	Rivulus marmoratus	75-80	L	Mangrove

Purplemouth moray	Gymnothorax vicinus	65-70	F	reef, rocky shore
Porcupine fish	Diodon hystrix	75-80	F	Reef
Cocoa damselfish	Pomacentrus variabilis	5--10	F	Reef
Southern Stingray	Dasyatis americanus	0-5, 60-65	0-5L; 60-65F	sandy bottom

* Refers to typical habitat of the life stage observed

† Considered to be a reef or back reef species, but commonly observed in mangroves in several areas (MacDonald and Weis, in review).

Figure VI.3: Bray-Curtis Ordination plot of fish species/5 m segment of mangrove. Different shapes represent different sites; open dots represent fringing sites, closed dots represent lagoon sites. Samples orient first by site and secondarily by Fringe or lagoon.



VI.8 Regression

When the same statistics were examined across the gradient using linear regression, after adjusting for colinearity distance was found to have a significant influence on two of them. SR_{all}, and total fish abundance both decreased linearly as distance from the edge increased. The trend was quite weak, explaining only 20% of variance in SR, although it explained nearly 45% of variance in abundance (SR: Linear regression, R^2=.20, p≤ .05, n=16. Abundance: R^2=.44, p≤ .01, fig. 4). Biomass also decreased in this manner but was not quite significant (R^2=.213, p≤ .07). In all of these cases the ratio of juvenile/adult fish stayed fairly constant (fig. 4). In both cases the slope of the regression line was shallow, indicating only slow changes along the gradient (fig. 4.) Regression of average size of fish/ distance showed significant results only in the most common family, the Lutjanidae. Average Lutjanid size increased significantly as distance to the edge decreased, particularly at the 10 m scale (Linear Regression: 5 m scale, R^2 = .488, p ≤ .0001, n=16. 10 m scale: R^2= .9343, p≤ .003, n= 8). No other family showed a significant change in size along the gradient, but most families were not as consistently present as the Lutjanidae.

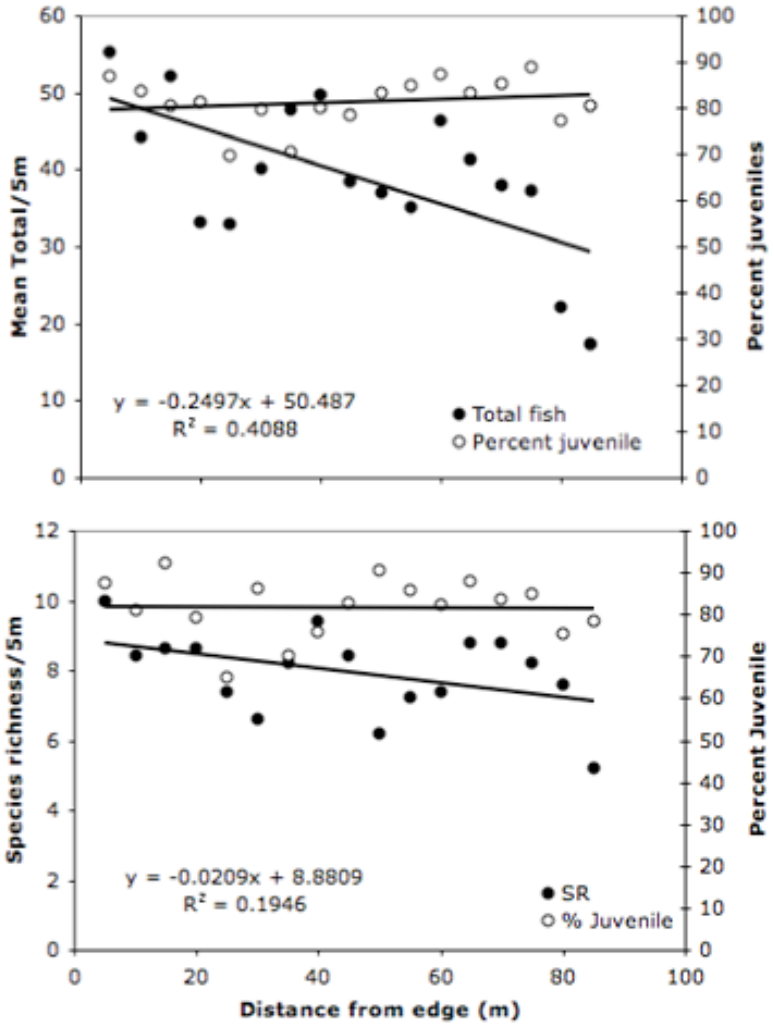


Figure VI.4: Linear regression of Fish Species Richness (Bottom) and abundance (top) by distance away from the mangrove boundary. Open circles indicate the percentage of each representing juveniles.

VI.9 Age Classes

The trends were virtually identical when juveniles and adults were considered separately as they were in the overall fish community. There were no significant differences in most measures closest to the edge, and for both juveniles and adults SR and abundance

decreased with increasing distance from the edge. All of the rare species individuals were juveniles.

VI.10 Root organisms

There were no significant differences in any of the measures of root organism abundance or diversity based on proximity to forest gaps. There were significant differences based on site (ANOVA $F_{16,4}$= 2.63-6.16, p≤ 0.001-0.04 depending on measurement, Table 1) although there was no clear lagoon v. fringe dichotomy. In multivariate space, Bray Curtis Ordination extracted 52.59% of variance in 2 axes, 74.16% in 3 axes. Unlike fish, however, observations did not cluster in distinct groups either by distance or by site (Fig. 5). Also unlike fish, linear regression did not show a linear increase or decrease along the distance gradient in any category or any epibiont taxa (typical R^2= .02).

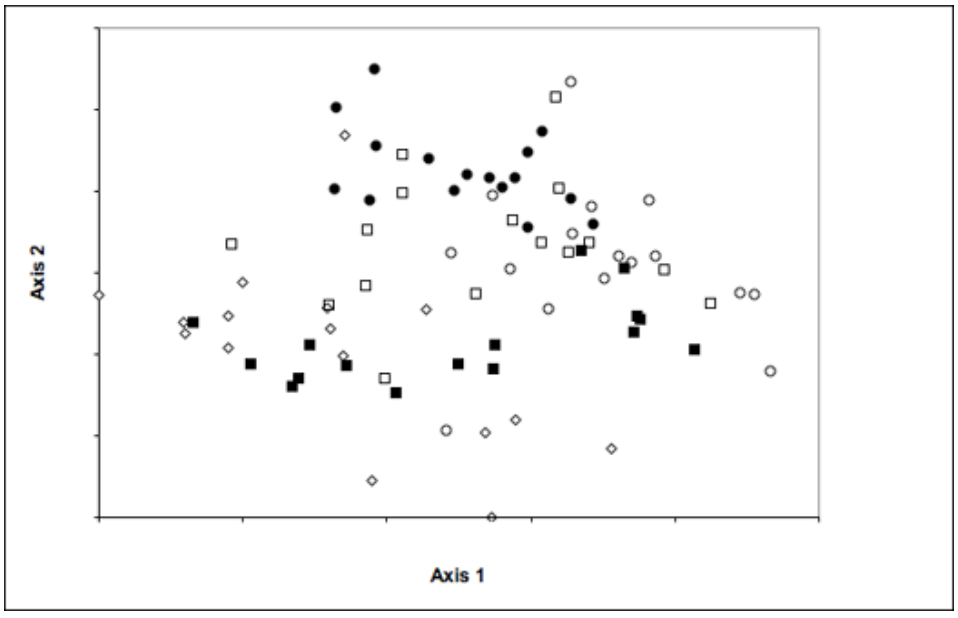


Figure VI.5: Bray curtis ordination plot of sessile prop-root organisms. Different shapes represent different sites; open dots indicate fringing sites, while closed dots indicate

lagoon sites. Lagoon sites separate by location along Axis 2; fringing sites show few distinctions. Lagoon v. fringe sites do not segregate coherently.

