

The Ecological Impacts of Mangrove Patch Perimeter on Fringe Prop Root-Dependent Communities

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ABSTRACT

The rapid changes in global climate and overexploitation of natural resources are significant factors when considering the persistence and function of mangroves. Mangroves serve as a refuge for a diversity of aquatic, terrestrial, and avian species that generate valuable ecosystem services for human communities that depend on these organisms. Through worsening natural and anthropogenic processes, such as intensified hurricanes and deforestation, the widespread loss of mangrove forests results in fragmentation, producing truncated, isolated mangrove patches. Specifically, in Bocas del Toro, naturally segmented mangrove patches of different sizes may impact mangrove-dependent organisms as a result of reduced habitat. To address this knowledge gap, we collected data on two mangrove fringe-dependent communities to identify significant differences in biodiversity, family evenness, and community structure as a function of different mangrove patch perimeters. Select fish families and epibiont categories displayed significant correlation to increasing mangrove patch perimeters. However, the results did not yield a significant relationship between different mangrove patch sizes and most population metrics of the dependent marine communities. Instead, mangrove patch size had little ecological impact, which expanded the previous hypothesis from patch size having a significant impact to patch assemblage playing a role in the diversity and presence of mangrove-dependent communities. Given that mangrove patches varied in size by several orders of magnitude and had similar fish and epibiont communities, smaller islands may have essential conservation values similar to larger habitat patches and provide redundancy that contributes to overall system equilibrium.

RESUMEN

Los cambios rápidamente del clima global y sobreexplotación de recursos naturales son factores significativos al considerar las persistencia y funciones de manglares. Manglares sirven de la refugia a una diversidad de especies acuáticas, terrestres y aviares que los producen servicios ecosistémicos valiosos por comunidades que dependen de los organismos. Por el empeoramiento de los procesos naturales y antropogénicos, como huracanes intensificados y deforestación, la pérdida generalizada de bosques

de manglares da lugar a la fragmentación, produciendo parches de manglares truncados y aislados. Particularmente en Bocas del Toro, parches de manglares naturalmente segmentados de tamaños diferentes podría afectar a los organismos que dependen de los manglares como resultado de la reducción del hábitat. Para abordar esta brecha de conocimiento, recopilamos los datos de dos comunidades dependientes de los manglares para identificar diferencias significantes de biodiversidad, uniformidad de familia, y estructura de comunidad en función de parches perimetros diferentes. Distintas familias de peces y epibiontes de las raíces expusieron las correlaciones significativas con el aumento del parches perimetros. Sin embargo, los resultados no produjeron una correlación significativa entre parches de manglares perimetros diferentes y la mayoría de las métricas de población de las comunidades marinas dependientes. En cambio, el tamaño de parche manglar tuvo poco impacto ecológico, que desarrolla un hipótesis que suggestar tamaño de parche tiene un impacto significativo a ensamblaje de parches desempeña un papel en la diversidad y la presencia de las comunidades manglares dependientes. Puesto que las parches manglares variaron en tamaño por ordenes de magnitud y tuvieron comunidades similares de peces y epibiontes, parches pequeños pueden tener valores esenciales de conservación similar a los parches grandes y pueden proveer redundancia ecológica que contribuya al equilibrio general del sistema.

INTRODUCTION

Mangroves are halophytic trees and shrubs that occupy coastal wetlands throughout subtropical and tropical latitudes (Hutchings and Saenger 1987). These tropical arboreal structures, particularly along the fringe, provide several ecosystem services that provide benefits to organisms living along coastlines worldwide as well as regulating processes with a global impact. Ecological benefits from mangrove forests include water quality improvement, wave amelioration, habitat creation, and carbon sequestration (Lin and Dushoff 2004; Waycott et al. 2011; Alongi 2014; Barreto et al. 2015; Whitfield 2016). These functions of mangrove forests not only contribute to mitigating climate change but foster an environment that can be inhabited by a variety of marine biota that benefit the forest. A broad array of tropical fishes found in mangrove habitats fall under distinct trophic groups – for example, macroalgae grazers, invertebrate feeders, and carnivores – that sustain healthy trophic food webs within this ecosystem (Wright 2019). Fringe mangroves also foster suitable habitat that encourages the diversity of epibionts, which are sessile organisms that attach to the aerial prop roots of mangroves. Epibionts, in return, provide beneficial services to the mangrove ecosystem. For example, epiphytic sponges perform water filtration,

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nutrient exchange, and habitat creation, which enhances the abiotic conditions of the surrounding environment for the dependent communities and trees themselves (Stachowicz 2001). Consequently, fringe mangroves exhibit facultative mutualism through the exchange of benefits between the tree and its dependents (Ellison et al. 1996). This quality highlights the importance of these ecosystems and how fringe mangroves can impact tropical marine biodiversity.

Unfortunately, between 1980 and 2010, the total mangrove forest area declined between 20% – 35% worldwide (Polidoro et al. 2010). Mangrove area is expected to continue declining by 1% per year due to worsening natural and anthropogenic events, which vary regionally (Goldberg et al. 2020). The most significant natural causes of mangrove loss are intensified, frequent storm surges and terrestrial droughts (Goldberg et al. 2020). However, these seemingly natural impacts are generated and amplified by anthropogenic activity, such as excessive carbon emission and destruction of ecological carbon sinks, which lead to warmer sea and air temperatures (Reguero et al. 2019; Environmental Defense Fund 2022). Anthropogenic mangrove degradation is mostly attributed to the expansion of aquaculture along with deforestation for coastal development (Barbier and Cox 2003; Thomas et al. 2017). Such significant loss through these destructive methods alters the biogeochemical and ecological processes that mangrove forests have provided for centuries and inevitably leads to less habitat protection, which is a significant component of this present study (Kathiresan and Bingham 2001).

