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Abundance, foraging levels, and dietary preferences of *Chaetodon capistratus* on reefs surrounding Porvenir Island in the Guna Yala Comarca of Panamá

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Abstract

Reef fish are a physically and functionally diverse group of organisms that live in close association with coral reef habitats. *Chaetodontidae* represents the most species rich family of corallivorous fish, and their reliance on corals as food resources has led to their designation as indicator species of coral cover and health. However, the majority of research on the foraging ecology of Caribbean Chaetodontids dates back several decades, and therefore does not account for recent changes in coral community composition as the result of disease, climate change, and other stressors. As the novel and deadly stony coral tissue loss disease (SCTLD) epidemic causes mass mortality of reef building corals on Caribbean reefs, corallivores are expected to be among the first species impacted by changing reef conditions. Therefore, baseline data on population sizes and behaviors are needed from healthy reefs in order to fully understand the shifts that are occurring on diseased reefs. Here, benthic surveys and focal follow methods were used to investigate the abundances, foraging behaviors, and dietary preferences of *C. capistratus* populations on reefs without SCTLD near Porvenir Island in the Guna Yala Comarca of Panamá. *C. capistratus* were found to forage more often than expected on less abundant coral species including *Siderastrea* spp., *Orbicella* spp., and brain corals, and less often than expected on more abundant coral species including *Agaricia* spp. and *Porites* spp. *C. capistratus* was also observed foraging on sand and algae substrates in addition to coral prey. Therefore, this research supports previous classifications of *C. capistratus* as an active generalist, but disputes the designation of *C. capistratus* as an anthozoan specialist. Contrary to previous findings, the abundance of *C. capistratus* was not positively correlated with coral cover. This is potentially explained by the wider dietary niche reported for the studied population in comparison to other populations of *C. capistratus.* The diverse diet observed here suggests that *C. capistratus* populations exhibit behavioral and dietary plasticity, and can exploit reefs with varying degrees of coral cover. This dietary flexibility may be important for the resilience of the species in the face of dramatic losses of live coral cover due to SCTLD.

Acknowledgements

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Introduction

Coral reefs are among the most biodiverse ecosystems in the world and provide habitats for between ¼ and ⅓ of all marine species, while occupying less than 1% of the ocean's area (Plaisance et al., 2011; Spalding et al., 2001**).** The organisms that reside on reefs exhibit a large degree of diversification and specialization, which allows for high species richness across relatively small spatial scales (Karlson & Hurd, 1993). Reef fishes are a physically and functionally diverse group of species characterized by their reliance on and association with coral reefs. Reefs provide food and protection for resident fish species and support a variety of interspecific symbioses (Choat & Bellwood, 1991). While coral cover and diversity are significant factors that affect the species abundance and richness of local fish populations, fish also influence coral communities in a variety of ways (Bouchon-Navaro & Bouchon, 1988). In particular, corallivorous fish are closely linked to coral as a food source, though their degree of dietary reliance on coral varies widely. Corallivores have been characterized as a distinct and specialized guild in tropical coral reef ecosystems and are often considered to be among the most evolutionarily developed species of reef fish (Randall, 1974).

Chaetodontidae, commonly known as butterflyfish, is the most species rich family of corallivores across the globe and includes around 130 species that live in close association with reef substratum (Liedke et al., 2015). This family has a complex evolutionary history extending back more than 50 million years (Bellwood & Wainwright, 2002). *Chaetodontidae* became associated with reef ecosystems during the Miocene, which was followed by rapid cladogenesis and the evolution of corallivorous strategies alongside the expansion of fast-growing corals (Bellwood et al., 2009). Bellwood et al. (2009) found that corallivory arose independently in the Chaetodontids at least five times in the last 15.7-3.2 Ma. This tightly linked evolutionary history between Chaetodontids and corals makes certain clades highly susceptible to global trends of changing coral community composition and coral population declines as a result of disease and climate change (Bellwood et al., 2009).

