



The Effects of Coral Presence among Red Mangrove (*Rhizophora mangle*) Prop Roots on Caribbean Fish Communities.

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UNIVERSITY OF MIAMI

THE EFFECTS OF CORAL PRESENCE AMONG RED MANGROVE (*RHIZOPHORA
MANGLE*) PROP ROOTS ON CARIBBEAN FISH COMMUNITIES

By

Jennifer Lynn Wright

A THESIS

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Masters of Science

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THE EFFECTS OF CORAL PRESENCE AMONG RED MANGROVE
(*RHIZOPHORA MANGLE*) PROP ROOTS ON CARIBBEAN FISH COMMUNITIES

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Coral reefs and mangroves play a variety of roles in the lives of reef fishes, serving as nursery, feeding, and breeding grounds. Mangroves, while often near reef ecosystems, do not typically have suitable conditions for coral recruitment and growth, though mangrove-coral habitats do occur. The distribution and extent of these mangrove-coral habitats, as well as the composition of the fish community that utilizes them, are poorly understood. In several locations throughout Bocas del Toro, Panama, many species of corals grow on and among submerged red mangrove (*Rhizophora mangle*) prop roots. This study aimed to analyze the reef fish community in a mangrove-coral habitat, quantifying the effect coral presence has on the red mangrove fish community. I conducted visual underwater fish surveys in coral and noncoral mangrove habitats throughout Bocas del Toro. Furthermore, I conducted an experiment in which I placed artificial coral among the mangrove prop roots to differentiate the effect of live coral vs. hard substrate on the mangrove fish community. Of the 28 fish species (encompassing 11 families and 4 trophic groups) observed, over 90% were juveniles, and 57% occurred at both coral and noncoral mangrove habitats. Noncoral sites had higher abundances of *Sphyraena barracuda* and invertebrate feeders. Coral sites

had greater species richness and higher abundances of roving herbivores (*Scarus* spp.) and territorial herbivores (*Stegastes* spp.). In an experimental component of the research, the addition of the artificial coral increased total fish abundance (particularly roving herbivores), indicating that roving herbivores are attracted to the hard substrate that corals provide. The addition of the artificial coral did not affect the abundance of territorial herbivores, indicating that these fishes may require more time to recruit or that they rely on biological cues from living coral. The mangrove-coral habitat in Bocas del Toro is functioning primarily as juvenile habitat for reef fishes, with more species (particularly *Scarus* spp. and *Stegastes* spp.) attracted to the mangrove-coral habitat compared to other mangrove fringe communities. The presence of coral has made the habitat more favorable for species who tend to prefer coral reef habitats, while the mangrove prop roots provide necessary shelter from predators and additional food resources for fishes. Specific effort should be spent conserving mangrove-coral habitats, as this habitat type is unique, seldom found, and provides the ability to conserve mangroves, corals, and reef fishes all within one location.

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TABLE OF CONTENTS

	Page
LIST OF FIGURES	v
LIST OF TABLES	vi
Chapters	
1 INTRODUCTION	1
1.1 Study objectives	5
2 STUDY AREA – BOCAS DEL TORO	6
3 MATERIALS AND METHODS	11
3.1 Visual Transect Surveys	11
3.2 Microhabitat Measurements	13
3.3 Artificial Coral Experiment.....	14
3.4 Statistical Analysis	15
4 RESULTS	17
5 DISCUSSION	26
5.1 Visual Transect Surveys	26
5.2 Artificial Coral Experiment	31
6 CONCLUSIONS	33
LITERATURE CITED	35

LIST OF FIGURES

Figure 1. Coral growing on and under mangrove prop roots with fish (<i>Lutjanus apodus</i>) swimming past (bottom right) in Bocas del Toro, Panama. <i>Photo credit: Heather Stewart.</i>	10
Figure 2. Location of coral (yellow circles) and noncoral (red squares) mangrove sites in Bocas del Toro, Panama. Yellow circles also indicate artificial coral placement locations.	12
Figure 3. (A) Finished piece of artificial coral (AC), and the formation of a quadrat along the mangrove fringe (B) pre-AC and (C) post-AC.	15
Figure 4. Canonical Correspondence Analysis (CCA) for square root-transformed (A) species abundances and (B) trophic group abundances vs. environmental variables and survey sites in Bocas del Toro, Panama. Yellow ellipses encompass coral sites; purple ellipses encompass noncoral sites. Species and trophic group codes are listed in Table 1. Environmental variable codes: Chlor = chlorophyll, DO = dissolved oxygen, EPRD = epibiont prop root diameter, Light = light intensity, PR = prop root density, Sal = salinity, Temp = temperature.	19
Figure 5. Comparison of mean fish community metrics between coral and noncoral sites. Error bars indicate standard error of the mean. Asterisk indicates significantly different value between coral and noncoral sites at $P \leq 0.05$ (*).	20
Figure 6. Comparison of mean trophic group abundances between coral and noncoral sites. Error bars indicate standard error of the mean. Asterisk indicates significantly different value between coral and noncoral sites at $P \leq 0.05$ (*) and $P \leq 0.01$ (**).	22
Figure 7. Box and whisker comparisons [showing minimum, 1 st quartile, median, mean (x), 3 rd quartile, and maximum] of significant environmental variables between coral sites (yellow) and noncoral sites (red). Asterisk indicates significantly different value between coral and noncoral sites at $P \leq 0.05$ (*), $P \leq 0.01$ (**), and $P \leq 0.001$ (***)	23
Figure 8. Comparison of mean fish community metrics before (pre-AC) and after (post-AC) artificial coral placement. Error bars indicate standard error of the mean. Asterisk indicates significantly different value pre-AC and post-AC at $P \leq 0.05$ (*).	24
Figure 9. Comparison of mean trophic group abundances before (pre-AC) and after (post-AC) artificial coral placement. Error bars indicate standard error of the mean. Asterisk indicates significantly different value pre-AC and post-AC at $P \leq 0.05$ (*) and $P \leq 0.01$ (**).	25

LIST OF TABLES

Table 1. List of the species observed during sampling with their respective species code, family, and trophic group. Trophic group: RH = Roving herbivore, TH = Territorial herbivore, IF = Invertebrate feeder, CR = Carnivore. Species habitat types: C = coral, NC = noncoral. Species marked with an asterisk (*) were grouped at the genus level for subsequent analyses.	17
Table 2. Results of parametric (Welch's two-sample <i>t</i> test: <i>T</i>) and nonparametric (Mann-Whitney two-sample test: <i>W</i>) one-tailed [greater at coral sites(*)] or two-tailed comparisons of fish community metrics between coral and noncoral sites in Bocas del Toro. Values in bold are significant at $\alpha = 0.05$	20
Table 3. Results of parametric (Welch's two-sample <i>t</i> test: <i>T</i>) and nonparametric (Mann-Whitney two-sample test: <i>W</i>) one-tailed [greater at coral sites(*)] or two-tailed comparisons of square root-transformed fish densities between coral and noncoral sites for the top 10 most abundant species (at all sites combined). Values in bold are significant after applying Hochberg correction with false discovery rate of 10%.	21
Table 4. Results of parametric (Welch's two-sample <i>t</i> test: <i>T</i>) and nonparametric (Mann-Whitney two-sample test: <i>W</i>) one-tailed (G = greater than, L = less than) or two-tailed (N) comparisons of square root-transformed fish densities between coral and noncoral sites for each trophic group. Values in bold are significant at $\alpha = 0.05$	22
Table 5. Results of parametric (paired Welch's two-sample <i>t</i> test: <i>T</i>) and nonparametric (paired Mann-Whitney two-sample test: <i>V</i>) one-tailed [greater post-AC (*)] or two-tailed comparisons of fish community metrics in quadrats pre-AC and post-AC. Values in bold are significant at $\alpha = 0.05$	24
Table 6. Results of parametric (paired Welch's two-sample <i>t</i> test: <i>T</i>) and nonparametric (paired Mann-Whitney two-sample test: <i>V</i>) one-tailed [greater post-AC (*)] or two-tailed comparisons of square root-transformed fish densities in quadrats pre-AC and post-AC based on trophic groups. Values in bold are significant at $\alpha = 0.05$	25

CHAPTER 1. INTRODUCTION

The Caribbean Sea is considered a diversity center for fishes (Veron 1995, Floeter and Gasparini 2000). Generally, species composition varies among different habitats (Talbot and Goldman 1972, McGehee 1994), but a strong taxonomic division between reef and nonreef faunas is difficult to define (Dominici-Arosemena and Wolff 2005). Therefore, “reef fishes” may be characteristic of—but not restricted to—coral reefs (Bellwood 1998, Robertson 1998). In general, adult reef fishes spawn on the reef or the continental shelf and the fertilized eggs develop into pelagic larvae (Igulu et al. 2011). After a span of several weeks to months, the larvae settle on the substratum; some larvae do not settle on the coral reef itself, but in nearshore habitats (Adams et al. 2006, Pollux et al. 2007).

When reef fishes reach maturity, it is assumed that they migrate to coral reefs because this habitat type is more suitable for adults (Dorenbosch et al. 2007), resulting in lower adult densities in coastal habitats (Nagelkerken et al. 2000a,b). Reefs provide spawning, nursery refuge, and feeding areas for a variety of fishes (Wilson et al. 2008). However, the impact of factors such as food availability and predation pressure depends not only on the type of habitat, but also on the way the habitats are arranged within the coastal landscape (Beets et al. 2003, Serafy et al. 2003, Grober-Dunsmore et al. 2004). Factors outside the reef itself can also influence fish communities, and it is now accepted that inshore tropical coral reefs do not function in isolation but rather as part of a larger habitat network, encompassing in many cases mangrove and seagrass habitats (Davis et al. 2014).