Alterations to these forests impact the ecological function of mangroves across a variety of scales. Particularly in Bocas del Toro, Panama, numerous mangrove forest sites have fallen victim to deforestation for agriculture, construction, and viewsheds (Granek and Fraiser 2007). Eastern Panama and Caribbean regions that overexploit mangroves are also areas most likely to experience the harsher consequences of climate change, specifically sea-level rise (Giorgi 2006; Woodruff et al. 2013). Landward sediment erosion significantly inhibits peat compaction — organic substrate accumulation beneath the roots — which mangroves use to adapt and combat threatening rising sea levels (Sánchez-Núñez et al. 2019). Further, such destruction leaves mangrove fringes more susceptible to natural threats, due to reduced root density, and anthropogenic pressures, resulting in a positive feedback loop of within-patch mangrove loss (Blanco-Libreros and Ramirez-Ruiz 2021). Considering the vast marine biodiversity found throughout the Caribbean and Latin America (Miloslavich et al. 2010), weakened mangrove structure through fragmentation is a major concern in ecological and biological studies. The livelihood of the flora and fauna that depend on these forests is greatly impacted since their once-fortified coastal buffer and habitat has become an unstable and vulnerable site (Bryan-Brown et al. 2020). Mangrove-endemic organisms are forced to either quickly adapt to or evacuate the

new and unfavorable conditions, which threatens established trophic interactions, endangered species refuge, and mangrove biodiversity (Luther and Greenberg 2009).

The sizes and orientations of coastal habitats have been found to have a noticeable impact on species biodiversity. For example, Crotty et al. (2018) discovered that increased habitat patch size directly increases the variety of mollusks that reside within the bounds of the surveyed marsh. While this patch theory has been integral in understanding marsh ecosystem dynamics, this theory can apply to understanding tropical mangrove ecosystems, considering the ecosystem services they provide and their high biodiversity. Root epibiont and fish communities that depend greatly on hanging, submerged fringe root formations display great diversity within and among different mangrove patches. For example, fringe forests on the windward side of mangrove patches have significantly lower epibiont diversity, resulting in an algae-dominant root structure in contrast to the occupancy of various epibiont phyla (i.e. Chlorophyta, Cnidaria, Mollusca, Porifera) along the leeward edge of the patch (Farnsworth and Ellison 1996). MacDonald and Weis (2013) reported a positive correlation between increased root organism species richness and increased fish species richness. Fish species richness has a strong correlation to diversity in fish trophic groups, which provides numerous ecosystem services — i.e., invertebrate population control, macroalgae grazing, and nutrient cycling — to create a balanced and healthy mangrove habitat (Halpern and Floeter 2008; Burkepile et al. 2013; Henderson et al. 2019). The success of these specific communities provides benefits to society and other habitats, from providing low-income fishing communities with job and food security to populating coral reefs with important grazers (Ellison 2014; Seemann et al. 2018).

Recognizing that reduced mangrove forest area by means of anthropogenic or natural fragmentation is crucial to understanding altered marine population dynamics and potential biodiversity hotspots in tropical regions, we undertook a study to analyze the impact of fragmentation on mangroves in Panama. This study utilized different analyses to address one central question: how does mangrove patch perimeter impact the presence and biodiversity of root epibiont and fish populations? These two foci were analyzed to evaluate the health and functionality of segmented mangrove patches in Bocas del Toro. The main goals of this study were to connect the concepts of mangrove fragmentation to biodiversity, expand upon the knowledge of potential mangrove patch weaknesses due to habitat size, and provide guidance on mangrove forest conservation within this region.

METHODS

Study Site

This study was conducted between July and August of 2022 on the Caribbean coast of northeast Panama, where