Various studies around the world have investigated *Chaetodontidae* abundance and foraging behavior in relation to coral cover and diversity. Bouchon-Navaro and Bouchon (1988) found that the density of Chaetodontid fishes was positively correlated with coral species diversity and live coral cover in the Red Sea but did not find any relationship between fish and coral species richness. The abundance of obligate corallivores was linked specifically to the distributions of branching coral colonies (i.e. *Acropora*), which can potentially be explained by the food availability and shelter offered by branching species. Cole et al. (2008) further investigated foraging of Chaetodontid species on the Great Barrier Reef and observed a preference for and spatial association with *Acropora* species. Researchers studying Chaetodontids in French Polynesia observed resource partitioning between sympatric obligate and facultative corallivores, with the more abundant species almost always being a scleractinian specialist (Harmelin-Vivien & Bouchon-Vavaro, 1983). Additionally, Gregson et al. (2008) found that the feeding rate of Chaetodontids on the Great Barrier Reef was positively correlated with the proportion of coral consumption, with obligate corallivores having higher feeding rates than facultative corallivores or non-corallivores. However, much of these studies have used correlational data between Chaetodontid abundance and coral prevalence to predict diet. Therefore, further behavioral studies that investigate foraging activities through bite observations are necessary to determine the specific dietary components and preferences of Chaetodontids.

The direct reliance of many *Chaetodontidae* species on corals as food resources has led to their designation as an indicator species of coral cover and health (Kramer et al., 2003; Hill &

Wilkinson, 2004). Obligate corallivores in the *Chaetodontidae* family have been found to be highly susceptible to declines in coral. Pratchett et al. (2006) observed significant population declines among coral-feeding Chaetodontids following a severe coral bleaching event on the Great Barrier Reef. Research on *Chaetodon octofasciatus* in Indonesia reported that populations showed resilience to increasing fishing pressures but were closely linked to high coral cover (especially of *Acropora* spp.) and therefore potentially susceptible to ongoing reef degradation in the region (Madduppa et al., 2014). Berumen and Pratchett (2007) found that the Pacific Chaetodontids, *Chaetodon plebeius* and *Chaetodon trifascialis,* had significantly higher growth rates, survivorship, and reproductive output when feeding on exclusive diets of their preferred scleractinian corals compared to exclusive diets of non-preferred scleractinian corals. This specialization can put these species at risk to resource depletion, although *C. plebeius,* the more generalist species, has been found to be more resilient to disturbances in coral reef habitats than *C. trifascialis* (Wilson et al., 2006). Emslie et al. (2011) also found considerable variability in the responses of Chaetodontids to different reef disturbances based on the type of disturbance, the extent of the disturbance, and the species of *Chaetodontidae*. Physical disturbances resulted in greater declines than biological disturbances, and Chaetodontids with the narrowest feeding preferences were always the most susceptible species to any type of disturbance. Therefore, while Chaetodontids may be generally viewed as indicators of coral health and cover, the effects of different stressors on specific populations should be individually investigated due to the high variability of response based on species and level of disturbance.

Chaetodon capistratus, a Caribbean Chaetodontid, has been studied across various sites in efforts to characterize its foraging ecology and dietary preferences. Birkeland and Neudecker (1981) identified the species as an active generalist of scleractinian corals and found that local fish abundance was correlated with local coral cover and diversity. However, research by Gore (1984) on the same species identified a preference for octocorals and zoanthids. Furthermore, a study conducted in the Guna Yala Comarca in Panamá found that *C. capistratus* preferred to forage on gorgonian corals, especially within the genus *Plexaura* (Lasker, 1985). There appears to be little consensus among these studies on the dietary preferences at the family level, or even species level, of Chaetodontids. Additionally, the majority of studies investigating these dietary preferences were conducted several decades ago. It remains unclear, therefore, whether *C. capistratus* diets have shifted in response to the magnitude of stressors impacting Caribbean coral communities in recent years.