Mangroves play a variety of roles in the lives of reef fishes, serving as additional nursery, feeding, and breeding grounds (Kjerfve and Macintosh 1997, Laegdsgaard and Johnson 2001, Verweij et al. 2006 a,b). Mangroves in the Caribbean strongly influence the fish community structure on neighboring coral reefs and serve as an intermediate nursery habitat that increase the survivorship of young fishes (Mumby et al. 2004). At least 17 reef fish species in the Caribbean utilize mangroves significantly as juveniles (Nagelkerken et al. 2000a,b), and it is likely that many of these juveniles have a high dependence on the mangrove habitat (Dorenbosch et al. 2007, Nagelkerken et al. 2017). For example, *Scarus guacamaia* has a functional dependency on mangroves and has suffered local extinction after mangrove removal (Mumby et al. 2004). Mangroves do not function equally as juvenile habitat for all fishes; some fish species may utilize mangroves as an alternative habitat (Beck et al. 2001), and others may not depend on the presence of mangroves at all (Dorenbosch et al. 2004). Mangroves may provide multiple above-mentioned benefits to fishes simultaneously, and the benefits are frequently species-, size class-, and life history-specific (Nagelkerken et al. 2000a, Manson et al. 2005, Verweij et al. 2006a, MacDonald and Weis 2013).

In both coral reef and mangrove habitats, the presence of structure is an important attribute to fishes, with many fish species attracted by structure-rich habitats (Chabanet et al. 1997, Jenkins and Sutherland 1997, Scharf et al. 2006). Habitat structure, as defined by McCoy and Bell (1991), combines elements of both heterogeneity and complexity and encompasses the composition, abundance, and spatial arrangement of physical matter within a habitat. In red mangrove shorelines throughout the Caribbean, the complex structure provided by the prop roots (also termed “aerial” or “stilt” roots) can reduce

predation risk while offering food abundance for juvenile reef fish species (Parrish 1989, Nagelkerken and Faunce 2008, Nagelkerken et al. 2010). In many areas, a diverse epibiont community of sessile organisms (e.g., algae, bivalves, sponges, etc.) lives directly on the submerged red mangrove prop roots, substantially increasing structural heterogeneity in the mangroves (MacDonald et al. 2008). On coral reefs, the number of shelter holes, rugosity, and percent coral cover have all been identified as important aspects of coral reef complexity structuring fish distribution (Luckhurst and Luckhurst 1978, Gratwicke and Speight 2005a,b).

While reef and mangrove habitats are highly productive on their own, their functioning is enhanced where connectivity facilitates the exchange of organisms among habitats (Berkström et al. 2012, Nagelkerken et al. 2015, Olds et al. 2013). Mangrove habitat configuration in relation to coral reefs and seagrass beds can relate to the fish community composition, species richness, and fish density (Dorenbosch et al. 2004, 2007, Igulu et al. 2014). The typical connectivity between these habitats in the Caribbean is described as red mangrove fringe communities followed by extensive seagrass beds, shallow coral reefs, and lastly deep reefs and offshore waters (Silvestri and Kershaw 2010). Links between coral reef, mangrove, and seagrass habitats are particularly important for reef fishes which often move among these habitats to spawn, disperse, feed, and seek refuge from predators (Igulu et al. 2014, Nagelkerken et al. 2017, Dubuc et al. 2019). This habitat connectivity also promotes the abundance of important functional groups and key ecological processes (e.g., herbivory, predation) in tropical seascapes (Olds et al. 2012, Peterson et al. 2013).

The distribution of mangrove, seagrass, and coral reef habitats is well-documented and monitored (e.g., Madin and Madin 2015, Thomas et al. 2017, Jayathilake and Costello 2018), and has become of particular interest in recent years due to declining habitat extent from development and climate change. Corals, while often near mangrove ecosystems, do not typically inhabit mangroves due to the frequently high sedimentation rates, lack of suitable substrate, and inadequate water quality (i.e., increased turbidity and decreased salinity and dissolved oxygen; Yates et al. 2014, Rogers 2017). Therefore, studies of corals dwelling in mangrove habitats are scarce (e.g., Macintyre et al. 2000, Rützler et al. 2000, Rogers 2009, Nguyen et al. 2019), and only a few comprehensive studies of these habitats have been performed to date (Yates et al. 2014, Rogers 2017, 2019, Camp et al. 2019). Of these comprehensive studies, only two have described the fish communities utilizing the mangrove-coral habitat (Rogers 2017, 2019). Moreover, the presence of this habitat type is known in only a few locations [e.g., northern Great Barrier Reef (Camp et al. 2019), US Virgin Islands (Yates et al. 2014), Belize (Rützler et al. 2000)], and the distribution and extent of this combined-habitat type is largely unknown. Mangrove-coral habitats, herein, refer to red mangrove communities with total substrate coverage consisting of at least 20% coral cover.

Yates et al. (2014) investigated a mangrove-coral habitat in the US Virgin Islands and found that it served as a nonreef coral refuge from thermal stress and ocean acidification. Additionally, while describing the mangrove-coral community in the US Virgin Islands, Rogers (2017) noted several adult fishes occurring in the mangrove-coral habitat including *Lutjanus griseus* and *Haemulon* spp. Currently, the search for potential refugia for reef fishes has focused on deeper reefs which often experience more stable

abiotic conditions compared to shallow reefs (Bridge et al. 2013, Jankowski et al. 2015, MacDonald et al. 2016). However, deeper reefs may not be suitable refugia for some fish species, such as herbivores, due to heavy predation pressure and lower habitat complexity (Kahng et al. 2010). Therefore, it is possible that the mangrove-coral habitat can serve not only as a refuge for corals, but also for coral reef fishes.

1.1 STUDY OBJECTIVES

Due to the limited knowledge of the mangrove-coral habitat and its spatial extent, the effect that corals have on the mangrove reef fish community is poorly understood. The goal of this study was to analyze the reef fish community in a mangrove-coral habitat, quantifying the effect coral presence has on the fringing red mangrove fish community. This study aimed to answer two main questions. First, how does the fish community differ between mangrove-coral habitats and other mangrove habitats? To answer this question, I conducted visual fish transect surveys at coral and noncoral mangrove fringe sites across the Bocas del Toro Archipelago. Second, is the difference in the fish community due to the physical structure of coral or a biological aspect of the living coral itself? This question was answered by conducting a field experiment, in which I added artificial coral to constructed quadrats within the mangrove prop roots to analyze the change in the mangrove fish community.

CHAPTER 2. STUDY AREA – BOCAS DEL TORO

The present study took place in the Bocas del Toro Archipelago in Caribbean Panama. This archipelago comprises an area of 3500 km², formed by six large forested islands and hundreds of small mangrove cays dominated by red mangroves (*Rhizophora mangle*; Guzmán 2003). About 12 million years ago, the Bocas del Toro Archipelago consisted of shallow-water fringing reefs around active volcanic islands (Coates et al. 2005). By the early Pliocene (3–5 million years ago), marine regression caused a rapid shallowing throughout the Bocas del Toro Basin (Coates et al. 2005). During this time, an extensive coral reef system developed on either volcanic basalt (Bastimentos Island) or siliciclastic sediments (Colon Island), reflecting the oceanographic changes as a result of shallowing and closure of the Isthmus of Panama (Coates et al. 2005).

The current islands in the Bocas del Toro Archipelago formed on top of coral reef facies, consisting mainly of *Agaricia* spp., *Colpophyllia natans*, *Dichocoenia stokesi*, *Manicina (Teleiophyllia) geisteri*, *Montastraea* spp., *Porites* spp., and *Stylophora granulata* (Coates et al. 2005). These red mangrove “fringe forest” islands are characterized by dense, well-developed prop root systems and are directly exposed to tides, waves, and strong winds (Lugo and Snedaker 1974). Surrounding these islands are seagrass beds (dominated by turtlegrass, *Thalasia testudinum*), fringing coral reefs (up to 20 m deep), and dozens of shallow reef patches (Guzmán 2003). The reefs are typically dominated by corals with a high stress tolerance, including *Porites* spp. and *Agaricia* spp. (Seemann et al. 2014, 2018). Bocas del Toro exhibits a less continuous zonation pattern, with mangrove cays and patches of seagrass and shallow coral reefs scattered throughout the archipelago (Guzmán and Guevara 1998).

Intense rain and irregular seasonal patterns characterize the Bocas del Toro region. There are two periods of low rainfall (March and September) and high rainfall (July and December; D'Croz et al. 2005). Rainfall is most intense at night and least intense in the late afternoon, a pattern common in tropical coastal areas (Kaufmann and Thompson 2005). Salinity at the surface is usually 30–34 ppt but can drop to as low as 20 ppt after heavy rain (Kaufmann and Thompson 2005). Mean sea surface temperatures vary from 27.5 °C (January–February) to 29.7 °C (September–October; Collin et al. 2009). Environmentally stressful temperatures can result from a month without rain, and an equal period of cloudy skies can decrease temperatures rapidly. The inner portion of the archipelago (Almirante Bay) experiences higher water temperatures and has larger temperature fluctuations compared to the seaward side (Kaufmann and Thompson 2005).

In the Bocas del Toro Archipelago, water interchange with the open ocean occurs through passages between islands and mangrove cays (D'Croz et al. 2005). Waves and currents have a strong effect outside of the archipelago, but the major islands act as a barrier, decreasing wind strength, wave height, and tidal amplitude for the inner water bodies (Dominici-Arosemena and Wolff 2005). The tidal range is small, ranging between 2 and 15 cm under standard conditions (Guzmán et al. 2005). Average wind speed is about 7 km/hr but can occasionally increase to 20 km/hr (Kaufmann and Thompson 2005). The strong northeast winds (known to occur from late December to March) bring in some offshore water, but most of the cooling observed is during the periods of heavy rainfall (Kaufmann and Thompson 2005). Oftentimes, inshore water is either warmer or colder than offshore water, and local solar radiation creates substantial differences from offshore waters, regardless of the amount of mixing (Kaufmann and Thompson 2005).