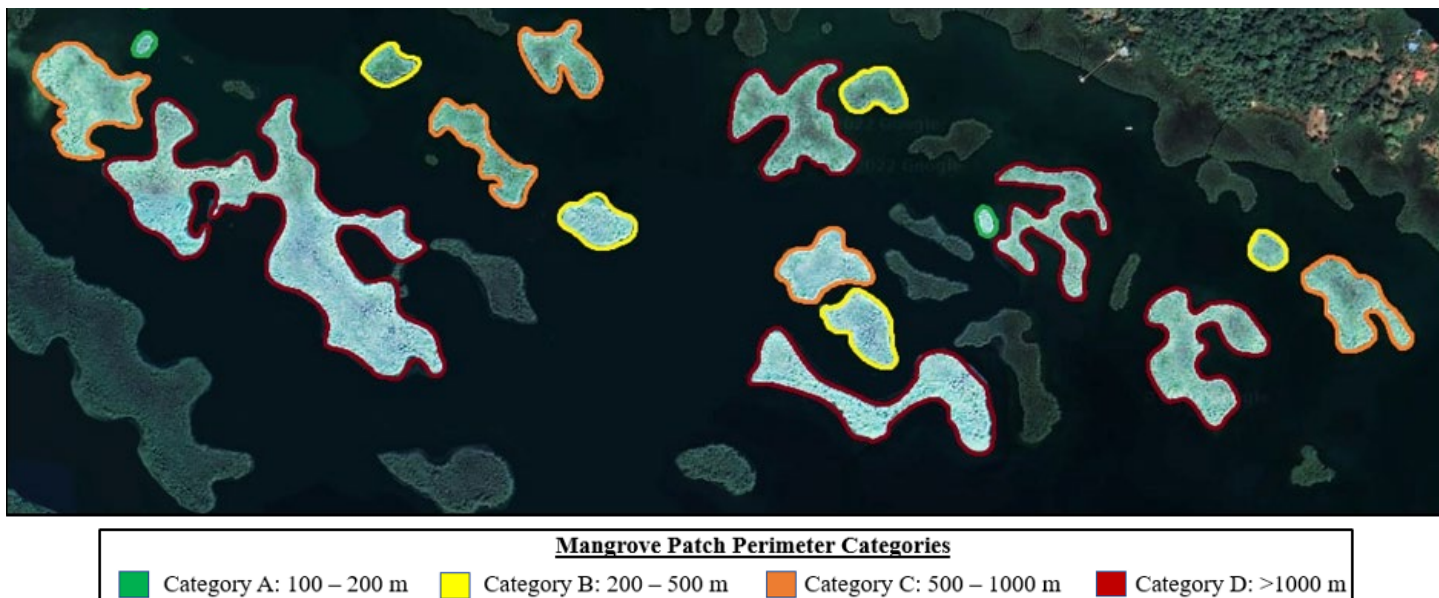


Figure 1. Map of the 20 sampled mangrove patches (highlighted) in Bahía Almirante. (©Google Earth)

the Bocas del Toro province expands over 250 km² of the mainland and various islands (Figure 1). The six main islands within this province – Isla Colón, Isla San Cristóbal, Isla Pastores, Isla Bastimentos, Isla Popa, and Cayo Solarte – surround and partially enclose Bahía Almirante. Tropical rainforests border the bay on the mainland and throughout the archipelago of Bocas, with several towns along the coasts.

For this study, 20 mangrove patches south of Cayo Solarte were selected for analysis (Figure 1). These patches consist of primarily red mangroves (*Rhizophora mangle*) and were selected because they had more than 50 meters of coastline. The perimeters were measured from Google Earth (using the measurement tool) and organized the mangrove patches into four perimeter categories (A: 100–200m, B: 200–500m, C: 500–1000m, D: >1000m) to ensure that there was equal number of surveys to reduce variability in the statistical analyses. These islands were usually surrounded by substrate ranging from fine silt to fine sand, and further from the peat bank, turtle grass (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), or a mix of both seagrass species occurred.

Once the mangrove patches were chosen and organized into the four perimeter categories, the following procedures were performed on the leeward side of each patch which was expected to have calmer tidal and boat activity; however, the overall tidal range in Bahía Almirante is relatively small — ranging from 2 cm to 15 cm above standard sea level (Guzman et al. 2005). The procedures include mangrove fish underwater visual surveys, which analyzed the population composition across the 20 patches, and epibiont assemblage analysis.

Mangrove-Fish Underwater Visual Surveys

For each mangrove patch, the researchers snorkeled along a

50-m transect, which was deployed on the leeward side following the natural contour of the forest canopy. The depth of the benthos varied depending on the site, with measurements between less than a meter to roughly three meters deep. To ensure that the survey captured the undisturbed activity of the fish, five minutes of minimal activity followed the deployment of the transect, in which the lead researcher waited to start the survey. Underwater visual surveys (UVS; Nagelkerken et al. 2000; MacDonald and Weis 2013) were conducted along the transect to count the number and species of each fish observed. This survey was timed to ensure that method replication at different patches was consistent, generally with a duration of 5 minutes. To acquire a full assessment of fish communities inhabiting each specific patch including transient species, five separate surveys, conducted between 9:00 and 16:00, were completed at each site. Fish were identified using a supplemental PowerPoint of mangrove fish species commonly found among Panamanian mangroves provided by Jen Wright (2020).

For post-UVS analysis, from the total number of fish families recorded, nine trophic families were selected based on the families analyzed in the Wright study (2019) and were the most common families seen throughout the surveys. The data were extracted and used to conduct general population analysis and statistical tests to identify any significant difference between fish family presence or abundance as a function of mangrove patch size.

Root Epibiont Analysis

Following the mangrove-fish survey, the mangrove root epibiont survey was conducted along the same 50-m transect. One root was chosen approximately every 2 m, yielding a total of 25 roots surveyed and analyzed at each site. Included in the survey, the hanging roots had to meet three requirements: (1) above the water's surface, there

had to be an indication of a mean high-water line (MHWL) as a reference to place the survey quadrat to be placed 40 cm below, (2) the submerged portion of the root had to be at least 50 cm long, and (3) the root itself could not be connected to the benthos. If these requirements were not fulfilled, the closest root that met the criteria was selected for analysis. The MHWL was established by a biological indicator—the presence of *Bostrychia* algae (Yokoya et al. 1999) – and measured 40 cm below the MHWL with a 1-m labeled PVC pipe. These three specific criteria were derived from various studies performed on mangrove roots in Panama (Sparks 2020; Stewart et al. 2022), since the overarching goal of this study was to capture data from an uninterrupted, subtidal epibiont assemblage. After confirming the measurements from the MHWL and submerged root length, a labeled PVC quadrat (50 x 10 cm) was held 40 cm below the *Bostrychia* line on the outward side of the root. Within the bounds of the measurement quadrat, two videos — each with a duration of roughly 20 seconds — and four pictures of the epibiont community were captured on an Olympus Tough TG-6 waterproof camera. Hanging root length, including the indicated MHWL, and presence count of the epibiont assemblages were recorded and organized into 14 categories: empty space, barnacle, bivalve, green algae, red algae, crustose coralline algae (CCA), turf algae, cyanobacteria, sponge, tunicate, tube worm, hydroid, anemone, and bryozoan. This process was repeated for the entirety of the 50 m transect, resulting in 50 videos and 100 pictures of 25 analyzed root-epibiont communities per mangrove patch.