The most recent and pressing threat to Caribbean coral reefs, and consequently Chaetodontids, is a novel disease known as stony coral tissue loss disease (SCTLD), which was first observed in Florida in 2014 (Precht et al., 2016). This disease is causing mass and rapid mortality in over 30 species of scleractinian corals, resulting in significant shifts in coral community composition and coral cover across the region. SCTLD is highly infectious and spreading quickly, though the pathogen remains unknown. The most recent studies have observed its presence as far south as the Honduran Bay Islands and St. Lucia, and it is expected to sweep through the entire Caribbean within the next few years (Kramer et al., 2019). Only one study thus far has evaluated the impact of SCTLD on any fish populations. Noonan and Childress (2020) found that *C. capistratus* populations increased alongside local outbreaks of SCTLD and observed an overall foraging preference for diseased coral. However, the lack of recent, pre-epidemic research on *C. capistratus* diets in relation to coral cover is a significant research gap that prevents full analysis of how population numbers and behaviors may have changed as a result of SCTLD. As the disease progresses southward through the Caribbean, the window to collect such data on pre-disease reefs is becoming smaller. Therefore, it is of the utmost importance to focus research efforts on collecting data from healthy sites.

Baseline data of coral prevalence in relation to *C. capistratus* foraging levels and dietary preferences from non-diseased reefs are needed in order to understand the scope of how SCTLD may be affecting corallivores. Findings from this research may have implications for understanding the resilience of overarching fish communities, and thus provide insight on the magnitude of change occurring on Caribbean reefs.

Research Location

The Isthmus of Panamá formed between 3-3.5 million years ago through tectonic movements occurring at the edges of the Pacific-Farallon, Caribbean, and South American Plates (O'Dea et al., 2016). A series of volcanic events ensued, producing a narrow strip of land that connected North and South America while dividing the Atlantic and Pacific Oceans (Cortes, 2007). Since the uplift of the isthmus, oceanographic conditions on either side of Panamá have slowly shifted to produce the tropical climate of the present day. The Caribbean coast is characterized by stable water temperatures, expansive coral reef systems and seagrass meadows, limited mangrove forests, and large carbonate plates (Cortes, 2007). Contrastingly, the Pacific coast is characterized by annual temperature shifts, seasonal upwellings, and contains extensive networks of mangrove forests, small patch reefs, and very few seagrass meadows (Cortes, 2007).

The Guna Yala Comarca is an archipelago of over 300 islands located along the eastern Caribbean coast of Panamá (Figure 1). The surrounding waters are dominated by coral reef and seagrass habitats along the continental shelf (Clifton et al., 1997). The islands and adjacent mainland are inhabited by the Guna people, who maintain autonomous control over the Comarca and have lived in the region for several hundred years (Apgar et al., 2015). The activities of the Guna people, such as subsistence fishing, commercial lobster harvest, and structural

Figure 1: The Guna Yala Comarca on a map of Panamá (accessed from Google Earth).

development, have impacts on the ecology of the coral reefs in the area. However, the ban on large-scale fishing operations within the Comarca by the Guna National Congress has resulted in diverse fish populations in comparison to industrially fished regions of the Caribbean (Clifton et al., 1997).

Guna Yala contains 638 km^2 of coral reefs, constituting 81% of Panamá's reef systems (Guzman, 2003; Andrefouet & Guzman, 2005). These reefs remain largely intact due to strict laws preventing SCUBA diving and low visitation rates from cruise ships (Clifton et al., 1997). Surveys have identified the reefs in western Guna Yala by geomorphological classifications: fringing reefs, deep reefs, patch reefs, barrier reefs, and reef complexes (Andrefouet & Guzman, 2005). Over 50 species of scleractinian corals occur in the region, and shallow, leeward reefs are dominated by *Acropora*, *Agaricia*, *Porites*, and *Millepora* species. Massive corals such as brain corals and star corals are also common. Gorgonian corals in the genera of *Plexaura* and *Pseudoplexaura* can be found in abundance in zones above 20 m (Clifton et al., 1997).