Bocas del Toro is considered an isolated site, where the reef fish populations are likely to be maintained by self-recruitment (Sponaugle et al. 2002, Dominici-Arosemena and Wolff 2005). The majority of the reef fish species recruit during the rainy season (Wilson 2001), although replenishment can occur year-round (Robertson et al. 1988, 1993). Within the archipelago, winds may play an important intermittent role in larval input to inshore coral reefs while currents primarily influence settlement and recruitment to exposed reefs (Cowen 2002). The most abundant fish families found on the coral reefs are Acanthuridae, Chaetodontidae, Labridae, Serranidae, and Scaridae (Dominici-Arosemena and Wolff 2005, Seemann et al. 2018). Within these families, there are several species known to dominate on the coral reefs: *Acanthurus bahianus*, *Chaetodon capistratus*, *Halichoeres bivittatus*, *Hypoplectrus* spp., *Scarus iseri*, *Sparisoma* spp., and *Stegastes* spp. (Dominici-Arosemena and Wolff 2005, Liu 2018, Seemann et al. 2018). Haemulids are also quite common on the reefs, and they are thought to migrate from adjacent mangrove areas (Dominici-Arosemena and Wolff 2005).

The mangrove fish communities in Bocas del Toro have a similar composition compared to the reefs. The most abundant families in the red mangrove habitats are Chaetodontidae, Gerreidae, Haemulidae, Lutjanidae, Scaridae, and Sphyraenidae (MacDonald et al. 2008, Seemann et al. 2018). Several species are known to dominate in the mangroves as juveniles: *Abudefduf saxatilis*, *C. capistratus*, *Gerres cinereus*, *Haemulon* spp., *Lutjanus apodus*, *S. iseri*, and *Sphyraena barracuda* (MacDonald et al. 2008, MacDonald and Weis 2013, Seemann et al. 2018). The fish community structure in Bocas del Toro seems to be a complex, indirect, and nonlinear consequence of structure and environmental conditions (Dominici-Arosemena and Wolff 2005). Fish abundance

and species richness increase toward more complex zones and densities of specialized feeders (e.g., herbivores) increase in sheltered zones (Dominici-Arosemena and Wolff 2005). The highest populated coral reefs in this area are near Bastimentos Island, Colon Island, and Caranero Island, where some of the massive coral reefs are located (Dominici-Arosemena and Wolff 2005). In Bocas del Toro, fish biomass and species richness are relatively low, and a greater proportion of the total fish biomass on coral reefs is comprised of herbivores in contrast to other Caribbean reefs (Dominici-Arosemena and Wolff 2005, Seemann et al. 2018). The coastal habitats throughout the archipelago are known to share species pools and are well connected, forming a heterogeneous seascape (Nguyen et al. 2019).

In Bocas del Toro, rapid human population growth and development connected with agriculture (e.g., banana industry) and tourism has led to severe ecological degradation of mangroves, seagrass, and coral reef habitats (Guzmán 2003, Cramer 2013, Seemann et al. 2014, 2018). Clearing and development of coastal areas (particularly offshore islands) have greatly increased, leading to a loss of over half of Panama's mangrove extent (Polidoro et al. 2010). Pressure from commercial and artisanal fisheries has forced several stocks of economically important species into collapse (i.e., Holothuroidae, Strombidae; Guzmán et al. 2005), and declines in abundances of larger predatory species (Haemulidae, Lutjanidae, Serranidae) and herbivorous species (Scaridae) have been observed throughout the archipelago (Aronson et al. 2003, Seemann et al. 2014). Coral cover and species richness have decreased in Bocas del Toro over the past two decades, declining from 29.7% coral cover (with 58 species) in 1999 to 13.6% coral cover (with 42 species) in 2011 (Guzmán 2003, Jackson et al. 2014). A dramatic

phase shift on these reefs has also occurred, where habitats previously dominated by reef-building corals (e.g., *Acropora* spp.) are now primarily covered by low-relief corals and macroalgae (McClanahan et al. 1999, Aronson et al. 2004, Jackson et al. 2014). In recent years, this decline in coral cover has been exacerbated by elevated macroalgal abundance which is a result of overfishing of keystone herbivores (Nugues et al. 2004, Kline et al. 2006). Through their consumption of algae, herbivores open space for young coral settlement and growth, playing a central role in the maintenance of coral reefs (Feitosa and Ferreira 2015, Cramer et al. 2017). In several locations throughout Bocas del Toro, many species of corals grow on and among submerged red mangrove prop roots, forming mangrove-coral habitats (Fig. 1). Coral species that have been identified in the mangrove-coral habitats in Bocas del Toro include, but are not limited to, *Agaricia agaricites*, *Agaricia tenuifolia*, *Agaricia lamarcki*, *Manicina areolata*, *Montastrea cavernosa*, *Porites astreoides*, *Porites furcata*, and *Siderastrea siderea*, (J Wright, pers. observ).



Figure 1. Coral growing on and under mangrove prop roots with fish (*Lutjanus apodus*) swimming past (bottom right) in Bocas del Toro, Panama. Photo credit: Heather Stewart.

CHAPTER 3. MATERIALS AND METHODS

3.1 VISUAL TRANSECT SURVEYS

The current study was conducted from February to March 2019 in Bocas del Toro, Panama. This period was during low rainfall and lower recruitment for most reef fishes in the archipelago. Visual surveys were conducted in two habitat types: mangrove fringe (1) with corals (“coral”) and (2) without corals (“noncoral”). I chose six study sites for each habitat type throughout the archipelago (Fig. 2) based on previous visual surveys and knowledge of mangrove-coral habitat location. Coral sites were required to meet the mangrove-coral habitat definition, described herein as red mangrove communities with total substrate coverage consisting of at least 20% coral cover. The sites were also visually assessed for suitability of transect surveys (i.e., at least 50 m of swimmable mangrove fringe). After choosing the coral site locations, noncoral sites were selected throughout the archipelago that were visually similar to the coral sites (primarily in terms of visibility, depth, and swimmable mangrove fringe). While choosing sites for both habitat types, an effort was made to encompass as much of the archipelago as possible.

To study the fish community, I used a modification of the visual “belt-transect” method described by Rooker and Dennis (1991). This is a popular reef fish survey method (Caldwell et al. 2016), and one that has been used extensively throughout the Caribbean (e.g., Faunce and Serafy 2006, Nagelkerken 2000a,b, Serafy et al. 2003). The method involved snorkeling a 30 m-long transect parallel to the mangrove fringe while looking 2 m landward from the submerged prop root edge and recording species, number, and size [total length (estimated to the nearest centimeter using a dive slate ruler)] of the fish taxa encountered. Throughout the sampling period, I (the only observer) surveyed the

entire fish community with the exception of cryptic species (Clinidae, Gobiidae; *see* Serafy et al. 2003). These fishes were excluded because they were not easily visible using the belt-transect method, making any counts of these fishes comparatively inaccurate to other fish species. I placed small, silvery, fork-tailed fishes that tend to inhabit the water column in large schools (e.g., Atherinidae, Clupeidae, Engraulidae) into a single group (referred to as small, water-column fishes; Serafy et al. 2003), and estimated their abundance on each transect to the nearest 50 individuals per transect. These fishes were analyzed separately since they were sighted sporadically and in high densities, consequently distorting the analyses (Ferreira et al. 2001). All visual surveys were conducted between 10:00 and 16:00, and time of day was standardized to reduce possible effects of diel rhythms and to minimize low light conditions. Transect locations were chosen at nonfixed starting points and each study site was sampled five times.

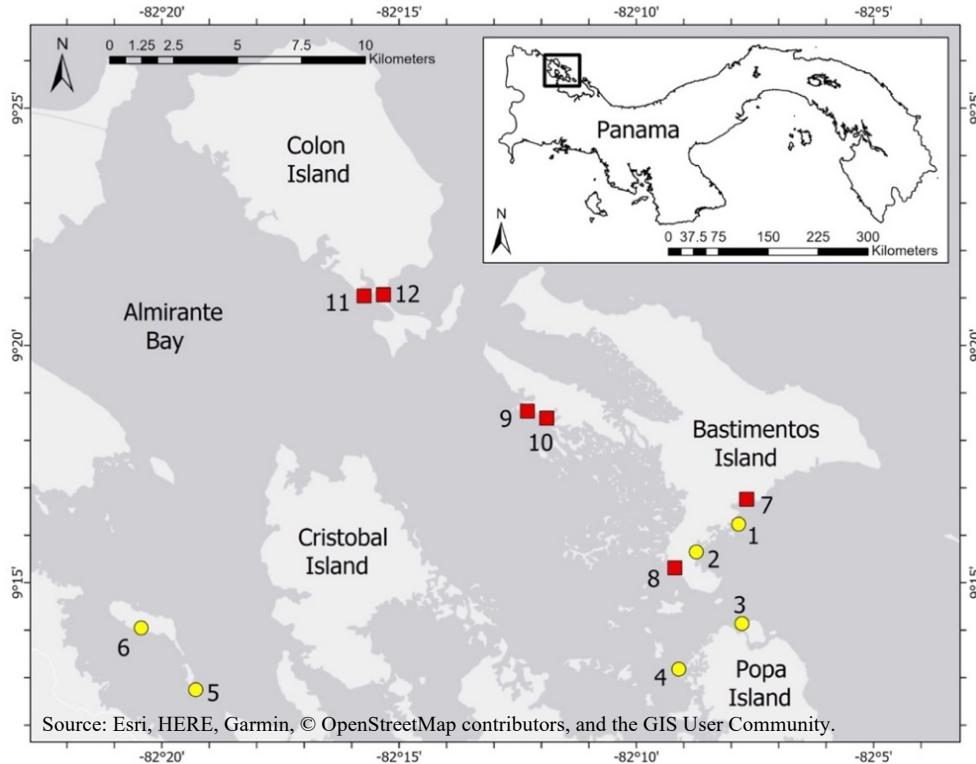


Figure 2. Location of coral (yellow circles) and noncoral (red squares) mangrove sites in Bocas del Toro, Panama. Yellow circles also indicate artificial coral placement locations.