Data Analysis

For the statistical analyses, I checked for normality (Shapiro-Wilk normality test) and homogeneity of variance (Levene test) in R, to ensure that the data met the assumptions of parametric statistical tests. If the assumptions for the parametric test analysis were not met, the Kruskal-Wallis and Welch’s one-way ANOVA tests were used in place of the parametric analysis of variance (ANOVA) tests.

For the UVS analysis, the data were analyzed from two perspectives, looking at fish family differences across mangrove patch categories and all island sites. The number of fish was pooled in each selected family and determined each family’s sample proportion with respect to the total fish count at each site. For categorical differences, the ANOVA and Kruskal-Wallis tests were conducted accordingly on the family percent occurrence to establish if there were significant differences between this factor and patch size. The family composition of each category and the total family abundance and percent occurrence were presented in an array of graphics using Microsoft Excel. For broad community analysis, regression analyses were conducted in Microsoft Excel and R to uncover any significant trends between each family proportion and all sampled mangrove patch sizes. Lastly, to analyze general fish family biodi-

versity across all patch sizes, the Shannon-Weiner biodiversity index was utilized to focus on relative fish family abundance, and the Pielou’s evenness index was utilized for species evenness.

The root epibiont data were converted into 20 presence-absence tables, then the count of filled-in blocks under each epibiont was extracted and organized based on mangrove patch perimeter categories. The total percentages of every selected epibiont (ex. Epibiont 1) in each patch size category (ex. Category X, comprised of 5 sites) relative to the total number of all epibionts were calculated using the following equation:

$$\text{Overall Epibiont \%}_{(\text{Category X})} = \frac{\# \text{ of Epibiont } 1_{X1} + \# \text{ of Epibiont } 1_{X2} + \# \text{ of Epibiont } 1_{X3} + \# \text{ of Epibiont } 1_{X4} + \# \text{ of Epibiont } 1_{X5}}{\sum \text{ Epibiont } 1_X + \sum \text{ Epibiont } 2_X + \sum \text{ Epibiont } 3_X + \dots + \sum \text{ Epibiont } 14_X}$$

These percentages were then organized into a csv file to conduct ANOVA and TukeyHSD analyses to discover significant differences between each epibiont’s average percentage and patch size category. The epibiont proportions per size category were arranged into four stacked bar charts using Microsoft Excel.

RESULTS

Underwater Visual Survey Analysis

In total, 15,036 fishes from 15 different families were accounted for across all 100 underwater visual surveys. Of these, 1564 fishes from nine trophic families were recorded and used for analysis (Table 1). These fish families were classified under various trophic groups and organized similarly to the study by Wright (2019).

The first analytical test was establishing the differences between each fish family’s composition, considering size categories and all sampled patch perimeters. From a categorical standpoint, most fish families within their respective patch perimeter categories presented a similar family

Table 1. An alphabetical list of the nine most prevalent fish families selected for analysis, accompanied by their common family name and trophic classification.

| Family | Common Family Name | Trophic Group |
|----------------|--------------------|-----------------------|
| Chaetodontidae | Butterflyfishes | Invertebrate feeder |
| Gerridae | Mojarras | Invertebrate feeder |
| Haemulidae | Grunts | Invertebrate feeder |
| | | Carnivore |
| Lutjanidae | Snappers | Carnivore |
| Poeciliidae | Mosquitofishes | Surface grazer |
| | | Invertebrate feeder |
| Pomacentridae | Damselfishes | Territorial herbivore |
| Scaridae | Parrotfishes | Roving herbivore |
| Serranidae | Sea basses | Carnivore |
| Syphraenidae | Barracudas | Carnivore |

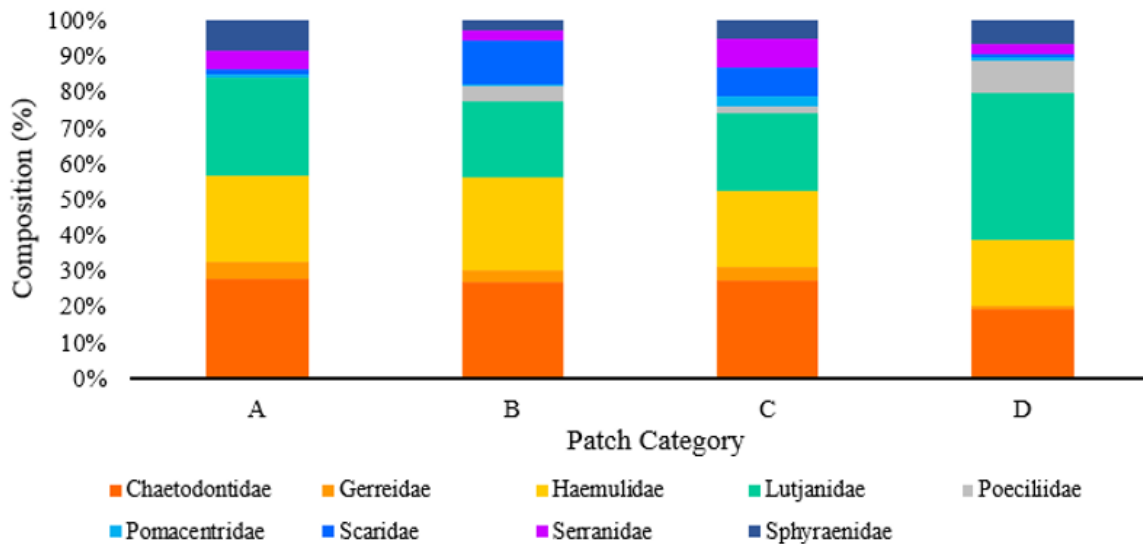


Figure 2. Fish family trophic groups' composition (%) by mangrove patch category in Bocas del Toro, Panama. Distribution of the number of fish within each family relative to the total fish count based on Patch Categories. Progression from small to largest patch perimeter length: A: 100–200m, B: 200–500m, C: 500–1000m, D: >1000m.