VI.11 Lagoon v. Fringe Comparison

For every diversity and abundance measure tested, fringing mangroves were significantly higher than the lagoon sites (SR_{all}, T Test, $p \leq 0.001$; SR_{comm}, Mann Whitney U test $p \leq 0.001$; Total fish, T- Test, $p \leq 0.001$; H' T Test, $p \leq 0.001$, Fish biomass, Mann Whitney U-Test $p \leq 0.02$. n= 48 fringe, 40 lagoon, Fig. 6). Root organisms, as observed in multivariate space, did not vary significantly between fringing mangroves and the lagoon in any measure of diversity or abundance/5m, (average $p \leq 0.6$), although while sponge diversity was higher in fringing mangroves and sponge area was proportionally higher in the lagoon.

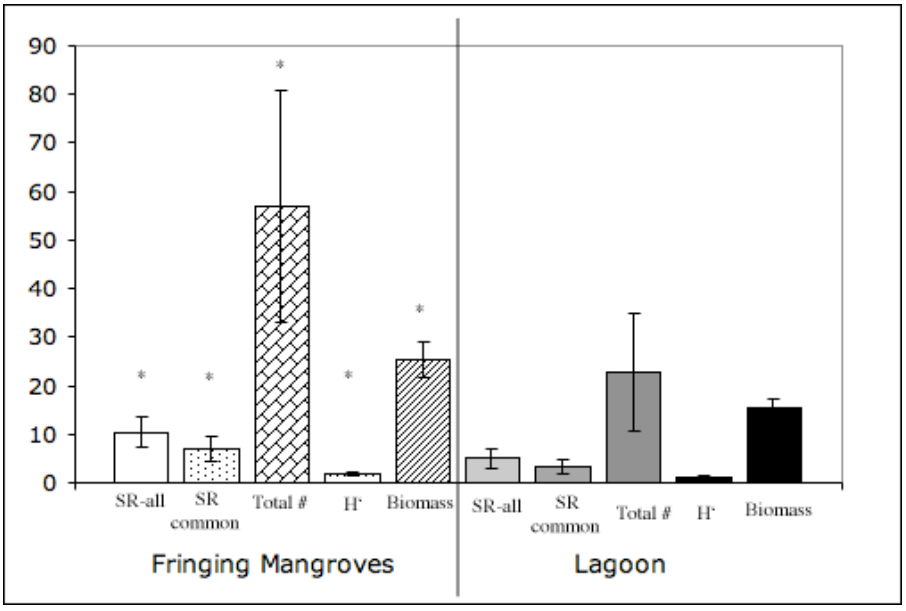


Figure VI.6: Fish community measurements by lagoon/fringe. Stars indicate significant differences between the 2 types; fringing sites were significantly higher for every measurement. Error bars indicate +/` 1 standard deviation.

VI.12 Abiotic factors

Neither depth nor density explained any appreciable amount of variation in fish or root species richness or abundance (Linear regression, average R^2= .005). Distance to reef and open ocean are covered in the results of the edge-interior gradient. Secchi distance was, not surprisingly, significantly higher in the fringing mangroves, averaging 9.85 m as opposed to 5.9m (2 sample T-test, $p \leq 0.001$, n=24).

DISCUSSION

VI.13 Fishes

The results of this study did not entirely support the hypothesis that fish diversity would be substantially higher along mangrove forest edges than in the interior of patches. It was likewise unexpected that communities of fish and epibionts on edges were more dissimilar to one another than to communities from patch interiors. The lack of consistency in root epibiont communities was also contrary to the hypotheses. The only result that did confirm the hypotheses was the higher incidence of rare fish closer to the forest edge. Nevertheless, the continuous nature of the gradient as evidenced by linear regression implies that edge effects do have an impact in mangroves but it is gradual; there is influence of the edge region farther into the forest than just the immediate forest-edge boundary.

The higher diversity along the forest-gap boundary is driven to a large extent by species that are primarily found in other habitats. There is already evidence that species assemblages in one habitat may be affected by neighboring habitats. Dorenbosch *et al.* (2005b) found a greater incidence of reef-associated and generalist species along the

seagrass/reef interface, and more purely seagrass associated species in the interior of the grass beds. Mangrove species are also more common in seagrass that is nearer to mangroves(Jelbart *et al*. 2007). In this study, the identity of the "visitor" species was determined by what sort of habitat was adjacent. The fringing mangroves were adjacent to coral rubble and patch reef and the edges had reef-associated species such as puddingwife (Labridae) *Halichoeres radiatus*, or banded butterflyfish *Chaetodon striatus*. In the lagoon, where the edges were adjacent to mud flats, species known to forage in mud flats such as the southern stingray *Dayatis americanus* were more common.

Beyond the immediate edge, the decrease in species present was very gradual, for both adult and juvenile fish. Even away from the edge, much of the diversity was still driven by species normally associated with other habitats. This study only dealt along the accessible outer 2 meters of the mangrove forest; on some level the entire study area is "edge" habitat, and certainly neighboring habitats (seagrass and mudflats) may have some influence on the outer levels of the mangrove forest at any point along the gradient. Pilot data taken in Panama suggests that the true interior of the forest- the back of the forest towards the upland areas- may not be very different from the outer reaches so long as there is sufficient water, but this awaits confirmation, and studies in the depths of the mangroves are difficult, dangerous and time consuming.

Likewise, the increasing biomass and, in the case of the Lutjanidae, average size, as distance from the edge decreased was also expected because of the influence of other habitats. The configuration of the forest gaps in Utila meant that the transects were not only oriented away from a gap, but also away from the nearest reef (or lagoon mouth for

those sites). Many Lutjanidae are believed to undergo ontogenetic diet and habitat shifts, moving away from nursery habitats toward the reef when a certain size is reached (Cocheret de la Moriniere *et al.* 2002, Cocheret de la Moriniere *et al*. 2003a). The increasing size of individuals, partially driven by a decrease in juveniles, is consistent with such a shift (Dorenbosch *et al.* 2005b). It was not expected, nor was it observed, to see any changes along the gradient in the size of fishes that do not move to the reef, e.g. the Gerreidae. In other families, such as the Haemulidae, such a shift was expected, but was not observed, most likely due to the inconsistent distribution of these species along the gradient. Large predators, particularly *Sphyraena barracuda*, showed no pattern as large juveniles and the occasional adult hunted throughout the mangrove/seagrass interface.