3.2 MICROHABITAT MEASUREMENTS

Water quality measurements were obtained at each site at least once (five times at most sites during each visual transect survey depending on availability or monitoring equipment). I measured water temperature, salinity, dissolved oxygen, pH, and total chlorophyll (chlorophyll *a* and *b*) using a YSI EXO2 multiparameter sonde. Light intensity was measured at each site using a HOBO MX2202 data logger. During each deployment, both HOBO and YSI EXO2 measurements were recorded every minute for a duration of 30 minutes. Depth was measured at each site to the low tide line during mean low tide using a 1-m long polyvinyl chloride pole marked every 5 cm. At each site, I measured prop root density and epibiont prop root diameter within two 1 m² quadrats at the beginning and end of the visual survey transects (0 and 30 m) for a total of 10 quadrats per site. Prop root density was measured by counting the number of prop roots within each quadrat. Epibiont prop root diameter was measured by using a tape to measure the maximum diameter of the attached organism assemblage on each root within the quadrat (Serafy et al. 2003). Since fish densities are often correlated to the degree of coral cover (Grigg 1994, Hixon and Beets 1993, Luckhurst and Luckhurst 1978), I visually quantified the total hard coral cover (both living and dead corals) at each site. To estimate coral cover, total cover was quantified within each quadrat to the nearest 5% in the following categories (totaling 100%): live coral, dead coral (both recently dead and dead for a prolonged period of time), coral rubble, seagrass, invertebrates, leaf litter, algae, sand, and silt. I distinguished coral rubble from dead coral as the former being encrusted and highly fragmented.

3.3 ARTIFICIAL CORAL EXPERIMENT

To analyze the effect of live coral vs. hard substrate on fish assemblages, I constructed one 1×1 -m quadrat at each coral site ($n = 6$), starting at the mangrove prop root edge and extending landward into the canopy 1 m. These quadrats were marked using zip ties and red-colored plastic square tags attached to prop roots at mean low tide water level (Fig. 3). Each quadrat was constructed in an area of the mangrove-coral habitat that *did not* contain coral (at least 1 m away from coral cover in all directions) and quadrats were surveyed four times in February before adding artificial coral (“pre-AC”). During each survey, I swam along the fringe to locate the quadrat and, once located, waited in position for 1 minute before starting the survey to lessen the effect of my initial presence on fish presence/abundance. After the initial waiting period, I surveyed the quadrats for 5 minutes (making observations 1 m from the quadrat) and recorded species, number, and size (total length) of all fish taxa encountered except for cryptic species.

To make the artificial coral, I followed a tutorial on YouTube (Carver 2011). The artificial coral was made using the following mixture: 3 parts crushed shells, 2 parts white Portland cement, and 2 parts large rock salt. The artificial coral was molded in bins with sand to resemble the shape and height of coral found at the coral sites. Each piece of artificial coral was left in the mold for 48 hours to harden and then soaked in seawater for 2 weeks to dissolve the rock salt. I changed the seawater every 48 hours to return the pH back to that of the pH at the coral sites, which averaged 8.01 (SD 0.04) (Fig. 3A). Three equally sized pieces of artificial coral (average LWH = $28 \times 18 \times 11$ cm) were added to each quadrat (Fig. 3B, C). After placing the artificial coral (“post-AC”), the quadrats were left unvisited for 3 weeks and then surveyed again four times in March 2019.

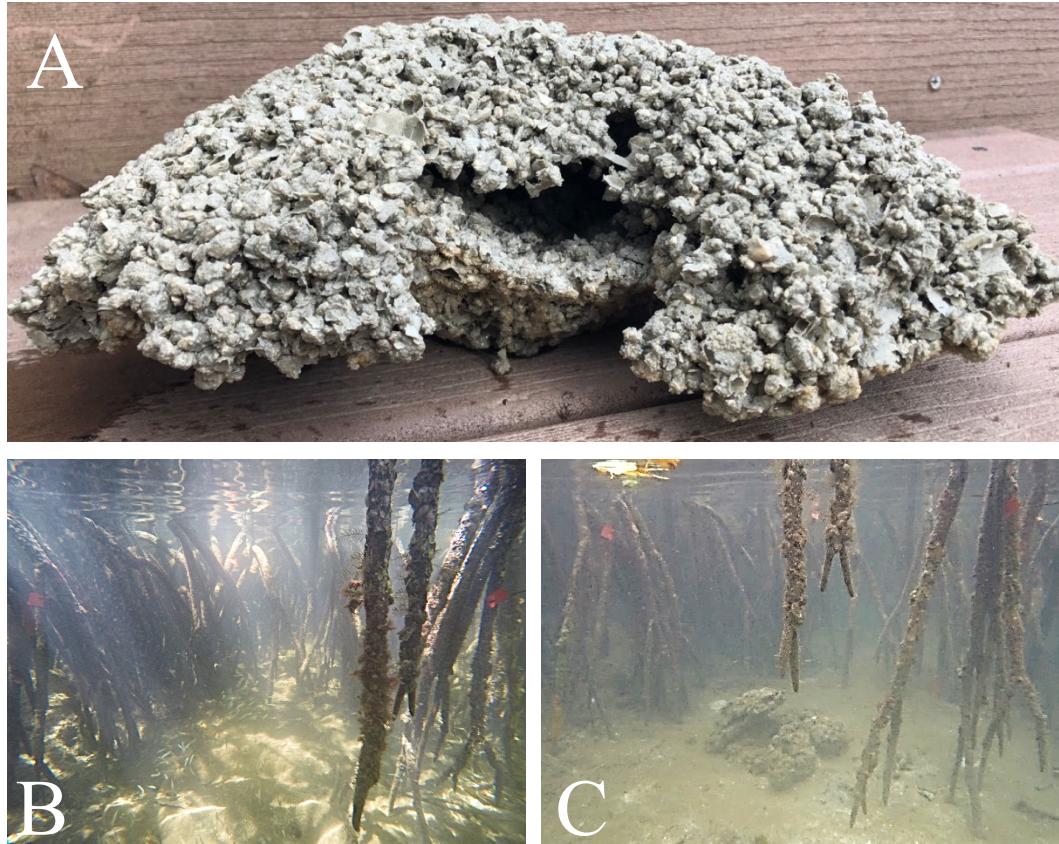


Figure 3. (A) finished piece of artificial coral, and the formation of a quadrat along the mangrove fringe (B) pre-AC and (C) post-AC.

3.4 STATISTICAL ANALYSIS

Prior to analysis, I (1) checked the data for normality (Shapiro-Wilk normality tests) and homogeneity of variance (F tests to compare two variances) and (2) pooled the observed abundance of each species across all five transects per site and for the four quadrat surveys at each coral site pre-AC and post-AC. These abundances were square-root transformed to down-weight the influence of the most abundant taxa and to normalize the data. Species were grouped together trophically following a modification of Ferreira et al. (2004) and Jones et al. (1991) as: “roving herbivores” (fishes that feed on detritus, turf algae, and macroalgae), “territorial herbivores” (fishes that feed on farmed turf-algae within their territories), “invertebrate feeders” (fishes that feed

primarily on crabs, molluscs, and other benthic invertebrates), and “carnivores” (fishes that feed on fishes and benthic organisms; Dominici-Arosemena and Wolff 2005). After checking for unimodality of species responses to the environmental variables (Hartigan’s dip test for unimodality), I examined the association between fish abundance and habitat characteristics using Canonical Correspondence Analysis (CCA). This ordination method is a powerful multivariate technique that is commonly used to analyze how multiple species (or trophic groups) respond simultaneously to environmental factors (e.g., Lara and González 1998, Dominici-Arosemena and Wolff 2005).

Parametric Welch’s two-sample t tests or nonparametric Mann-Whitney two-sample t tests (when transformations failed to normalize data) were used to compare fish community metrics (abundance, Shannon-Wiener diversity, species evenness, species richness, juvenile:adult ratio), species, trophic groups, and small, water-column fishes between coral and noncoral sites, and experimental quadrats pre-AC and post-AC. I distinguished juveniles vs. adults based on each species maturation size obtained from FishBase, the global database of fish species (or based on juvenile vs. adult colorations for *Stegastes* spp.; Dorenbosch et al. 2004). Environmental parameters between coral and noncoral sites were compared (after checking for multivariate outliers, linearity, multicollinearity, and equality of covariance matrices) using a multivariate analysis of variance (MANOVA). To lower the likelihood of type I error, I applied Benjamini-Hochberg (BH) corrections to species t tests and the MANOVA test with a maximum false discovery rate of 10%. All analyses were performed in RStudio (2019) v1.2.1335 using the packages tibble, data.table, vegan, and diptest. Bar charts and box and whisker plots were created in Microsoft Excel v16.30.

CHAPTER 4. RESULTS

In total, I found 28 fish species in 11 families and 4 trophic groups, and 57% of the species occurred at both coral and noncoral sites (Table 1). I grouped abundances of *Hypoplectrus* spp., *Scarus* spp., and *Stegastes* spp. at the genus level due to low species counts and functional similarities of species within each genus.

Table 1. List of the species observed during sampling with their respective species code, family, and trophic group. Trophic group: RH = Roving herbivore, TH = Territorial herbivore, IF = Invertebrate feeder, CR = Carnivore. Species habitat types: C = coral, NC = noncoral. Species marked with an asterisk (*) were grouped at the genus level for subsequent analyses.