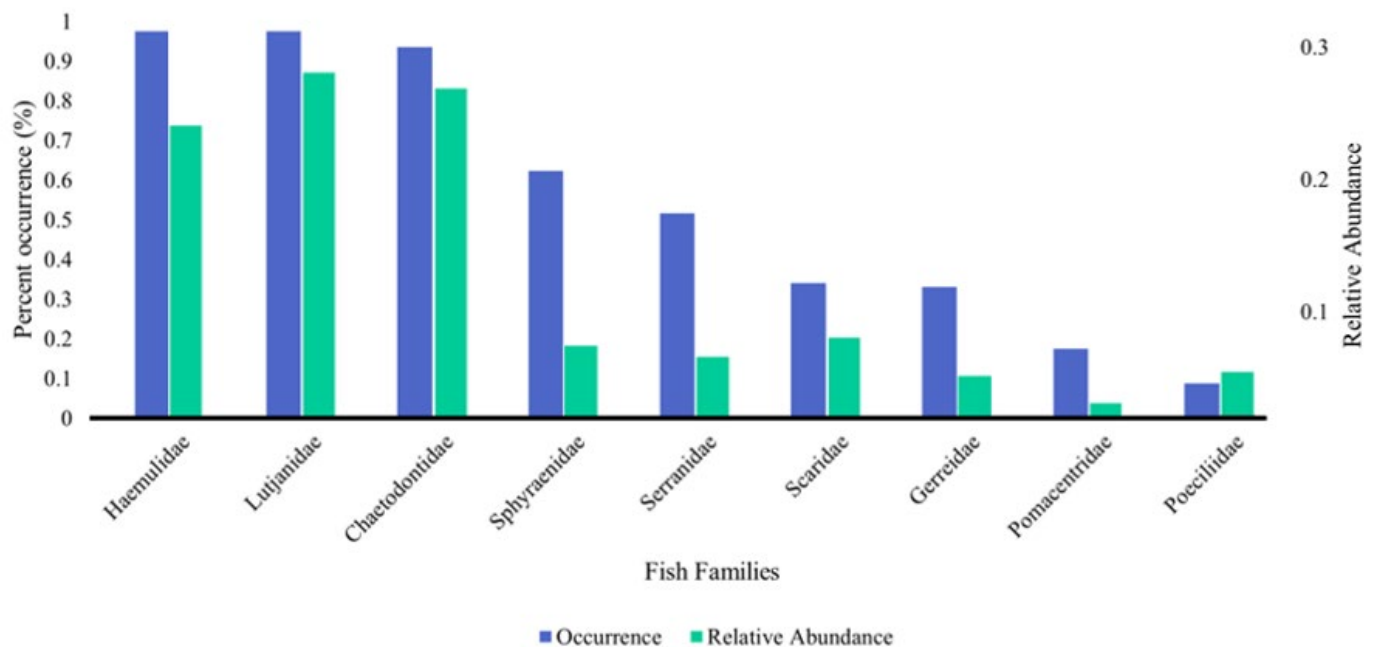


Figure 3. Population analytics of selected fish families found south of Cayo Solarte. Percent occurrence of fish from the selected fish family (%) refers to the number of times each family was recorded divided by 100 surveys. Relative abundance refers to the total number of fish from each family compared to the total fish population.

composition (Figure 2). There were differences between the overall percentage of select fish families in different categories, which was confirmed by generalized linear model analysis for family diversity and species evenness. The correlation between either of these two factors and patch perimeter failed to display significant results, which further supported the categorical findings of nearly uniform familial composition across the variety of patch perimeters (diversity: $p = 0.509$; evenness: $p = 0.981$).

The next step was to analyze significant differences in specific fish family abundances across categories and

all island perimeters. This analysis focused on the specific number of fish, instead of the overall proportion, to investigate the population dynamics of different sites based on perimeters. Each category had the following total fish count from the selected fish families: A: 389; B: 463; C: 376; and D: 293. Although the largest patch perimeter (D) had a noticeably smaller population size compared to the other categories, there were no significant differences between the overall populations within the categories after running an ANOVA on the normally distributed data ($F(16,3) = 0.947$, $p = 0.441$).

Although the total number of fish provided nonsignificant results across all patch sizes, a secondary question arose: per family, would there be differences between patch sizes? To that effect, using the number of fishes from all families by patch size, a one-way ANOVA test presented significant results ($F(425,38) = 3.801$, $p < 1 \times 10^{-6}$). The post-hoc comparison with Bonferroni-holm correction revealed that some families were significantly different from patch size to patch size (i.e., the Gerreidae population in A was significantly smaller than the Chaetodontidae population in B, $p = 0.008$). Regarding intra-family population comparison across patches, the number of fish in the Chaetodontidae family within B was significantly greater than the Chaetodontidae population in D ($p = 0.0139$). This may have been a result of the particular resources (i.e. proximity to food availability and protection) found around the smaller mangrove patches.

Another noteworthy finding was the prevalence of fish families Chaetodontidae, Haemulidae, and Lutjanidae (Figure 3). These specific families had the highest relative abundance across all sites and perimeter categories, with

the relative abundance of Chaetodontidae ranging from 19% to 27%, Haemulidae ranging from 18% to 25%, and Lutjanidae ranging from 21% to 41%. In fact, most of the significant population differences discovered in the one-way ANOVA were derived from these three most abundant families.