It was also contrary to expectations that the percentage of juveniles did not increase as distance into the patch increased, which was also seen in the 2005 Dorenbosch study. Interior habitat may be better nursery habitat for some species, due to increased predation risk closer to the edge (Fagan *et al*. 1999) . However, most evidence for increased predation risks on an edge comes from terrestrial systems, an exception being increased predation on scallops (Bologna and Heck 1999). Smaller juveniles would be furthest from making an ontogenetic shift to the reef, and thus could be expected to be concentrated further from the adult habitat. The fact that this did not happen suggests that the characteristics that make mangroves into a desirable nursery habitat are not enhanced any farther into a secondary patch. The constant juvenile/adult ratio also suggests that conditions are equally unfavorable for juveniles as adults as distance from the edge increases, although overall there are more juveniles. As noted above, the even

distribution of juveniles suggests a gradual shift toward the reef and out of the mangroves; as size increases, individuals slowly shift toward the mangrove edge, rather than departing abruptly upon attainment of maturity.

Dorenbosch (2005) also observed differences in fish densities depending on distance relative to the reef or seagrass edge, but found that rather than overall differences the positional densities varied depending upon the type of fish. The difference in the mangroves was not significant in a static sense; it only became apparent in this system as a gradual increase. The presence of rare species in the edge regions is not sufficient to explain the difference, and no particular type of species was particularly abundant in edge areas to explain the difference. Nevertheless, as in Dorenbosch (2005), many nursery species, e.g. Haemulidae, did peak in the interior of the fringe rather than the edge, while a greater variety of species were more abundant near the edge. The greater diversity and abundance at the edge of these large mangrove stands is contrary to what Jelbart *et al.* (2006) observed in seagrass. Predation is generally higher along patch edges leading to a more inhospitable environment for fish (Hovel 2003). More research is necessary to be certain, but it is possible that the greater resources available where more habitats intersect supports a greater abundance of fish, despite any presumed predation risk. It also seems that mangroves are not completely analogous to seagrass in this respect.

It was surprising that edge fish assemblages did not have any common features in multivariate analysis. As discussed above, more species from adjacent habitats (e.g. reef) are present in the edge regions, presumably leading to a distinct edge assemblage made up of species from multiple habitats. It would be expected that communities in lagoon

edges would cluster together, and those of fringing edges would cluster together as in both those cases the edges are adjacent to similar habitats. This was not the case, and entire transects were more closely associated than different edges were to one another, even though in some cases the edge zones were physically closer to one another than each edge was to the opposite end of its transect. However, a study of infaunal assemblages on a similar scale to this study found that larger scale processes had a larger effect on seagrass species assemblages than edge effects did (Bowden *et al*. 2001). It certainly seems to be the case here that large scale processes affecting the species composition of a given mangrove stand (e.g. settlement) take precedence over within-patch effects. The large variation in responses to patch size and edge may also reduce similarity between different locations (Bell *et al*. 2001). In this case all of the mangrove patch sizes were very large (200 m minimum, usually several km in length), so differences in patch size were not a factor.

VI.14 Prop-root Organisms

Unlike the fish community, there were few differences in prop-root epibionts along the gradient. This was partially to be expected, in that sessile organisms cannot easily move back and forth between habitats. Individuals that typically reside in particular habitat type are adapted to that habitat and will typically settle there. When sessile organisms settle in environments other than the one to which they are adapted (e.g. prop roots instead of corals) most likely they will quickly be out-competed by the natives (Wulff 2005). Nevertheless, variation in physical conditions along the gradient, particularly near the cut, should have been sufficient to favor certain organisms, especially the omnipresent Rhododphyta. The opening of the mangrove forest increases

light penetration and should favor algae (Chapter 4; MacDonald and Weis in review). Not only was there no notable difference in algal cover closer to the edge of the gaps, but there was no appreciable increase in overall epibiont cover either, as should have been encouraged by greater light. One possibility, especially inside the lagoon, is that an increase in turbidity near the gaps caused by greater sedimentation from terrestrial sources counteracted any increased light penetration.

There has been little study of edge effects on sessile marine organisms. (Airoldi 2003) did find that increasing distance from a patch edge did impact the colonization of certain algal species (but not limpets), although that study took place in much smaller patches, and also suggested that algal density ought to be higher near the edge. The conclusion from the present study is that conditions in the interior of a mangrove stand are as conducive to epibiont growth and diversity as conditions near the edge.

This study also demonstrates that scale has a significant influence on the outcome. Trends that are very evident at the scale of an entire 40 m transect do not automatically apply at 5 m increments. For instance, clear correlation between epibionts and fish diversity/biomass discussed in (chapters 1-3; MacDonald and Weis 2007) was simply not evident in 5m increments. Likewise, depth and density of prop-roots, which were shown to influence fish communities and behavior in previous studies (Cocheret de la Moriniere *et al*. 2004, Ellis and Bell 2004, MacDonald and Weis 2007) were not observed at this scale. Part of the problem is that in general, small scale examination of highly mobile organisms such as fish is prone to variation and error as the fish move; this makes snapshot examinations of fish on this level, even repeated observations, inherently risky. The same is not true for sessile organisms; However, for some, there is no evidence that

increased sampling extent affects results. Epiphytic biomass, for instance, has been found to be constant across a wide range of scales, although measures such as diversity typically vary with the scale of the study (Moore and Fairweather 2006).

VI.15 Lagoon v. Fringing Mangroves

The distinct communities of the lagoon and fringing sites was not unexpected. For one thing, the surrounding habitat has a large effect on species composition of motile fauna within a given habitat patch (Tanner 2006, Jelbart *et al.* 2007); the lagoon mangroves are surrounded mostly by mud and some seagrass, where the fringing mangroves are surrounded by more contiguous grass beds and coral. Another consideration is that physical conditions in the lagoon, particularly turbidity, are very different from the fringe. Visibility in the lagoon was much lower, (but was sufficient to see clearly across the width of the transect even at its worst). The census indicated different species, e.g. more Tetraodontids (not analyzed) and Rivulus in the lagoon, compared with more Haemulidae and Labridae in the fringing mangroves. These differences were reflected in the multivariate analysis.

Likewise, the lagoon did not impact root epifauna to nearly the same degree as it did the fish fauna. Diversity and abundance in the lagoon, with the exception of sponge species richness, was comparable to that of fringing mangroves. There were also no distinct lagoon/ fringe epibiont community trends; species overlap was such that ordination had only limited success separating the transect segments, either by distance from the edge or by lagoon/fringe distinctiveness. This lends weight to the argument that light penetration alone does not determine algal growth; total algal coverage in the two

habitat types was very similar in the lagoon and the fringe, despite vastly higher turbidity inside the muddy lagoon. In fact, despite a few differences in species, most taxa were quite evenly matched both inside and outside the lagoon.