Family	Species	Code	Trophic group
ACANTHURIDAE (surgeonfishes)	<i>Acanthurus chirurgus</i> C, NC	ACHI	RH
BELONIDAE (needlefishes)	<i>Abelennes hians</i> C, NC	AHIA	CR
CHAETODONTIDAE (butterflyfishes)	<i>Chaetodon capistratus</i> C, NC	CCAP	IF
GERREIDAE (mojarras)	<i>Eucinostomus melanopterus</i> C, NC	EMEL	IF
	<i>Gerres cinereus</i> C, NC	GCIN	IF
HAEMULIDAE (grunts)	<i>Anisotremus virginicus</i> NC	AVIR	IF
	<i>Haemulon carbonarium</i> NC	HCAR	CR
	<i>Haemulon flavolineatum</i> C, NC	HFLA	CR
	<i>Haemulon plumieri</i> C, NC	HPLU	CR
	<i>Haemulon sciurus</i> NC	HSCI	CR
LABRIDAE (wrasses)	<i>Halichoeres bivittatus</i> C	HBIV	CR
LUTJANIDAE (snappers)	<i>Lutjanus apodus</i> C, NC	LAPO	CR
	<i>Lutjanus griseus</i> C, NC	LGRI	CR
	<i>Lutjanus jocu</i> C, NC	LJOC	CR
	<i>Lutjanus synagris</i> NC	LSYN	CR
	<i>Ocyurus chrysurus</i> NC	OCHR	CR
POMACENTRIDAE (damselfishes)	<i>Abudefduf saxatilis</i> C, NC	ASAX	TH
	<i>Stegastes adustus</i> C, NC *	STEG	TH
	<i>Stegastes dienceaus</i> C *	STEG	TH
	<i>Stegastes partitus</i> C *	STEG	TH
	<i>Stegastes planifrons</i> C *	STEG	TH
	<i>Stegastes variabilis</i> C *	STEG	TH
SCARIDAE (parrotfishes)	<i>Scarus iseri</i> C, NC *	SCAR	RH
	<i>Scarus taeniopterus</i> C *	SCAR	RH
	<i>Sparisoma viride</i> C	SVIR	RH
SERRANIDAE (sea basses)	<i>Hypoplectrus nigricans</i> C, NC *	HYPO	CR
	<i>Hypoplectrus puella</i> C, NC *	HYPO	CR
SPHYRAENIDAE (barracudas)	<i>Sphyraena barracuda</i> C, NC	SBAR	CR

The species abundance CCA showed a difference in species composition between coral and noncoral sites (x -axis eigenvalue = 0.345, y -axis eigenvalue = 0.218; Fig. 4A). Coral sites (1–6) clustered around species *H. bivittatus*, *Hypoplectrus* spp., *Scarus* spp., and *Stegastes* spp. Noncoral sites (7–12) were more clustered around Gerridae species and *S. barracuda*. The noncoral sites showed a greater variation among sites, primarily along the second axis. Noncoral site 8 was heavily influenced by a high abundance of *Anisotremus virginicus*, and noncoral site 11 appeared to be influenced by two species of Haemulids: *Haemulon plumieri* and *Haemulon sciurus*. Coral sites 3 and 4 showed a slight separation from the other coral sites, primarily due to an increase in pH and an increase in the abundance of *Ablennes hians* for site 4.

The trophic group abundance CCA again showed a difference in fish community composition between coral and noncoral sites, although weaker than the previous CCA (x -axis eigenvalue = 0.178, y -axis eigenvalue = 0.036; Fig. 4B). All coral sites (sites 1–6) appear on the left side of the first axis, whereas all noncoral sites appear on the right side (Fig. 4B). Roving herbivores and territorial herbivores were more abundant at the coral sites, whereas invertebrate feeders were more abundant at the noncoral sites (Fig. 4B). Coral sites 3 and 4, similar to noncoral site 11, appeared to have an increase in salinity and a decrease in light intensity; coral sites 5 and 6 displayed an opposite trend. As previously shown, coral site 1 appeared to be most heavily influenced by an increase in temperature, dissolved oxygen, and prop root density. The environmental variables included in both species- and trophic group-CCAs were chosen to maximize the species-environment correlation.

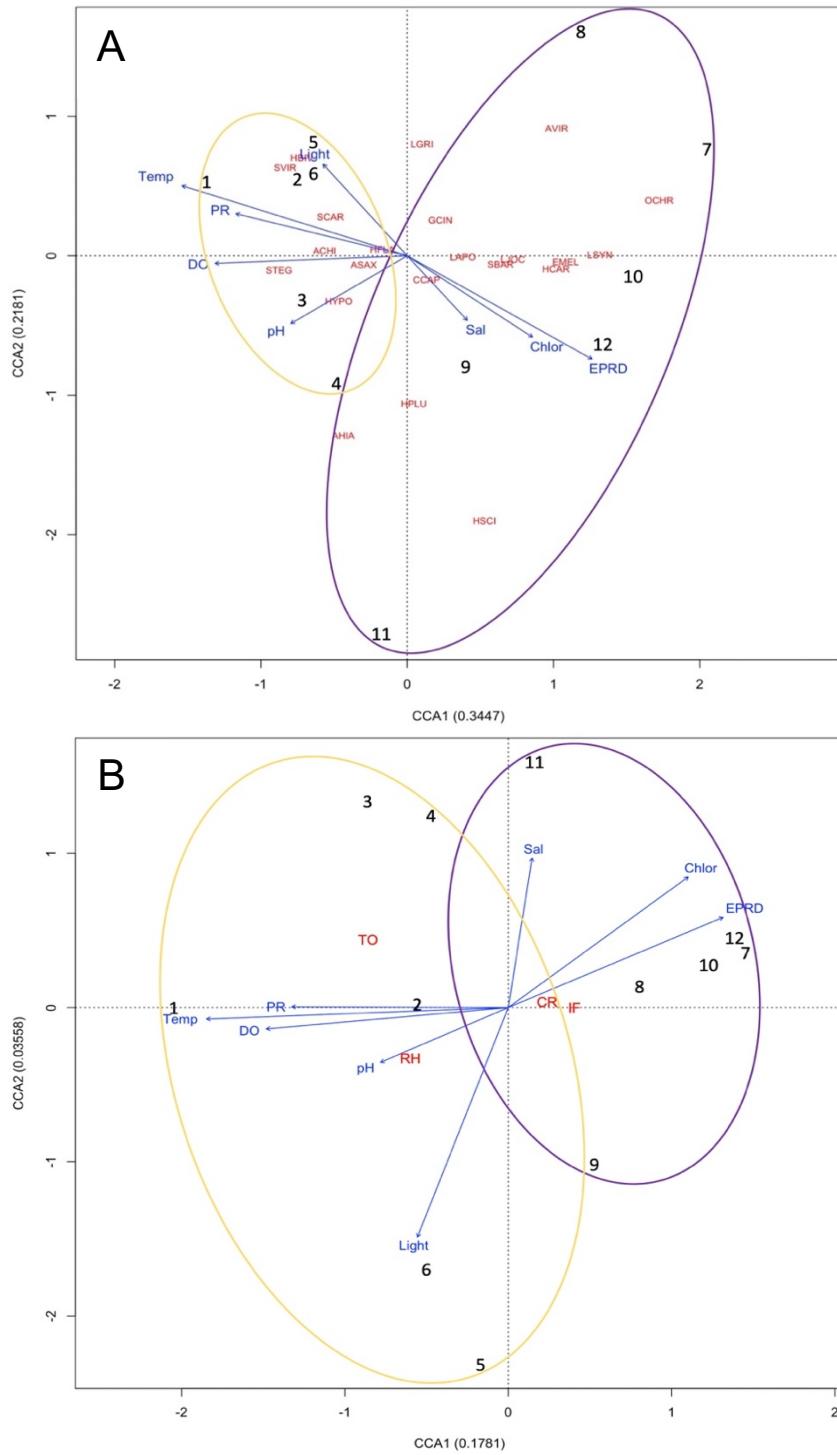


Figure 4. Canonical Correspondence Analysis (CCA) for square root-transformed (A) species abundances and (B) trophic group abundances vs. environmental variables and survey sites in Bocas del Toro, Panama. Yellow ellipses encompass coral sites; purple ellipses encompass noncoral sites. Species and trophic group codes are listed in Table 1. Environmental variable codes: Chlor = chlorophyll, DO = dissolved oxygen, EPRD = epibiont prop root diameter, Light = light intensity, PR = prop root density, Sal = salinity, Temp = temperature.

The two-sample t tests showed that species richness was significantly higher at coral sites compared to noncoral sites (Table 2, Fig. 5). Adult fishes were too scarce for a meaningful analysis of juvenile:adult ratios between sites (over 90% of the fishes encountered at both habitat types were juveniles). The adult fishes observed at coral sites were primarily *Stegastes* spp. (35%), *C. capistratus* (21%), *Haemulon flavolineatum* (18%), and *L. apodus* (15%). Adults fishes observed at noncoral sites were primarily *A. virginicus* (35%), *C. capistratus* (32%), and *L. apodus* (16%).

Table 2. Results of parametric (Welch's two-sample t test: T) and nonparametric (Mann-Whitney two-sample test: W) one-tailed [greater at coral sites(*)] or two-tailed comparisons of fish community metrics between coral and noncoral sites in Bocas del Toro. Values in bold are significant at $\alpha = 0.05$.