A generalized linear model analysis was conducted to analyze the fish family abundance in relation to patch perimeter. The result was nonsignificant ($p = 0.2$), indicating a lack of sufficient correlation between fish count and patch perimeter. However, when analyzing individually per fish family population, Lutjanidae was the only family to provide significant results ($p = 0.0137$). Specifically, the proportion of Lutjanidae within its respective patch community increased with increasing patch perimeter (Figure 4). To further investigate lutjanid prevalence across patch sizes, a one-way ANOVA using the binned population for this family was conducted. This test provided the significant finding that the largest perimeter range category (D) had the overall highest proportion of Lutjanidae compared to all other Lutjanidae proportions in the remaining categories (ANOVA: $F(16,3) = 3.831$, $p = 0.0304$).

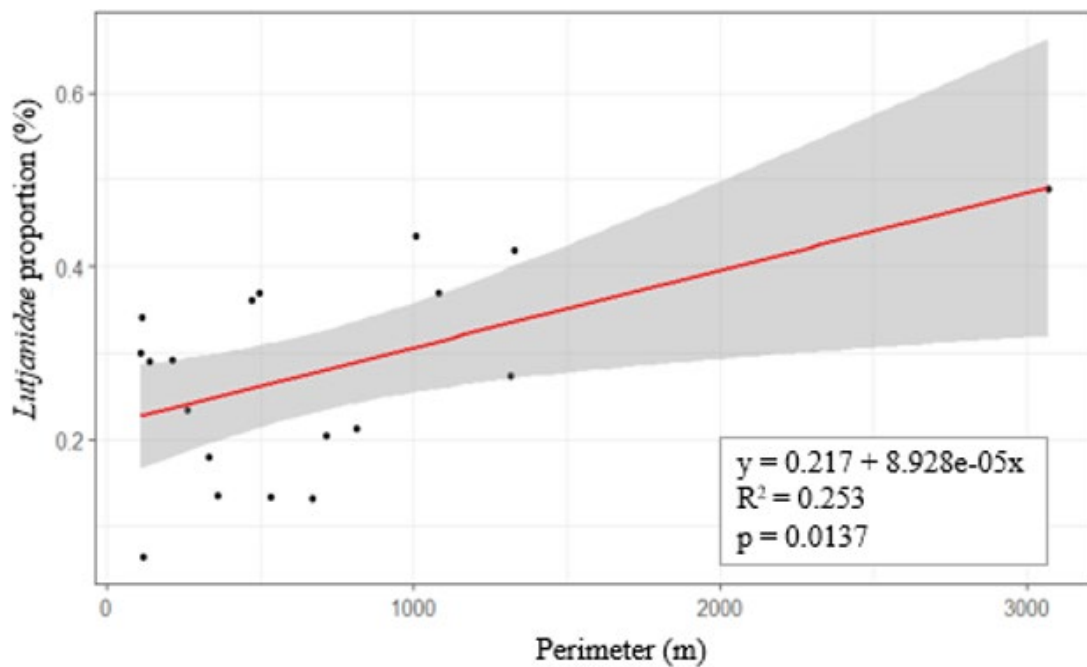


Figure 4. Fish family Lutjanidae proportion across increasing patch perimeter. Proportion (%), also referred to as relative abundance within each sampled site, of this selected family yields a positive correlation with greater mangrove patch perimeter. The p-value is deemed significant according to $\alpha (0.05 > 0.0136)$.

| Category | Anemone | Barnacle | Bivalve | Bryozoan | CCA | Cyanobacteria | Empty | Green Algae | Hydroid | Red Algae | Sponge | Tubeworm | Tunicate | Turf Algae |
|----------|-----------|-----------|-----------|----------|----------|---------------|-----------|-------------|-----------|-----------|-----------|-----------|-----------|------------|
| A | 3 | 2 | 47 | 3 | 5 | 57 | 16 | 81 | 6 | 57 | 83 | 15 | 40 | 41 |
| | 0.006579 | 0.00438 | 0.1031 | 0.006579 | 0.01096 | 0.125 | 0.035088 | 0.177632 | 0.01316 | 0.125 | 0.182018 | 0.032895 | 0.087719 | 0.089912 |
| B | 12 | 9 | 66 | 5 | 8 | 9 | 18 | 88 | 15 | 57 | 83 | 25 | 50 | 9 |
| | 0.026432 | 0.019824 | 0.145374 | 0.011013 | 0.017621 | 0.019824 | 0.039648 | 0.193833 | 0.03304 | 0.125551 | 0.182819 | 0.055066 | 0.110132 | 0.019824 |
| C | 5 | 5 | 73 | 0 | 2 | 69 | 14 | 87 | 8 | 58 | 62 | 18 | 43 | 45 |
| | 0.010225 | 0.010225 | 0.149284 | 0.000000 | 0.00409 | 0.141104 | 0.02863 | 0.177914 | 0.01636 | 0.118609 | 0.126789 | 0.03681 | 0.087935 | 0.092025 |
| D | 1 | 14 | 47 | 0 | 5 | 48 | 9 | 99 | 7 | 49 | 76 | 21 | 48 | 22 |
| | 0.002242 | 0.03139 | 0.105381 | 0.000000 | 0.011211 | 0.107623 | 0.020179 | 0.221973 | 0.015695 | 0.109865 | 0.170404 | 0.047085 | 0.107623 | 0.049327 |

Table 2. Categorized epibiont count calculated from Presence-Absence tables. Counts (in bold) were determined by the number of filled-in (present) blocks found within each bin for its corresponding epibiont. Percentages were calculated using Equation 2. Progression from Category A to Category D is representative of increasing patch perimeter with the following measurements: A: 100–200m, B: 200–500m, C: 500–1000m, D: >1000m.