Conclusion

Even with the clear gradients in fish abundance and diversity, it is difficult to say with certainty that the observed trends are not responses to other factors. As noted above, due to an accident of geography in four out of five cases distance away from the edge also corresponded to distance away from the reef, and it can not be determined which trends might be a result of which condition. Furthermore, of the trends demonstrated by linear regression, only 45% of variance was explained by distance from the edge, so clearly other factors are involved as well, which await discovery.

Chapter VII: Inter-mangrove movements and behavior of common species

INTRODUCTION

Mangroves are known to harbor many species of juvenile fish, and are believed to be important habitats for maintaining fish populations on reefs (Parrish 1989, Dorenbosch *et al*. 2004a, Mumby *et al*. 2004, Dorenbosch *et al*. 2005a). In the Caribbean, juveniles of the genus *Lutjanus* and *Haemulon* are especially abundant (Nagelkerken and van der Velde 2002). Juveniles settle in shallow, near shore habitats, often mangroves; smaller juveniles 70 mm or less of some species have been found almost exclusively in mangroves (Rooker 1995). With growth they undergo ontogenetic diet shifts and seem to be found mostly on reefs as adults ((Rooker 1995, Cocheret de la Moriniere *et al*. 2002). Full maturity is reached at about 30 cm TL. Spawning occurs offshore.

Some research suggests that for some species, e.g. the schoolmaster snapper *L. apodus*, the dependence on mangroves for part of its life cycle may be obligate (Nagelkerken *et al*. 2002, Halpern 2004). While *L. apodus* and other reef fish species preferentially use mangrove habitats as juveniles, not all mangroves are equally valuable in this regard (Chittaro *et al*. 2005b). Abundance of fish may vary considerably among nearby mangrove stands.

How fish actually utilize this habitat is not entirely clear. Within the mangroves, the behavior and movement of juvenile fish is not very well known. So far, it has been difficult to link individual adults found on a particular reef to a particular mangrove stand as juvenile habitat, if such a link exists. There is some evidence that movement in some species is size-dependent; a study of *Lutjanus argentimaculatus* , indicated that smaller

fish travel smaller distances than larger fish (Russell and McDougall 2005), but in general there is little information on this topic. The majority of individuals in that study, regardless of habitat studied, did not move more than a kilometer, although some shifted habitats from salt or brackish into fresher water (Russell and McDougall 2005). In contrast, adult red snapper, *Lutjanus campechanus* moved long distances, up to hundreds of kilometers (Patterson *et al*. 2001). Studies suggest that for some fish species, adults do not travel far from their recruitment estuary (Gillanders 2002).

There have been a few studies that observed marked individuals in an attempt to understand between- and within-habitat movements. All of these found evidence of site fidelity in juvenile Lutjanidae and Haemulonidae, although two of these studies were very short term (Watson *et al*. 2002, Dorenbosch *et al*. 2004b, Verweij and Nagelkerken 2007, Verweij *et al*. 2007). Many reef fishes do exhibit high site fidelity over the long term, partially as a result of unwillingness to traverse open areas (Chapman and Kramer 2000, Jones 2005). Some species utilize an extremely small area, less than 1 m^2 (Luckhurst and Luckhurst 1978b). In mangroves, site-fidelity was also observed in various species of fishes in Indonesia (Weis and Weis 2004).

For the most part, it is not well known whether fish travel extensively within the mangrove fringe. This study used mark and recapture techniques to track the movement of juvenile *Lutjanus apodus* and some other species in fringing mangroves and seagrass in Bocas Del Toro, Caribbean Panama, hypothesizing that juvenile fish would move little within mangroves.

MATERIALS AND METHODS

VII.1 Study Site:

The study was conducted in Isla Colon, Bocas Del Toro Province, in northeastern Panama. Located at the edge of the Bahia Almirante, Colon is the main island and population capital of the Bocas Del Toro Archipelago. Most of the island facing the bay is fringed with mangrove forests of varying ages and expanse; clearing of mangroves for agriculture and tourist development is widespread. The study was conducted in the Southwestern part of the island, facing the bay, in fringing mangroves (mostly unbroken except for the occasional dock) about 4 kilometers outside of the area's main town (Fig. 1).

FIGURE VII.1: Map of Bocas Del Toro, Panama, with tagging location highlighted.

VII.2 Mark/recapture

Juvenile reef fish, primarily *L. apodus*, were captured and released in a 40 meter stretch of fringing mangroves, as well as in associated seagrass habitats. (The nearest reef was in a boating corridor and not suitable for trapping; two pilot traps caught only cardinalfish *Apogon* spp.) Individuals were captured with two types of gear; 1.) collapsible 45 X 24 X 24 cm minnow traps with 6 cm openings, set every 4 m underneath overhanging roots and branches at the mangrove-seagrass interface or in the seagrass between 2 m and 10 m from the interface, and 2.) a small fyke net -wings 6.1 meter on either side of a 0.61 m funnel. Each wing of the fyke net was anchored to solid prop roots 5 m apart behind the overhanging branches and roots so that the entire set up created a 5 X 6.1 m isosceles triangle of net directing any fish leaving the mangroves toward the funnel net. 60% of the trapping effort was dedicated to mangroves and 40% to seagrass (the fyke net was not suitable for seagrass). All sampling was conducted between May 24 and August 20, 2006. Captured fish were measured, tagged subcutaneously with injections of acrylic paint (Lotrich and Meredith 1974) and released exactly where they were caught. Recaptured individuals were marked again with each subsequent re-capture. The marks were placed in the tissue immediately beneath the dorsal fin. A unique combination of color with the position and shape (e.g. left side, towards front, oblong) allowed fish to be identified either individually or narrowed the possibilities to within two. Specific combinations of color, position and shape were assigned to specific capture locations; only fluorescent colors were used in order to make the marks visible under water. The study area was marked off in 5m increments to make distance estimations more accurate.

When Catch Per Unit Effort (CPUE) reached zero for three consecutive days for a given trap, the trap was moved within a 1 m radius of its previous location. Every 2 days the fyke net was moved 5 m along the study area, and when it reached the end of the study area it was moved in the other direction. All traps and nets were examined and emptied twice daily.

To supplement the trapping, especially given low CPUE, every 10 days the study area was surveyed by snorkel, weather permitting, for a total of eight daytime and three night surveys. A single observer divided the 40 m area into a 2 X 40 m belt transect and very slowly swam the length of the transect, noting marked fish and all others of marked species observed during the transects. Sizes were estimated using a reference ruler attached to a slate. When a marked fish was encountered, the observer kept observing the fish until the color and arrangement of the tag had been positively identified before moving further along the transect. These surveys were conducted only on clear days when visibility was sufficient to observe the tagged fish.

VII.3 Data analysis:

Re-captured or observed individuals were used to estimate the maximum distance traveled since last capture or observation based upon the location of each capture. The amount of time since the last capture or observation was also noted. In cases where it was not possible to determine exactly which individual was captured, the most conservative (largest possible difference, most recent capture) estimate was used. Due to the low number of individuals repeatedly recaptured, home range could not be calculated.