Community metrics	T/W	df	P
Species richness *	29.500 (W)	10	0.037
Fish abundance *	0.985 (T)	10	0.174
Species diversity *	-0.302 (T)	10	0.616
Species evenness	-1.153 (T)	10	0.276

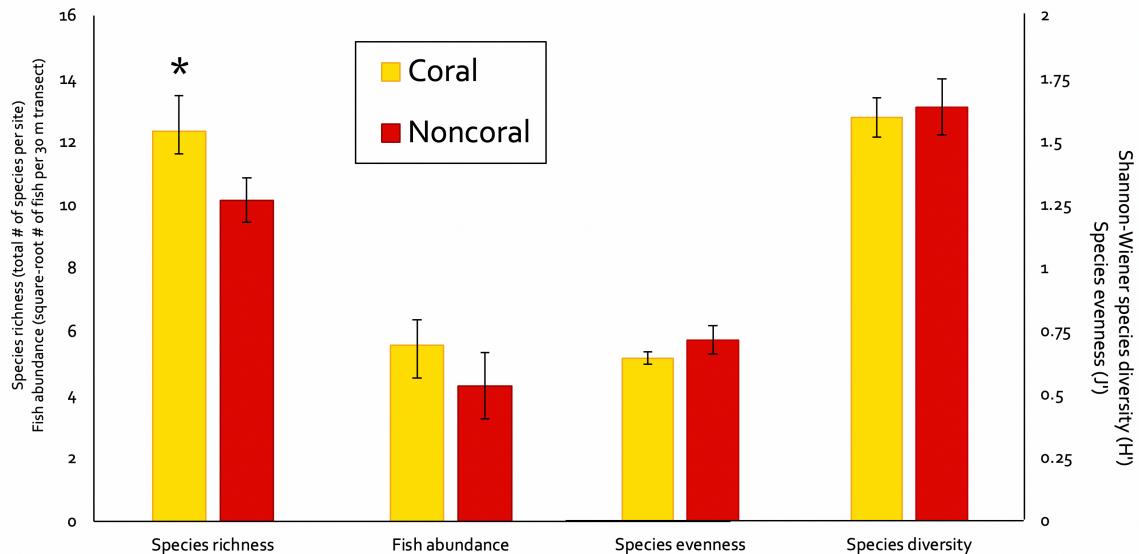


Figure 5. Comparison of mean fish community metrics between coral and noncoral sites. Error bars indicate standard error of the mean. Asterisk indicates significantly different value between coral and noncoral sites at $P \leq 0.05$ (*).

The top ten most abundant species observed during the visual surveys (at coral and noncoral sites combined) are listed in Table 3. The most abundant species were from the families Chaetodontidae, Gerridae, Haemulidae, Lutjanidae, Pomacentridae, Scaridae, Serranidae, and Sphyraenidae. Two species had significantly higher abundances at coral sites (*Scarus* spp. and *Stegastes* spp.) and one species had significantly higher abundance at noncoral sites (*S. barracuda*; Table 3).

Table 3. Results of parametric (Welch's two-sample *t* test: *T*) and nonparametric (Mann-Whitney two-sample test: *W*) one-tailed [greater at coral sites(*)] or two-tailed comparisons of square root-transformed fish densities between coral and noncoral sites for the top 10 most abundant species (at all sites combined). Values in bold are significant after applying Hochberg correction with false discovery rate of 10%.

Species	<i>T/W</i>	df	<i>P</i>	Hochberg correction
<i>Scarus</i> spp.*	3.820 (<i>T</i>)	10	0.002	0.010
<i>Sphyraena barracuda</i>	4.000 (<i>T</i>)	10	0.028	0.020
<i>Stegastes</i> spp.*	29.000 (<i>W</i>)	10	0.030	0.030
<i>Anisotremus virginicus</i>	9.000 (<i>W</i>)	10	0.074	0.040
<i>Haemulon flavolineatum</i>	1.944 (<i>T</i>)	10	0.081	0.050
<i>Hypoplectrus</i> spp.	28.000 (<i>W</i>)	10	0.119	0.060
<i>Lutjanus apodus</i>	-0.912 (<i>T</i>)	10	0.383	0.070
<i>Chaetodon capistratus</i>	-0.479 (<i>T</i>)	10	0.643	0.080
<i>Haemulon plumieri</i>	15.500 (<i>W</i>)	10	0.732	0.090
<i>Gerres cinereus</i>	0.084 (<i>T</i>)	10	0.935	0.100

The Welch's two sample *t* test (two-tailed) also showed that abundances of small, water-column fishes were significantly higher at non coral sites [mean 12.96 (SE 1.31)] compared to coral sites [mean 7.36 (SE 1.68)] (*T* = -2.625, *P* = 0.025).

Two trophic groups had significantly higher abundances at coral sites (roving herbivores and territorial herbivores) and one trophic group had significantly higher abundance at noncoral sites (invertebrate feeders; Table 4, Fig. 6).

Table 4. Results of parametric (Welch's two-sample *t* test: *T*) and nonparametric (Mann-Whitney two-sample test: *W*) one-tailed (G = greater than, L = less than) or two-tailed (N) comparisons of square root-transformed fish densities between coral and noncoral sites for each trophic group. Values in bold are significant at $\alpha = 0.05$.

Trophic group	<i>T/W</i>	df	<i>P</i>	G or L
Roving herbivores (RH)	3.534 (<i>T</i>)	10	0.003	G
Territorial herbivores (TH)	31.000 (<i>W</i>)	10	0.019	G
Invertebrate feeders (IF)	-1.833 (<i>T</i>)	10	0.048	L
Carnivores (CR)	-1.621 (<i>T</i>)	10	0.068	N

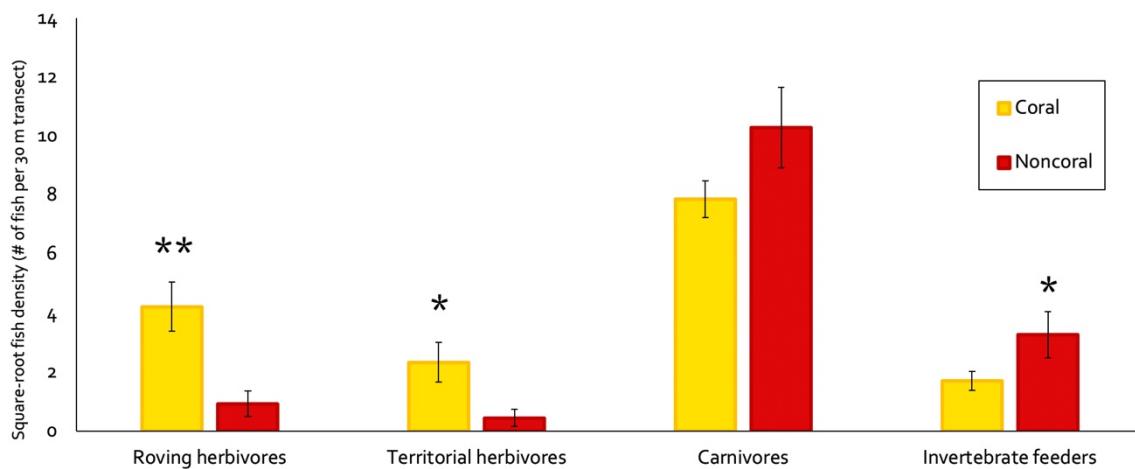


Figure 6. Comparison of mean trophic group abundances between coral and noncoral sites. Error bars indicate standard error of the mean. Asterisk indicates significantly different value between coral and noncoral sites at $P \leq 0.05$ (*) and $P \leq 0.01$ (**).

Depth was relatively consistent among sites (ranging from 0.7 to 1.0 m deep) and was not significantly different among habitat types (Welch's two sample *t* test: $T = -1.581$, $P = 0.145$). As revealed by the results of the CCAs (Fig. 4), there was a separation between coral and noncoral sites for species and trophic groups based on the environmental variables. Although not all statistically significant, temperature, prop root density, dissolved oxygen, light intensity, and pH generally increased toward coral sites and epibiont prop root diameter, salinity, and chlorophyll generally increased toward noncoral sites. This pattern was confirmed by the MANOVA test for several variables. Temperature ($P = 0.001$), prop root density ($P = 0.006$), and dissolved oxygen ($P = 0.027$) were all significantly higher at coral sites and epibiont prop root diameter ($P = 0.002$) was significantly higher at noncoral sites (Fig. 7). The two strongest variables determining fish species and trophic group distribution were temperature and epibiont prop root diameter.

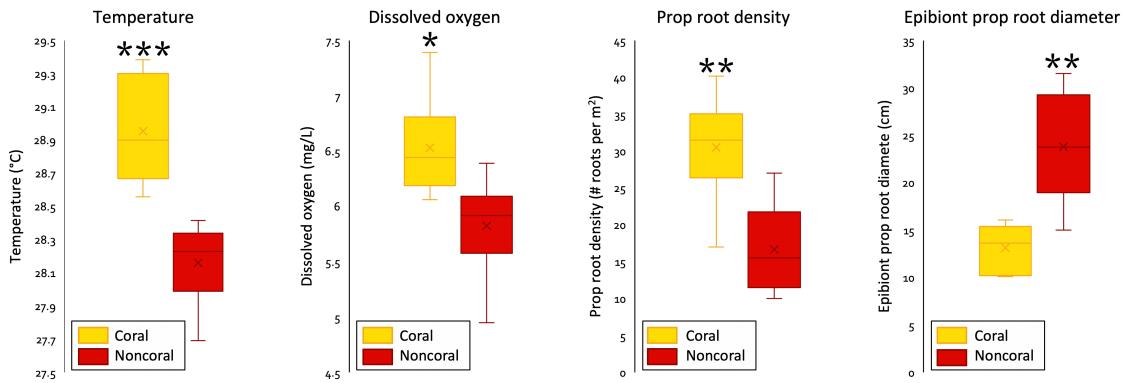


Figure 7. Box and whisker comparisons [showing minimum, 1st quartile, median, mean (x), 3rd quartile, and maximum] of significant environmental variables between coral sites (yellow) and noncoral sites (red). Asterisk indicates significantly different value between coral and noncoral sites at $P \leq 0.05$ (*), $P \leq 0.01$ (**), and $P \leq 0.001$ (***)�.

There were also several differences between the experimental quadrats pre-AC and post-AC. The two-sample *t* tests also showed that fish abundance significantly increased in experimental quadrats post-AC (Table 5, Fig. 8).