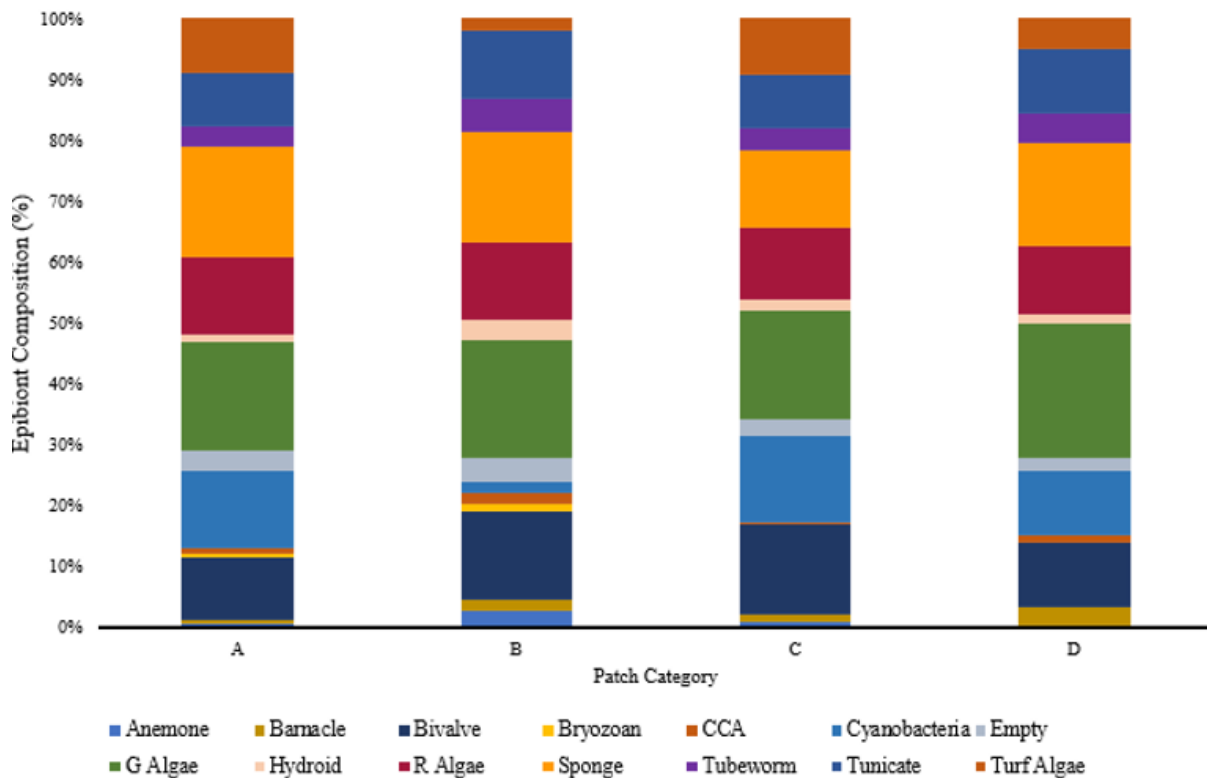


Figure 5. Root epibiont composition (%) by mangrove patch category. The percentage of each epibiont was established and organized by increasing patch size. With few discrepancies, the epibiont composition poses a similar community structure across binned sites. Progression from Category A to Category D is representative of increasing patch perimeter with the following measurements: A: 100–200m, B: 200–500m, C: 500–1000m, D: >1000m.

Root Epibiont Analysis

The Green Algae, Sponge, and Bivalve epibionts were found to be the most abundant within categories (Table 2), with “Present” percentages ranging from 17% to 22%, 12% to 18%, and 10% to 14%, respectively.

Although there are visible differences in the epibiont composition in patch categories (Figure 5), such as Category B having a drastically smaller Cyanobacteria and Turf Algae presence compared to others, the subsequent statistical tests (ANOVA, Kruskal-Wallis, and Welch’s one-way ANOVA) showed that there were no significant differences present between the overall epibiont percentages and mangrove patch size categories.

To determine if epibiont presence increases with increasing patch perimeters, a generalized linear model analysis was performed for the presence count of each root-dependent organism at every sampled site. After investigating every regression between each epibiont’s presence count and increasing perimeter, there were no significant correlations found, supporting the results from the categorical comparisons.

DISCUSSION

Root-Dependent Fish Community

The nine most prevalent fish families of varied trophic groups were chosen to identify trends or common congregation sites based on the trophic groups, i.e., to identify if

the mangrove patch perimeter had any influence on the aggregation or distribution of fish families with different ecological functions. Examples of trophic ecological functions include algae overgrowth control from herbivores and fish population control from carnivores. This study found no such relationship as the inhabitation, fish family evenness, and fish family diversity were all found to be statistically nonsignificant based on mangrove patch perimeter length. This finding presents an interesting example of ecological uniformity. The overall habitat condition and regional proximity of the selected mangrove sites may explain the similarity of fish family distribution, and rather than looking at individual mangrove patches as their own system, this assemblage of islands creates a nearly unified system.

The sampled mangrove islands had perimeters that ranged between approximately 100 – 3000 m. The seemingly broad array of perimeters pales in comparison to the vast mangrove areas studied by Shideler et al. (2017), who conducted fish biodiversity studies based on mangrove habitat size. In their study, the species richness of mangrove-reef fish was found to have a positive correlation with mangrove areas greater than 80 km². Their study focused more on the species richness and biodiversity of mangrove-reef fish, while the present study was aimed toward family evenness and family diversity between mangrove islands with different perimeters. Furthermore, the Shideler et al. study analyzed mangrove island area, investigating species richness and diversity around and within mangrove islands. The results of their study contrast with this present study since mangrove patch interiors provided more areas for predator protection within the complex system of prop roots. Even with these differences, a general takeaway is that fish distribution can be influenced by habitat perimeter. Future studies should choose mangrove islands of much greater perimeters to test if fish family diversity and evenness are impacted at a larger mangrove island scale.