RESULTS

Thirteen species were captured in either type of gear over the course of the survey, five of which- *Haemulon parra*, *Haemulon sciurus*, *Gerres cinerreous*, *Lutjanus apodus*, and *Lutjanus synagris* were tagged. The gear and capture location of each species is summarized in Table 1. Tagged individuals ranged between 4 and 24 cm TL, with a mean of 9.1 cm. The vast majority of tagged individuals were less than 12 cm TL, with only 5 individuals 15 cm or larger. The largest individual to be re-sighted or recaptured was 14 cm TL.

Table VII.1:Total capture events and sightings, including recaptures and resightings, arranged by gear and species. Observed numbers include all individuals of noted species observed during visual census, both tagged and untagged. Species not in bold were non-target species that were not marked.

			Gear		
Species (common)	Species (Latin)	Location	Traps	Fyke Net	Observed
Schoolmaster	***L. apodus***	**Mangrove**	**37 §**	**28**	**87**
Lane Snapper	***L. synagris***	**Mangrove/seagrass**	**12**	**1**	**2**
Sailor's grunt	***H. parra***	**Mangrove**	**6**	**9**	**5**
Bluestriped grunt	***H. sciurus***	**Mangrove/seagrass**	**7**	**3**	**4**
Yellowfin Mojarra	***G. cinereous***	**Mangrove**	**3**	**2**	**7**
Green Moray	*Gymnothorax funebris*	Mangrove	0	2	Not surveyed
Tonguefish	*Symphurus sp.*	Mangrove	1	0	Not surveyed
Striped parrotfish	*Scarus iseri*	Mangrove	1	0	Not surveyed
Barbfish	*Scorpaena*	Mangrove	3	0	Not

	brasiliensis				surveyed
Barracuda	*Sphyraena barracuda*	Mangrove	1	6	Not surveyed
Toadfish	*Amphichthys cryptocentrus*	Seagrass	4	0	Not surveyed

§ Includes 2 injured or small individuals that were not marked

Among the tagged species, the most commonly tagged and recaptured species was *L. apodus*. Of 47 different individual *L. apodus* marked, 29, or 61%, were recaptured or observed at least once during the study period. In contrast, of 13 individual *L. synagris* tagged, zero were recaptured. The recapture statistics for each tagged species are summarized in Table 2. Of these 29 *L apodus*, six were captured or re-sighted three times, four were captured four times, and two were captured five times in 58 total recapture events.

Table VII.2: Mark/recapture results for all species

Species	**Number Tagged**	**Number / % recaptured or observed**	**1 recapture**	**2 recaptures**	**3+ recaptures**
L. apodus	47	29 (61)	17	6	6
L. synagris	13	0 (0)	0	0	0
H. parra	12	4 (33.3)	4	0*	0*
H. sciurus	7	3 (42.8)	3	1	0
G. cinereous	4	2 (50)	2	0	0
Total	83	38(45.8)	26	7	6

- includes an individual observed to be preyed upon right after the first recapture

VII.4 Catch Per Unit Effort:

CPUE was very low: CPUE was only 0.792 fish/gear item/day during the study period. No marked individuals were observed anywhere but the mangrove fringe. CPUE for all gear declined over the course of the study period, with the sharpest decreases in trap efficiency; daylight visual observations stayed fairly constant (Fig. 2). Nighttime visual census noted exactly two *L. apodus*, both untagged, one in mangroves, and one in seagrass. No other target species were observed during nighttime census.

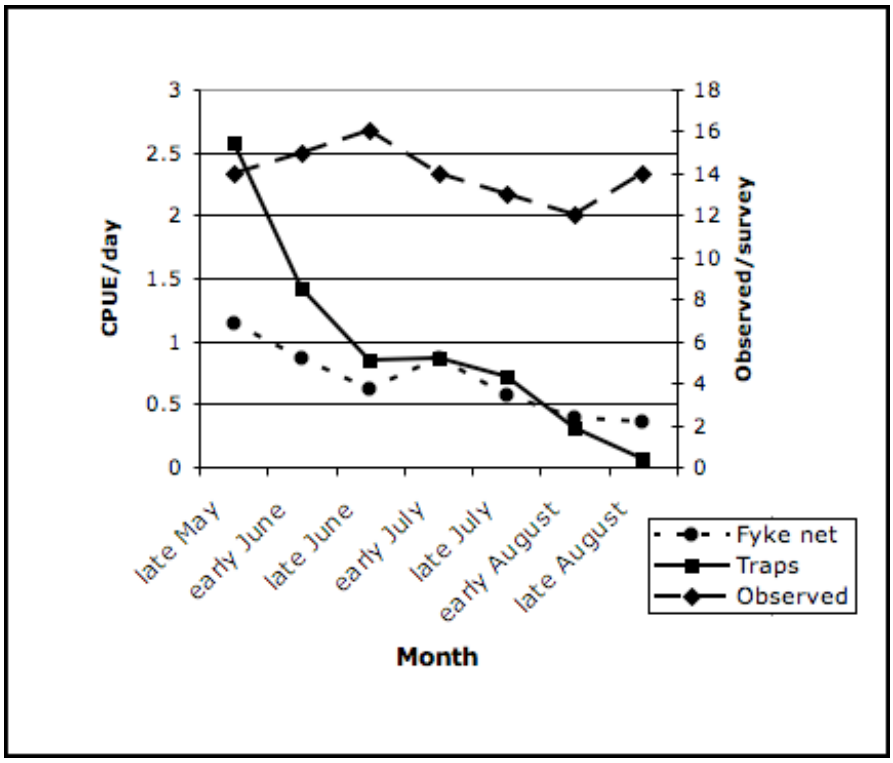


Figure VII.2: Catch Per Unit Effort (days) and observations/survey over time.

VII.5 Distance travelled

The majority (79%) of juvenile *L. apodus* were recaptured within five meters of their release location (Fig. 3). The mean maximum distance traveled was 4.06 meters, the longest observed distance was 10 meters, and the shortest was one meter. Those individuals that were recaptured twice or more had a higher mean maximum distance

traveled, 6.17 meters. The difference was significant (Mann-Whitney U test, $p \leq 0.0012$, n= 17 recaptured 1 time, 12 recaptured 2+ times). Other species travelled even shorter distances between captures, averaging 2.2 m (Fig. 3).

VII.6 Persistence Time

The mean number of days between first and last capture in *L. apodus* was 22.9 days; the shortest interval was one day and the longest was 85 days (Fig. 4) Other species generally had fewer captures with shorter intervals in between (Mean = 8.2 days, Fig. 4).