Table 5. Results of parametric (paired Welch's two-sample *t* test: *T*) and nonparametric (paired Mann-Whitney two-sample test: *V*) one-tailed [greater post-AC (*)] or two-tailed comparisons of fish community metrics in quadrats pre-AC and post-AC. Values in bold are significant at $\alpha = 0.05$.

Community metrics	<i>T/V</i>	df	<i>P</i>
Fish abundance *	21.000 (<i>V</i>)	5	0.016
Species evenness	-2.454 (<i>T</i>)	5	0.058
Species richness *	0.913 (<i>T</i>)	5	0.202
Species diversity *	-0.011 (<i>T</i>)	5	0.504

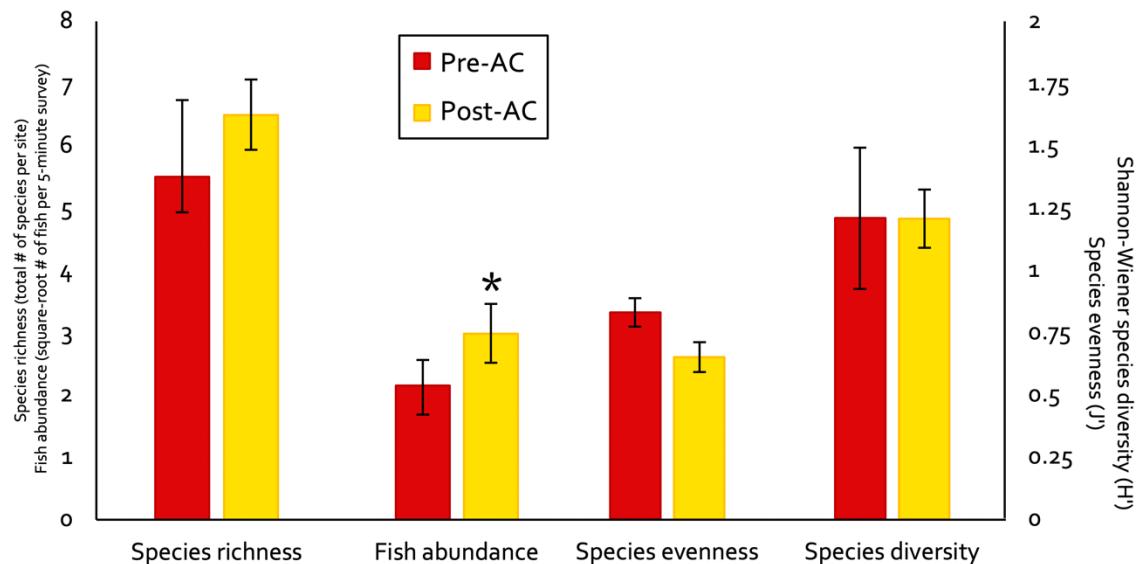


Figure 8. Comparison of mean fish community metrics before (pre-AC) and after (post-AC) artificial coral placement. Error bars indicate standard error of the mean. Asterisk indicates significantly different value pre-AC and post-AC at $P \leq 0.05$ (*).

I did not compare the pre-AC and post-AC quadrats based on species or families due to a high rate of zeros within the dataset. From a trophic group standpoint, however, there was a significant increase in carnivores and roving herbivores in the quadrats post-AC (Table 6, Fig. 9). Although not statistically significant, one juvenile territorial herbivore (*Stegastes variabilis*) was seen inhabiting the artificial coral at site 1 during the final post-AC quadrat survey.

Table 6. Results of parametric (paired Welch's two-sample t test: T) and nonparametric (paired Mann-Whitney two-sample test: V) one-tailed [greater post-AC (*)] or two-tailed comparisons of square root-transformed fish densities in quadrats pre-AC and post-AC based on trophic groups. Values in bold are significant at $\alpha = 0.05$.

Trophic group	T/V	df	P
Carnivores (CR)	4.360 (T)	5	0.007
Roving herbivores (RH) *	2.036 (T)	5	0.049
Territorial herbivores (TH) *	6.000 (V)	5	0.091
Invertebrate feeders (IF)	11.000 (V)	5	0.410

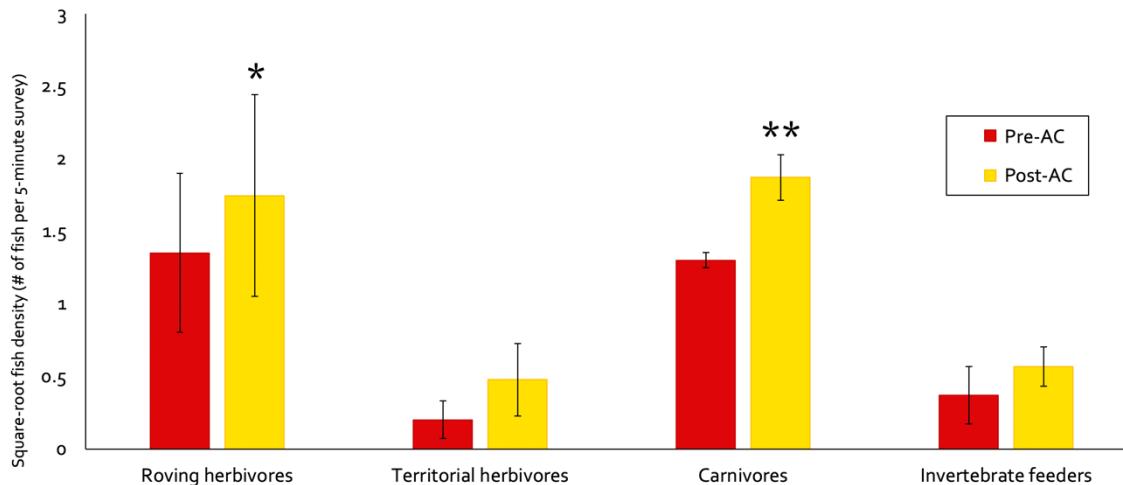


Figure 9. Comparison of mean trophic group abundances before (pre-AC) and after (post-AC) artificial coral placement. Error bars indicate standard error of the mean. Asterisk indicates significantly different value pre-AC and post-AC at $P \leq 0.05$ (*) and $P \leq 0.01$ (**).

CHAPTER 5. DISCUSSION

5.1 VISUAL TRANSECT SURVEYS

MANGROVE AND MANGROVE-CORAL HABITAT SIMILARITIES.—The present study highlights the effect that coral presence within the submerged mangrove prop roots has on the mangrove reef fish communities in Bocas del Toro, Panama. Between both habitat types, I found 28 fish species in 11 families and 4 trophic groups, with juveniles accounting for over 90% of the fishes encountered in each habitat type. This suggests that the mangrove-coral habitat in Bocas del Toro is functioning primarily as a juvenile habitat for reef fishes. Additionally, 57% of the species found occurred at both coral and noncoral sites. This supports studies that have shown that although fishes show a clear preference for a specific habitat, most fish species utilize multiple habitats simultaneously (Nagelkerken et al. 2000b, Shideler et al. 2017, Bradley et al. 2019, Sambrook et al. 2019).

In both habitat types, *C. capistratus* and *L. apodus* represented a large portion of the adult fishes observed. Both of these species are thought to be less site-attached in their adult life stages than other fishes, moving between rocky shorelines, mangrove patches, and coral reefs (Verweij et al. 2007, Jaxion-Harm et al. 2012). Also similar between coral and noncoral sites were the abundances of Haemulidae and Lutjanidae species, suggesting that the presence of coral within the mangroves is not affecting habitat utilization by these families. Studies in the Caribbean have suggested that many of these species (e.g., *H. sciurus*, *H. flavolineatum*, *H. plumieri*, *L. apodus*) are heavily dependent on mangroves as nursery habitats (e.g., Nagelkerken et al. 2002, Nagelkerken and van der Velde 2002), and the number and biomass of these species on coral reefs is significantly increased with proximity to mangrove habitats (Mumby et al. 2004).

Haemulids and Lutjanids have also been found at higher densities in mangroves closest to reefs as opposed to inland and expansive mangroves (Faunce and Serafy 2008). Since both coral and noncoral sites were located at mangrove shorelines relatively open to water with nearby reefs, it is understandable why these two habitat types displayed similar utilization by these families. The high abundance of these species in the mangrove-coral habitat in this study also seems to be consistent with the mangrove-coral habitat in the US Virgin Islands, where Rogers (2017) noted high abundances of *Lutjanus griseus* and *Haemulon* spp. In the current study, all visual surveys were conducted during daylight hours. Nocturnal behaviors among fishes are highly variable; these patterns can vary among species and life-stages, as well as between and within habitats (Hammerschlag et al. 2017). Therefore, future studies should include nighttime surveys to better describe mangrove-coral habitat utilization by all fishes.

MANGROVE HABITAT.—Differences in prey availability among trophic groups are an important factor in defining fish distributional patterns, and the presence of diverse and abundant food resources allows for the occurrence of additional fish species (Dominici-Arosemena and Wolff 2005). Noncoral sites showed an increase in epibiont prop root diameter and in the abundances of *S. barracuda*, invertebrate feeders, and small, water-column fishes. Adult *S. barracuda* abundance on coral reefs has been correlated to juvenile abundance in mangrove habitats, and mangroves are regarded as the most important biotope for *S. barracuda* juveniles (Nagelkerken et al. 2000b, Jones et al. 2010). Every *S. barracuda* encountered during the study was juvenile, and the diet of these juveniles is composed almost exclusively of teleosts (e.g., small, water-column

fishes; Hammerschlag et al. 2010). Therefore, it is possible that the greater abundance of *S. barracuda* at noncoral sites was caused by an increase in prey availability. *Sphyraena barracuda* are generally found as solitary individuals (Paterson 1998) and are habitat generalists, able to inhabit a variety of environments while preying upon fishes in various conditions (Blaber 1982, Faunce and Serafy 2008). Therefore, the abundance of *S. barracuda* seems primarily influenced by the location (and abundance) of their prey.