Six species in the family *Chaetodontidae* are found throughout the Caribbean, and three species, *Chaetodon capistratus, Chaetodon striatus*, and *Chaetodon ocellatus* occur on reefs in the northwestern region of Guna Yala (Humann & DeLoach, 2003). Of these three species, *C. capistratus* is the most common and can be observed on reefs from 1-20 m in depth.

The reefs of the Guna Yala Comarca have yet to show signs of SCTLD (Kramer et al., 2019). Therefore, Guna Yala represents one of the few locations where baseline data on coral prevalence and *Chaetodon* foraging ecology can be recorded on healthy reefs.

Research Question

What are the population abundances, foraging levels, dietary components, and food preferences of *Chaetodon capistratus* in reefs surrounding Porvenir Island in the Guna Yala Comarca?

Methods

This study was conducted on reefs near Porvenir Island (9°33'30" N, 78°56'49" W) in the western region of the Guna Yala Comarca. Porvenir Island is located roughly 12 km north of the Carti Port. The island is surrounded by patch and fringing reefs to the south, and barrier reefs to the north. Reef depths vary from less than 1 m to greater than 10 m (Clifton et al., 1997).

Reefs were sampled over 10 days from November 18th through November 27th, 2021. All visited reefs were between 1-3 m in depth to ensure high levels of visibility and allow for data collection to be conducted by snorkeling. Reefs were chosen through stratified haphazard selection, with no specifications regarding tourism or fishing pressures, directionality, geomorphological classification, or coral type (Hill & Wilkinson, 2004). In total, seven different reefs were sampled during the research period (Figure 2). The sampled reefs were Porvenir South, Lemon Cays, Smithsonian Reef, Aguadargana Reef Complex, Barrier Reef, Perro Chico South, and Nalunega reef (see Appendix I for coordinates).

Figure 2: Seven sampled reef sites surrounding Porvenir Island in the Guna Yala Comarca (accessed from Google Earth). Sampled reefs included (1) Porvenir South, (2) Lemon Cays, (3) Smithsonian Reef, (4) Aguadargana Reef Complex, (5) Barrier Reef, (6) Perro Chico South, and (7) Nalunega Reef.

At each reef, three, 30 m transects were randomly laid. After laying a transect, a five-minute wait period was observed (English et al., 1997). Following this wait period, the abundance of *C. capistratus* within 4 m on either side of the transect (8 m total width) were counted during a continuous swim along the line (Noonan & Childress, 2020). After this first pass, another five-minute wait period was observed. Abundances were recorded during a second pass swimming the opposite direction along the transect.

Following the abundance counts, coral cover and prevalence were recorded within 10, 1 m^2 quadrats placed randomly along the length of each transect (English et al., 1997). The quadrat was divided in squares of 10 cm^2. 81 data points identifying the benthic substrate were collected at crosshairs in each quadrat grid.

Two more abundance counts were conducted along each transect after the benthic survey, for a total of four passes and abundance counts per transect. Immediately following the completion of the benthic survey, a five-minute wait period was observed (English et al., 1997). After five minutes, abundances were recorded during a third pass swimming along the transect. Following this count, a final, five-minute wait period was observed. Abundances were then counted during a fourth pass swimming in the opposite direction along the transect.

Foraging behavior was observed using focal follows of *C. capistratus* individuals on the same reefs where benthic surveys were conducted. An individual was identified through random roving near the transect (Jones & Thompson, 1978), and then followed for five continuous minutes. During this time, every substrate the individual bit was identified and recorded (Birkeland & Neudecker, 1981). When the substrate was a scleractinian or octo- coral, it was identified by genus or species and the number of bites counted (Noonan & Childress, 2020).