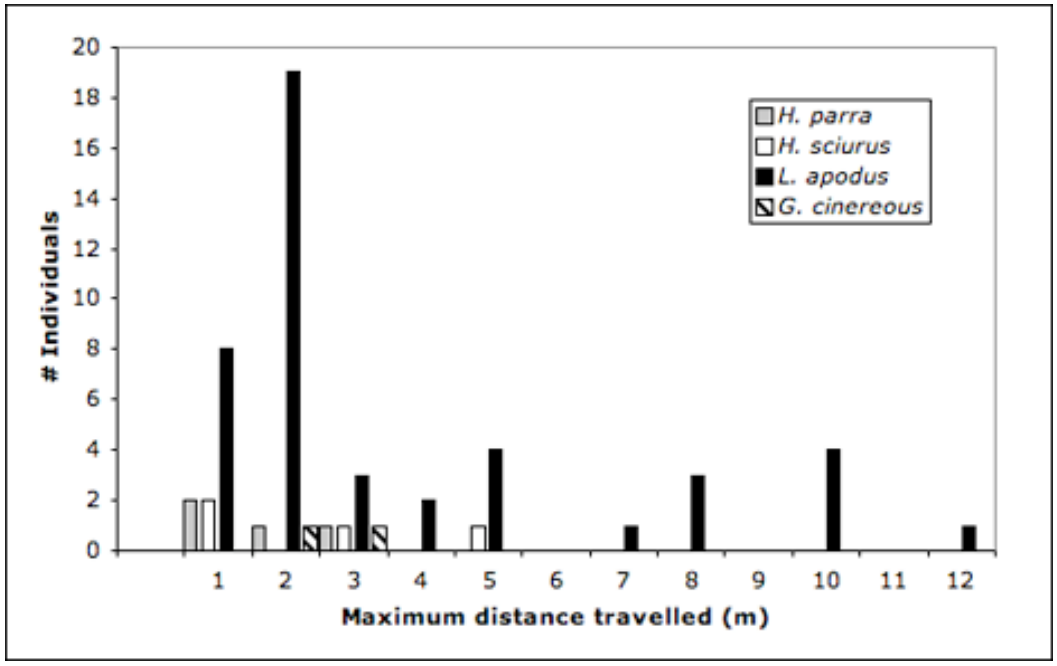


Figure VII.3: Histogram of distance traveled (m) by all tagged species in mangroves or seagrass (n=38).

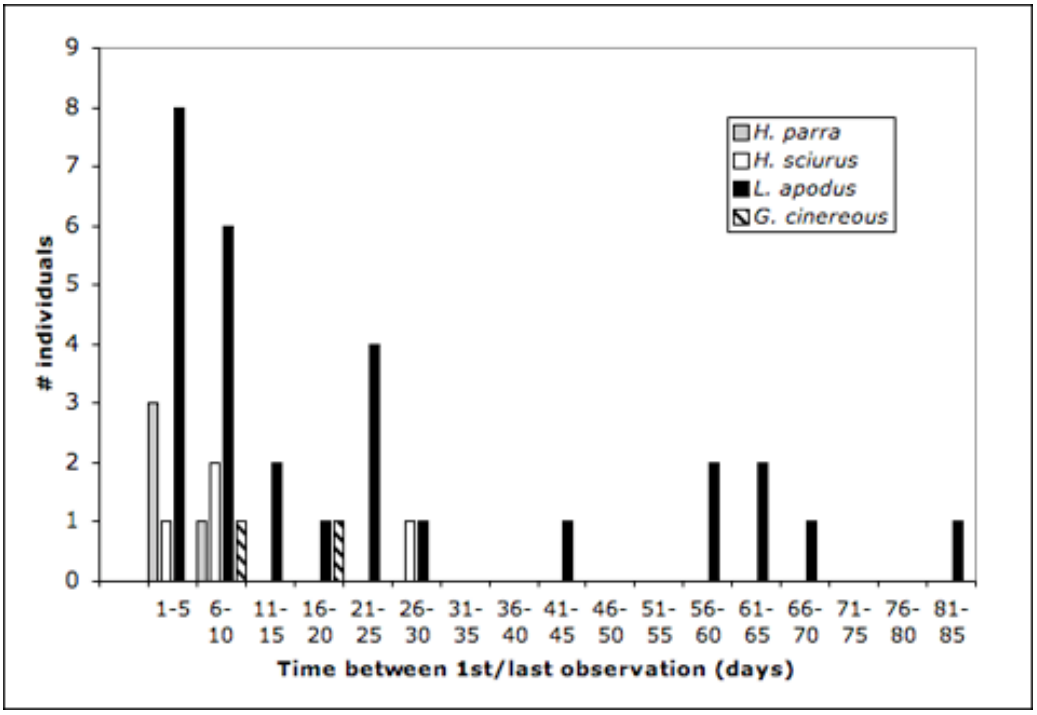


Figure VII.4: Histogram of elapsed time between captures (days) for juvenile fishes in mangroves (n=38).

DISCUSSION

While in the mangroves, juvenile *L. apodus*, by far the most common species, seem to exhibit limited site fidelity over the short term, but what happens over longer time scales is unclear. While the other species in the study exhibited a similar pattern, the low number of tags and recaptures makes it more difficult to draw conclusions.

While some individuals persisted in the study area for nearly three months, the majority of individuals were only re-sighted over the short-term, and disappeared afterwards. It is impossible to determine whether the decrease in sightings and recaptures over time reflects a dispersal of individuals out of the study area, an increase in mortality, or both. Fish abundance is known to peak in mangroves on a seasonal basis, typically but not always the rainy season, when this study was conducted, so it is unlikely a major shift

in overall fish presence occurred (Stoner 1986, Barletta *et al*. 2003, Lugendo *et al*. 2007). The mangrove fringe at the study site continues for kilometers, so habitat is widely available; fish have the option to stay within one habitat but not necessarily one location.

The persistence time was even lower for other species; the longest time between first and last sighting was only 26 days. The low "n" may be confounding those results; longer times may have been observed if more individuals had been tagged. One species, *L. synagris*, was never recaptured or observed. A primarily seagrass species (as juveniles), this species either suffers higher mortality or travels longer distances. Despite the lower "n," the proportion of *L. synagris* re-sighted (0) is disproportionate to the number caught, and suggests that this species has low site-fidelity.

CPUE in general declined during the study period, although observations stayed fairly constant. Trap efficiency tends to be lower in more heterogeneous environments anyway (Robichaud *et al*. 2000). Traditional mark-recapture studies of fish in reef environments also typically have a low recapture rate (Adams *et al*. 2006), so the low CPUE was not unexpected, although the difficulty in catching fish does not explain why the success rate decreased over time. It is possible that individuals may become used to the gear over time, and are able to avoid capture; CPUE dropped most dramatically in traps, while staying constant in observations. Any fish capable of navigating the complex environment of the mangroves may be able to escape easily from a trap.

Verweij and Nagelkerken (2007) and Verweij *et al*. (2007) both found that larger *L. apodus* and comparably-sized *Haemulon spp*. (to the fish marked in this study) used a larger area, but that individuals spent the majority of their time within a 10m radius area; these results are consistent with the present findings. Those studies also found evidence

that fish leaving a particular site may return to that site after an absence; such movements are not inconsistent with these findings. Other species also use a smaller percentage of overall home range (Bradbury *et al.* 1995).