Given that the two farthest sampled mangrove patches were roughly 2300 m away from each other (with other patches in between), proximity and orientation may have had a significant impact on the uniformity of fish family composition in the patches south of Cayo Solarte. Sufficiently scattered with just enough space away from the mainland of Solarte, the leeward side of the patches provided a relatively and similarly calm environment for various fish families to reside. The ecological function of mangroves serving as fish habitat applies to all 20 patches in this given region. More specifically, food availability and predator protection are both common resources provided by mangrove ecosystems, and this select mangrove patch assemblage is likely to be no exception (Cocheret de la Moriniere et al. 2003). These selected patches contained great abundances of fish, invertebrates, plants, and organic matter that would be sufficient for fish families of different trophic groups to congregate and disperse across different patches with similar abiotic and biotic features.

Overall, particularly in Bocas del Toro, fish distribution yields complex, non-linear patterns given the diverse ecosystems they inhabit: coral reefs, sea grass beds, exterior and interior mangrove forests, and coexisting mangrove-coral habitats (Dominici-Arosemena and Wolff 2005; Shideler et al. 2017; Wright 2019; Stewart et al. 2021). While the complexity of fish distribution may be an ambiguous answer to evenness and diversity among these sampled sites, the presence of certain fish families was of no surprise. The three most abundant fish families found in this study—Chaetodontidae, Haemulidae, and Lutjanidae—align with similar fish family findings in Bocas del Toro (MacDonald et al. 2008; Seemann et al. 2018). The relative dominance of these three specific families indicates the prevalence of fish within the invertebrate feeder and carnivorous trophic groups, which describes the ecological status of this mangrove patch assemblage. Carnivorous and invertebrate feeder species have a greater trophic impact on other marine fauna rather than benthic or epiphytic flora, and therefore allow sufficient growth of marine plants to take place and to be used for consumption and habitat (Bellwood et al. 2004; Krajewski and Floeter 2011; Burkepille et al. 2013). Of these significantly prevalent fish families, the positive correlation with the population proportion of the Lutjanidae family and increasing mangrove perimeter may be indicative of the spatial preference for snappers. Given that the two most frequently observed Caribbean snappers, gray snappers (*Lutjanus griseus*) and schoolmaster snappers (*Lutjanus apodus*), commonly grow up to roughly 40 cm (Fishbase.us), it can be inferred that their larger size requires these fish to seek more space for predator protection, and also for more food availability (Cocheret de la Moriniere et al. 2003). It is interesting to note that, although this study was limited to one distinct region of the semi-enclosed Bahia Almirante, the fish family composition found in mangrove patches examined was similar to the fish composition in other surveyed regions (Dominici and Wolff 2005; Macdonald and Weis 2013).

Root-Dependent Epibiont Community

The root epibiont communities also displayed a similarly uniform structure regardless of mangrove patch perimeter. The patch proximity and habitable conditions of this region could explain the similar composition of the observed epiphytic taxa across different sizes of these mangrove patches (Farnsworth and Ellison 1996). The prevalence of green algae, sponges, and bivalve suggests that there are favorable regional conditions around the mangrove patches south of Cayo Solarte, such as sufficient input of sunlight, nutrients, and microscopic plankton (Ellison et al. 1996; Kabir et al. 2014). These epibionts are similar to the epiphytic communities found by Stewart et al. (2022) - a study focused on sessile root epibiont composition on mangrove roots south of Cayo Solarte. In that study, sponges and red algae were found to be the most abundant, which supports the trend

that there are habitable conditions for the more abundant epibionts found in Bahía Almirante. Moreover, the proximity of these mangrove patches may have also allowed for quicker water-borne expansion of these specific epibionts via larval and spore dispersal (van den Hoek 1987; Mariani et al. 2006).

CONCLUSION

The mangrove-dependent organism compositions of Bocas del Toro patches were relatively consistent in relation to mangrove patch sizes. Our results suggest that mangrove patches regardless of size serve as important refuges for fish across various trophic levels, habitats for sessile organisms, and provide numerous mechanisms to supply both via sufficient canopy width for shade and submerged prop hanging roots for habitat substrate. Knowledge about separated mangrove patches has been expanded: biotic uniformity is present in closely oriented mangrove islands which suggests that protective measures should be put in place for the entire mangrove ecosystem, not just for individual patches. Though segmented, each mangrove patch harbored and sustained mangrove-dependent biodiversity as if the smaller patches were an extension of the larger ones. Regional government sectors and environmental organizations should support long-term studies, broad-scale mangrove monitoring – specifically in areas with high anthropogenic disturbance – and litigation to address the damage done to these valuable ecosystems amid climate change and deforestation, regardless of habitat perimeter.

Intensified climatic events and expanding deforestation put more mangrove habitats at risk and disrupt the equilibrium in which this uniquely connected ecosystem relies on. In that case, future mangrove patch studies should analyze the changes in the mangrove-dependent biodiversity and physical patch attributes of mangrove patches over time, considering differing amounts of anthropogenic activity within the area. Conducting similar research over longer periods would not only bring to light the extent to which mangroves are impacted by non-uniform environmental changes but would also expand our understanding of how environmental change impacts important mangrove-dependent biota.

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