Other substrate types include fleshy algae, sand, anemones, cyanobacteria, *Porolithon pachydermum,* zoanthids, tunicates, and trash. The number of bites to each of these substrates was recorded. Individuals were followed and observed as closely as possible without influencing behavior (Reese, 1975). Fish did not seem to exhibit abnormal behavior in response to the observer. Focal follows at a given reef were conducted sequentially over a two-hour period **(**Birkeland & Neudecker, 1981).

Statistical Analysis

All data analysis was conducted using RStudio (version 1.2.5033, “Orange Blossom”) and Microsoft Excel. Maps were generated using Google Earth. Abundance data was averaged across the four passes of each transect, and summed across all transects. From this data, population abundances were determined for *C. capistratus* per 1,680 m^2 of reef. A Kendall rank correlational test was used to test for associations between the abundance of *C. capistratus* and proportion of coral cover across transects. Coral cover was calculated as the total cover of scleractinian and octo- coral species that have been observed to be fed upon by *C. capistratus* in previous studies (Birkeland & Neudecker, 1981; Lasker, 1985; Gore, 1984), or were foraged upon by *C. capistratus* in this study. Therefore, *Millepora* spp. were excluded when calculating coral coverage because there is no evidence from previous literature nor this study that these species are a food resource for *C. capistratus.*

The number of points recorded for each substrate type was compiled for all quadrats across a single transect. From these values, benthic composition was calculated as the proportion of each observed substrate category. These proportions were averaged across the three transects per site to give an average benthic composition per site. These site averages were also used to calculate an overall average benthic composition across all sites. The benthic survey data was used to calculate the expected dietary composition of *C. capistratus* based on the prevalence of different coral species and assuming opportunistic, non-preferential feeding. Expected diet was calculated based on reported food resources of Chaetodontids, following a null prediction of no shift in diet from previous literature; therefore, categories of benthic substrates that were not observed to be foraged on by *C. capistratus* individuals across the Caribbean (i.e. *Millepora* spp., *P. pachydermum,* cyanobacteria, trash) were excluded when calculating expected dietary composition (Birkeland & Neudecker, 1981; Lasker, 1985; Gore, 1984).

The number of bites per different food resource was compiled for each focal follow and used to determine the proportion of each food in the diet of *C. capistratus*. These proportions were averaged by site, and across all six sites, and served as the observed dietary composition. The average observed diet of *C. capistratus* individuals at each site was compared to the calculated expected diet per site using a Chi-square goodness-of-fit test. The average, across-site observed diet was compared to the across-site expected values using a Chi-square goodness-of-fit test to determine whether individuals demonstrated preferences for specific foods.

Foraging data was also compiled across all sites to determine the intensity of feeding on different food resources. Intensity was determined as the average number of bites taken in a row from a certain food, and the total number of bites of each food taken over the course of the five-minute follow period. The average number of bites taken in a row from each food was compared using a Kruskal-Wallis rank sum test. The average number of bites taken from each food over five minutes was also compared using a Kruskal Wallis rank sum test. For both tests, the categories of *Acropora* spp., *Gorgonia ventalina, Erythropodium caribaeorum,* anemones, and zoanthids were excluded due to few observations ($n<5$).

Overall foraging levels of *C. capistratus* individuals were calculated as the number of total bites over a five-minute period. Foraging levels were averaged across all individuals per site, and across all six sites where focal follows were conducted.

From the focal follow and benthic survey data, foraging levels, dietary composition, and food preferences were determined for *C. capistratus.*

Ethics

Prior to conducting any research, my project was approved by the Institutional Review Board (IRB) of the School of International Training. For this process, I submitted my research proposal and methods through the Human Subjects Review Application Form. Because no humans were directly involved in data collection, my project did not require a full IRB review.