In Curacao, *L. apodus* were observed less frequently in mangroves than other areas, but mangroves are much more abundant in the Bocas del Toro area than that one (Verweij *et al.* 2007). In smaller mangrove patches, *H. flavolineatum* tagged in mangroves were re-sighted in mangroves around half the time, a rate very similar to this study, but were also re-sighted in other habitats (Verweij and Nagelkerken 2007). In the current study, no marked individuals were found to move between habitats; every re-sighted individual was re-sighted (or re-captured) in the same habitat where it was tagged. *L. apodus, H. sciurus,* and other species are known to move from mangroves, where they rest diurnally to other habitats at night to feed (Rooker and Dennis 1991, Nagelkerken *et al.* 2000a) Both of the aforementioned studies by Verweij *et al.* found such movements.

Therefore, it was unexpected that no mangrove-tagged individuals were ever captured in seagrass or vice-versa. In another study, smaller individuals of *O. chrysurus* were observed to stay within one habitat while larger conspecifics were observed in adjacent habitats, but the duration of that study was much shorter (Watson *et al.* 2002). Given the difficulty of both capturing and observing individuals in a highly heterogeneous environment like mangroves, it is also plausible that some tagged individuals were simply missed by the census. However, given the lack of evidence for movement between habitats, it is also possible that the presence of consistent, extensive mangrove habitat reduces the need for such movements. Differences in the configuration

of the mangrove-seagrass-reef habitat may affect fish use of these habitats (Dorenbosch *et al*. 2007).

In the present study there was no correlation between increasing body size (TL) and distance traveled, as some studies have noted (Jones 2005). While in the mangroves, young *L. apodus* may have similar movements regardless of body size. Most of the individuals in this study were too small to start their presumed ontogenetic shift to other habitats. From a conservation standpoint, these results suggest that enough mangroves should be preserved to satisfy their needs before these shifts take place.

Chapter VIII: Conclusions

Taken together, the preceding chapters suggest a number of possible contributors to variation in the value and use of mangroves as fish habitat. While causes of between-mangrove variation addressed by previous authors- especially depth, geography, and influence of neighboring habitats-were also observed, this study identified a suite of other inter-mangrove differences capable of impacting how fish use this habitat, including the influence of other organisms in the system, the impact of edges and other habitat differences, and the movements and behavior of the fish themselves. All of these may play a role in different areas, at different times or different conditions.

The sessile epibionts did influence fish communities, as fish diversity and biomass increased linearly as these criteria increased in sessile epibionts. The degree of the correlation depends to a large extent on the identity and size class of the fish and epibionts in an area, as some organisms, particularly hard substrate types like barnacles or colonial annelid tubes seemed to influence the greatest number of fish. Results were most significant for all size classes taken together, suggesting that these organisms play a greater role enhancing mangroves as general fish habitat rather than specifically as nursery habitat.

One problem was sorting out the effects of concurrently existing changes in abiotic conditions, which cannot be readily controlled in a field environment. For instance, multiple regression suggested that depth also influenced fish diversity in Panama, although this correlation was not found in Honduras. While some other abiotic conditions appeared to have minimal influence in both sites (distance to neighboring habitats, density of prop roots, turbidity, distance to open sea), in both sites it is not

possible to rule out the possibility that the fish and epibionts correspond because other conditions, e.g. nutrients, or even nutrient cycling caused by the fish themselves, are positive factors for both fish and epibionts independently. Nevertheless, the presence of the same trend in two completely separate areas with very different fish and epibiont communities, and in two different seasons (dry in Honduras, rainy in Panama) suggests that the observed correlation is more than coincidence.

In order to address the issue of causality, separate field experiments were conducted to experimentally manipulate epibionts, both real and artificial, to determine if epibionts, or at least their physical characteristics, are capable of causing differences in a local fish assemblage. The first experiment, utilizing artificial mangrove plots, showed that in principle that heterogeneous structure such as that caused by the presence of mangrove epibionts, can indeed drive changes in the mangrove community. In that experiment, treatments with the most heterogeneous structure had significantly greater abundance and species richness of fish in two separate years. These treatments also attracted a more abundant and diverse fish assemblage than those with live epibionts, which had yet to reach full growth and successional stage and thus had lower three-dimensional structure. All of the artificial mangrove plots had significantly greater fish abundance than comparable plots of seagrass alone.

In a related experiment, the density and diversity of existing epibionts was physically reduced in real mangrove islands. In most cases, fish density increased significantly in control transects but stayed level where epibionts were removed. Biomass followed a similar pattern, decreasing in most treatment transects, and remaining even in controls. Taken together, these two experiments suggest a causal relationship between an

increase in fish and epibionts, as their presence or removal, while abiotic conditions were kept constant, significantly affected fish diversity, biomass, or abundance. In field conditions, the effect may depend upon the size and species present, not only of the fish, but also of the epibionts.

The possibility that the fish-epibiont correlation is caused by fish grazing on mangroves can be discounted after fish were excluded from the surface of mangrove roots by a caging experiment. After caging, all roots, even those uncaged, showed some changes in epibiont species assemblage and percent cover, but only those roots which had been scrubbed clean and had mesh size large enough to admit some fish showed significant changes. Algae significantly decreased underneath the smallest mesh cages, suggesting that light, rather than predation or grazing, has a large impact on prop-root epibiont communities.

The results from the cages indicate that the mangroves are a dynamic environment where community changes may take place over the short term, a fact also observed in the other experiments. Fish density, especially in Panama decreased as the summer progressed, possibly a result of variation in spawning times in common species. The study site, regardless of other conditions, significantly affected fish assemblage. In every study including the artificial mangrove roots, multivariate analysis and most univariate analyses indicated that the immediate location of the site had a significant impact on the fish community, even among sites that are close together and share abiotic conditions.

In order to attempt to sort out differences caused by site, replicate sites in Honduras were examined in different environments, including both lagoon and fringing mangroves, as well as a distance gradient away from gaps in the mangrove stands.

Differences were observed under both conditions; community assemblage in the lagoon was different from the assemblage found in the fringe, while diversity, abundance, and biomass were lower inside the lagoon to a greater degree than can be explained by the higher turbidity in the lagoon,. Edges, had an influence; species richness and abundance of juvenile and adult fish showed a significant linear decrease away from the edge and into the interior of the mangrove stands. This effect was quite gradual rather than an abrupt difference next to the edge, suggesting that edge effects in mangrove are gradual and penetrate far from the edge. The abundance and richness nearer the edge seem to be driven primarily by influence of species most often found in other habitats, however. The average size of individuals of common species slowly decreased away from the edge as well, consistent with a gradual ontogenetic shift from juvenile to adult habitat. While abiotic factors showed little influence, it was impossible to sort out effects caused by the edge from effects caused by the proximity of adult habitats.

As with the other experiments, analysis showed greater similarity between observations taken in the same site than observations identical in distance from the edge at different, even nearby, sites. This suggestion suggests that larger scale processes are also at work; a likely candidate is that fish settling in cohorts wind up in the same general area, and then sort into different sections, with different conditions selected or utilized according to life stage and/or species. In a related finding, prop-root epibionts showed no significant change along the gradient away from the edge, although these communities were also different based upon site. They did not sort according to lagoon or fringe, either. As a result, the correspondence of fish communities with epibionts observed at the

scale of entire transects did not exist at the level of five meter increments. It is likely that experimental scale has a significant impact on results in many cases.