A high proportion of the adults observed at the noncoral sites were *A. virginicus*. This species is fairly common throughout the Bocas del Toro Archipelago and has been found in higher densities in mangroves than shallow back-reef habitats (Aguilar-Perera and Appeldoorn 2008, MacDonald and Weis 2013). The density of *A. virginicus* in mangrove habitats has been most commonly associated with deeper water sites (e.g., Drew and Eggleston 2008), but depth was relatively constant throughout the sites in the present study and, therefore, did not have a significant effect on species or trophic group abundances. Additionally, *A. virginicus* has been shown to be more abundant in mangrove habitats with larger sponge epibiont communities (MacDonald and Weis 2013). The noncoral sites had higher abundances of invertebrate feeders (primarily *A. virginicus*); it is possible that the larger epibiont communities on the prop roots at noncoral sites (although epibiont community composition was not quantified) provided better feeding opportunities for this trophic group.

MANGROVE-CORAL HABITAT.—The positive relationship between habitat structure and species richness has been attributed to the increase in substrate coverage, refuge holes, and the variety of microhabitats available (MacArthur and Levins 1964, Pittman et al. 2007). Coral sites contained significantly higher species richness compared to noncoral sites. This is understandable, as species richness has been shown to increase with increasing with percentage hard substrate and variety of growth forms (Gratwicke and Speight 2005a,b), which were both greater at coral sites compared to noncoral sites. This high species richness is also alluded to by Rogers (2017), who noted a large number of species (with high abundances of *Haemulon* spp. and *Lutjanus* spp.) occurring in the mangrove-coral habitat in St. Johns, US Virgin Islands. However, fish species abundance and richness in the mangrove-coral habitat in St. Johns are thought to have decreased in the area following hurricanes Irma and Maria in 2017 (Rogers 2019).

Roving herbivores (*Scarus* spp.) showed significantly higher abundances at coral sites compared to noncoral sites. *Scarus* spp. have been found to prefer back-reef habitat as juveniles (Adams and Ebersole 2002), although other studies have shown equal juvenile *S. iseri* use of mangrove and reef habitats (Nagelkerken and van der Velde 2002). Mangroves appear to be an abundance-limiting factor for several species of *Scarus* in the Caribbean, and abundances of *Scarus* spp. have been positively correlated with mangrove forest area (Serafy et al. 2015, Shideler et al. 2017). It is likely that the mangrove-coral habitat is providing ideal conditions for these juvenile fishes, providing the predation protection typical of mangrove habitat, while supplying preferred food sources for these fishes typical of coral reef habitat.

Territorial herbivores (e.g., *Stegastes* spp.) also showed significantly higher abundances at coral sites compared to noncoral sites. Territorial herbivores are present in high numbers in sheltered zones of massive coral reefs, and several species of *Stegastes* spp. are known to prefer shallow coral reef habitat as juveniles (Dominici-Arosemena and Wolff 2005, Chaves et al. 2012). Nagelkerken and Faunce (2008) found that densities of *Stegastes partitus* increased significantly after the removal of artificial mangrove units on the coral reef, indicating that the presence of the artificial mangrove prop root structure was not attractive to this species. *Stegastes* spp. occur primarily on the reef and it has been argued that these largely territorial fishes cannot afford to recruit to mangrove habitats and migrate to the coral reef in a later life-history stage (Shulman 1985, Nagelkerken and van der Velde 2002). Therefore, the presence of coral within the mangrove prop roots is likely the primary cause for mangrove-coral habitat utilization by *Stegastes* spp. At coral sites, a high proportion of the adults observed were *Stegastes* spp. These territorial fishes defend small areas (<2 m²; Harrington and Losey 1990) and show strong site fidelity (Shulman 1985, Gutiérrez 1998, Caldow and Wellington 2003, Abrey 2005), possibly explaining their adult abundance in the mangrove-coral habitat.

During the visual surveys, I excluded cryptic species from my observations due to the difficulty of surveying them using the belt-transect method. Cryptic fishes are often abundant, can be staple food sources, and can be important in nutrient recycling on coral reefs (Brandl et al. 2018). Therefore, the presence/abundance of cryptic fishes at mangrove-coral sites may be important in maintaining a habitat where corals are able to grow and thrive. Future studies should survey these sites again specifically focusing on cryptic fishes to determine their role in this ecosystem.

5.2 ARTIFICIAL CORAL EXPERIMENT

Herbivorous fishes can cover over 80% of the surface of reef habitats in Bocas del Toro, and this trophic group may greatly depend on the physical structure of the coral reef (Ferreira et al. 1998, Dominici-Arosemena and Wolff 2005, Chaves et al. 2012, Seemann et al. 2018). The addition of artificial coral resulted in an increase in overall fish abundance and, more specifically, an increase in the abundance of carnivores and roving herbivores. The increase in fish abundance was understandable, since increased total fish abundance is correlated with height of substrate (which was increased in the quadrats post-AC; Gratwicke and Speight 2005b). The general increase in structural complexity and substrate height may have led to the increased total fish abundance, which in turn increased carnivore abundance due to greater prey availability. This possibly explains why there was an increase in carnivore abundance in quadrats post-AC but not an increase in carnivore abundance at coral sites vs. noncoral sites (where fish abundance was not significantly different between sites). Abundance of roving herbivores has been found to be highest on coral reefs compared to other habitat types, and herbivore abundance has been positively correlated with coral cover (Eggertsen et al. 2019). The increase in roving herbivores within the quadrats post-AC is thought to be specifically influenced by the addition of the artificial coral hard substrate. This complements the visual transect surveys that showed higher abundance of roving herbivores at coral sites compared to noncoral sites. Therefore, it is likely that a structural element of the coral is attracting the roving herbivores.

Contrastingly, the addition of the artificial coral did not significantly affect the abundance of territorial herbivores (i.e., *Stegastes* spp.), although territorial herbivores were more abundant at coral sites compared to noncoral sites. Rooker et al. (1997) found that both natural and artificial reefs contained relatively equal (and high) abundances of pomacentrids, and the abundance of *Stegastes* spp. has been shown to increase relative to mean coral height (Harborne et al. 2012) and structural complexity of coral reefs (Ebersole 1985, Lirman 1994, 1999). The lack of increase in territorial herbivores (i.e., *Stegastes* spp.) in the quadrats post-AC may be explained by several factors. First, *Stegastes* spp. are extremely territorial fishes and once they settle into a habitat, their home ranges remain spatially limited (Sammarco 1983, Sponaugle et al. 2012), making it unlikely for nearby adult *Stegastes* spp. to inhabit the artificial coral. Second, it is possible that *Stegastes* spp. require settlement cues from living coral to navigate to the settlement habitat (Sponaugle et al. 2012, Dixson et al. 2014). Third, the post-AC quadrats were surveyed three weeks after artificial coral placement, giving limited time for *Stegastes* spp. larvae recruits to be exposed to the artificial coral. One juvenile (*S. variabilis*) was observed inhabiting the artificial coral during the final quadrat survey post-AC on March 15 (one day after the first quarter moon and during the minimum tide amplitude). This is consistent with D'Alessandro et al. (2007), who found that *S. partitus* larval supply peaked during quarter moons and minimum amplitude tides. Further monitoring of the post-AC quadrats is needed to determine if new *Stegastes* spp. larvae recruits will settle on the artificial coral structure.

CHAPTER 6. CONCLUSIONS

Understanding the utilization of mangrove-coral habitats by reef fishes is an important step in determining the role that this poorly described habitat serves within the coastal landscape. The first question that this study aimed to answer was: how does the fish community differ between mangrove-coral habitats and other mangrove habitats? The mangrove-coral habitat in this study is functioning primarily as a juvenile habitat for reef fishes, containing many of the same species (and increased species richness) as other mangrove communities in the archipelago. Abundances of economically important Haemulidae and Lutjanidae species were similar in both habitat types. The mangrove habitat had higher abundances of invertebrate feeders and *S. barracuda*, and it is likely that this was a result of increased prey availability/abundances of epibionts and small, water-column fishes, respectively. The mangrove-coral habitat had higher abundances of roving herbivores (*Scarus* spp.) and territorial herbivores (*Stegastes* spp.). For *Scarus* spp., it is likely that the mangrove-coral habitat has ideal conditions for these juvenile fishes, providing predation protection via mangroves and preferred food sources via coral. For *Stegastes* spp., coral presence within the mangroves is likely the main cause for their mangrove-coral habitat utilization.

The second question that this study aimed to answer was: is the difference in the fish community due to the physical structure of coral or a biological aspect of the living coral itself? The addition of artificial coral resulted in an increase in overall fish abundance (specifically roving herbivores and carnivores). The increase in roving herbivores complemented the increase observed at coral sites vs. noncoral sites and indicates that this trophic group is attracted by the hard substrate that the coral provides.

The lack of increase in territorial herbivores (contrastingly to the increase observed at coral sites vs. noncoral sites) is most likely explained by the small home ranges of these species and need for a longer sampling period after artificial coral placement to encompass larval supply cycles. In Bocas del Toro, pressure from commercial and artisanal fisheries has caused declines in abundances of larger predatory species (Haemulidae, Lutjanidae, Serranidae) and herbivorous species (Scaridae) throughout the archipelago. These fishes have specific functional roles in maintaining ecosystem balances, and the continued loss of these species may have devastating effects on the surrounding coastal landscape. Specific attention should be paid to mangrove-coral habitats, as this habitat type provides the ability to conserve mangroves, corals, and reef fishes all within one location. Further monitoring of the mangrove-coral habitats should continue to develop longer-term datasets (encompassing seasonal variations as well as nighttime observations) to better analyze the mangrove-coral habitat and its role within the tropical mangrove-seagrass-reef seascape.

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