While my project posed no direct harm to human subjects, I lived among and regularly interacted with Guna community members. Therefore, my presence and research actions posed some risk to the community. To minimize these risks, I adhered to all rules at Hotel Porvenir and complied with the requests of the Guna individuals with whom I interacted. I was respectful and conscientious of their cultural norms and lived within those expectations to the best of my ability. I was mindful of the space of the hotel owners and other guests, kept my belongings in my room, and collected all my trash over the course of my stay to dispose of in Panama City.

Additionally, there were concerns regarding ecosystem health to be considered while conducting fieldwork. Corals are highly susceptible to water-borne diseases and pathogens if their tissue is damaged. Therefore, it was crucial that I limited contact with them and the reef crest. When laying my transect, I ensured that both ends were placed on non-coral substrate. When retrieving the transect line, I wound up the tape slowly and carefully, making sure that it was not caught under any pieces of coral. Additionally, while swimming over the transect tape or following individual fish around, I was careful to remain several feet above the reef at all times. I was conscientious to keep my body oriented in a horizontal position or with my head down and feet above, to ensure that I did not accidently kick the reef with my fins. I only put my feet down and walked where the ground was sandy or rocky, and in general tried to swim even when the water was not deep in order to protect sand dwelling organisms (and myself from being bitten/stung by said organisms). I also was careful not to leave any of my equipment in the ocean, as plastic materials take many years to degrade. To ensure that this did not happen, I frequently checked that none of my equipment was loose or at risk of floating off. Finally, I refrained from using excessive amounts of sunscreen by wearing swim leggings and a swim shirt when snorkeling, and restricted use of sunscreen to my face and neck. Additionally, the sunscreen that I used was mineral-based and reef safe. In these ways, I sought to minimize the risks that my presence posed to the reef ecosystem.

Results

A total of seven reefs were visited over the course of a 10-day sampling period. 21 transects were laid, along which benthic surveys and abundance counts were conducted. An average of 21 *C. capistratus* individuals were observed per 1,680 m^2 of reef. There was no significant correlation between the abundance of *C. capistratus* and coral cover across the sampled reefs ($p>0.05$).

A total of 60 individuals were observed through focal follows on six reefs (Porvenir South, Lemon Cays, Smithsonian Reef, Aguadargana Reef Complex, Perro Chico South, and Nalunega Reef. No *C. capistratus* individuals were encountered over the two-hour search period at the seventh reef (Barrier Reef) where a benthic survey was conducted, and therefore no behavioral data were recorded for that site. The observed diets of *C. capistratus* within each site were significantly different than the expected diets based on food resource availability at each site (all p-values<0.001). *C. capistratus* diets across all sites also differed significantly from the expected diet based on average food availability across all sampled reefs (X^2=9160.9, df =19, p<0.0001) (Figure 3). Across all sites, *C. capistratus* individuals tended to consume less of all non-coral food sources than was expected from the assumption of non-preferential, opportunistic foraging based on substrate composition (Appendix II). These non-coral categories included algae, sand, sponges, anemones, zoanthids, and tunicates.