One factor that can potentially affect results by scale, at least for fish studies, is the movement of fish within the mangroves. If fish choose a spot and stay in it for long stretches, a study that chooses that area will find significantly different fish communities than another spot where this has not occurred. In order to examine that possibility, juvenile reef fishes were visually tagged in Bocas Del Toro, Panama, in both mangrove and seagrass habitats over the course of three months. The movement and persistence of tagged individuals of common species was calculated based on recaptures and visual census in the trapping area. All recaptures were within a ten meter radius, but very few individuals persisted in one spot longer than a week or two. No evidence was observed of movement between mangrove and seagrass habitats, but CPUE was overall quite low. Unless mortality is extremely high for this population, juvenile fish are apparently moving around considerably within mangroves. Although site fidelity has been observed in other studies, at the scale of these transects fish staying in a particular location is probably not a major driver of fish community variation, at least in Bocas Del Toro.

Overall, the complexity and diversity of mangrove habitats as fish communities is driven by many factors and takes place over the scale of individual roots to entire stands. Abiotic variables such as depth, geographic location, time of year, month, as well as biotic variables such as the influence of neighboring habitats or the species and age-class of the fish play a role.. Large-scale processes, possibly settlement, seem to take precedence over smaller scale variables, influencing the basic outline of the fish community, which may then vary according to conditions and scale. The take away

conclusion is that subtidal mangroves are extremely complex ecosystems inextricably entwined with other habitats such as seagrass or reef, making it difficult to analyze variation within the mangrove on its own. All of these variables contribute to the complexity and variation found in subtidal mangroves, but none of them provide a complete explanation.

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APPENDICES

APPENDIX 1:

Epibiont community composition on islands 1-3 before selective removal of epibionts. P indicates that a given species is present; R indicates that the species was present and then removed as part of the experiment.

Epibiont	**Island**			**Shape**	**Consistency**
	1	2	3		
Algae					
Bostrychia sp.	P	P	P	Covers root in a layer	soft
Ventricaria Vetricosa	**R**	**R**			
Coralline algae spp.				Covers root in a layer	hard
Anemones					
Stichodactyla Helianthus	P	**R**		n/a-predatory	soft
Annelids					
Seballastrarte magnifica	P		**R**	tube	medium
Colonial Annelids sp.	P			Very rugose	hard
Bivalves					
Chlamys sp.	**R**	P	**R**	Flat/perpendicular to root	hard
Isognomon alatus	P	P	P	flat	hard
Cnidarians					
Porites porites	P	P		Branches	hard
Agaricia agaricites	P			shelf	hard
Millepora alcicornis	P	P		spikes	hard
Agaricia tenuifolia			P	shelf	hard
Porites astreoides		P		massive	hard
Sertularella sp. (hydroid)	**R**		P	n/a predatory	soft

Gymnangium sp.			**R**	n/a predatory	soft
Crustaceans					
Balanus sp.	P	P	P	rugose/holes	hard
Sponges					
Dysidea etheria	**R**	P		Blocky/conulose	soft
Haliclona implexiformis		**R**	P	mounds	soft
Haliclona manglaris	P	P	P	Thin cushion	soft
Lissodendoryx colombiensis	**R**	P	P	Rugose-tubes	soft
Lissodendoryx issodictyalis		**R**		massive	soft
Amphimedon sp.			P	Rugose-tubes	
Mycale microstigmatosa	P	P	P	matlike	soft
Niphates erecta			**R**	rugose	soft
Spongia pertusa			**R**	massive	soft
Tedania igris	P	**R**	P	massive	soft
Unidentified	P (2 spp.)	P (2 spp.)	P (2 spp.)	Matlike/massive	soft
Tunicates					
Phalussia negra	**R**			tubular	soft
Microcosmus exasperatus	P		**R**	tubular	soft
Ascidia curvata			P	tubular	soft
Hermania pallida	P	**R**		tubular	soft
Other					
Cyanophyta	**R**	P		Matlike/ filamentous	soft

APPENDIX 2:

Summary of MANOVA Statistics for response to epibiont reduction by fish size class, Chapter III, Effect of Epibiont Removal

Size Class (cm)	Treatment		Location		Treatment*Location	
	$F_{60,6}$	P≤	$F_{60,4}$	P≤	$F_{60,12}$	P≤
0-10	8.130	0.0001	11.407	0.0001	4.782	0.0001
10.1-20	6.494	0.0001	13.307	0.0001	3.855	0.0001
20<	1.660	0.133	7.087	0.0001	3.239	0.0001

APPENDIX 3:

Summary of MANOVA statistics by fish species, Chapter III, effect of epibiont reduction

Species	**Treatment**		**Location**		**Treatment*Location**	
	$F_{60,6}$	**P≤**	**$F_{60,4}$**	**P≤**	**$F_{60,12}$**	**P≤**
Chaetodon capistratus	2.43	0.028	5.35	0.0001	2.73	0.002
Haemulon spp.	7.59	0.001	33.13	0.0001	4.15	0.0001
Sphyraena barracuda	1.82	.096	3.81	0.005	2.90	0.001
Stegastes Adustus	3.66	0.002	23.78	0.0001	2.80	0.002
Lutjanus Apodus	7.0	0.0001	16.34	0.0001	2.41	0.006
Gerres cinereous	9.12	0.0001	29.72	0.0001	9.75	0.0001
Scarus iseri	1.03	0.408	18.14	0.0001	0.71	0.741
Abudefduf saxatilis	1.92	0.079	24.06	0.0001	3.06	0.001
Hypoplectrus puella	1.42	0.207	4.93	0.001	2.81	0.001
Halichoeres bivittatus	4.05	0.001	21.19	0.0001	2.36	0.007
Ginglymostoma cirratum	6.39	0.0001	44.0	0.0001	7.5	0.0001

Curriculum Vita

James MacDonald

Education

May 2008 **Rutgers University, New Brunswick, NJ**
Ph.D., Ecology and Evolutionary Biology

May 2001 **Columbia University, New York, NY**
B.S., Environmental Biology

May 1997 **Columbia University, New York, NY**
B.A. in Anthropology, 1997

Professional Experience

Fall 2002-present **Teaching Assistant**, *Rutgers University Division of Life Science, New Brunswick, NJ*

Fall 2007 **NCEP Intern** *American Museum of Natural History, New York, NY*

Summer 2007 **Mangrove Scientist** *Operation Wallacea, Utila, Honduras*

2002 - 2004 **Mini Course Instructor**, *Newark Museum, Newark, NJ*

2001 - 2002 **Biodiversity Assistant/Urban Park Ranger,** *Department of Parks and Recreation, New York, NY*

2001 - 2002 **Science Writer/Expert Reviewer** *The Princeton Review, New York, NY*

1998 - 2000 **Manager for contract services**, *Columbia University Residence Halls, New York, NY*

Publications

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