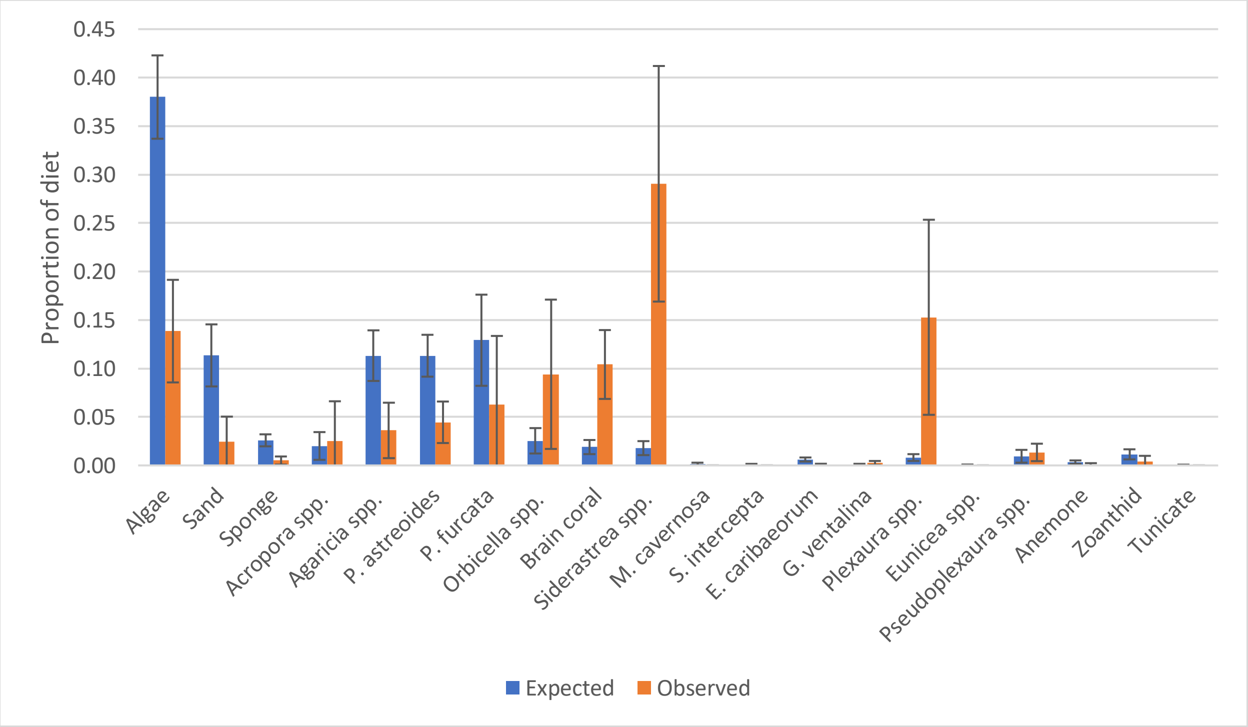

Figure 3: Expected and observed proportions of different food resources in the diet of *C. capistratus*. Expected proportions were calculated from benthic surveys. Observed proportions were calculated from bites during focal follows. Error bars represent +/- SE. X^2 = 9160.9, df = 19, p < 0.0001.

Porites astreoides, *Porites furcata*, *Agaricia* spp. and *Erythropodium caribaeorum* were also observed in lower-than-expected proportions in *C. capistratus* diets. *Porites astreoides*, *Porites furcata*, and *Agaricia* spp. were the three most prevalent scleractinian coral species at the sampled sites, comprising over 35% of possible food resources as determined by benthic surveys. However, cumulatively these three species only comprised 14.4% of the observed diet.

C. capistratus individuals consumed higher proportions of *Acropora* spp., *Orbicella* spp., brain corals (genera *Pseudodiploria*, *Colpophyllia*, and *Favia*), *Siderastrea* spp., *Gorgonia ventalina*, *Plexaura* spp., and *Pseudoplexaura* spp. than what was expected based on availability.

These 7 groups comprised only 10% of available food resources, but cumulatively made up 68% of the observed diet.

Montastraea cavernosa, *Stephanocoenia intercepta*, *and Eunicea* spp., were not observed to be foraged upon, despite occurring in low abundances in the benthic surveys.

There was a significant difference in the number of bites taken consecutively from each food resource (p<0.0001). Fewer consecutive bites were taken from algae in comparison to brain corals, *Orbicella* spp., *Pseudoplexaura* spp., *Plexaura* spp., and *Siderastrea* spp. More consecutive bites were taken from *Siderastrea* spp. than from algae, *Agaricia* spp., brain corals, *P. astreoides, P. furcata, Plexaura* spp., and sand (Appendix III).

There was also a significant difference in the average total number of bites taken from each food resource over the five-minute follow period (p<0.0001). *C. capistratus* individuals took on average the most bites from *Siderastrea* spp. over five minutes, followed by *Plexaura* spp., algae, brain corals, and *Orbicella* spp (Figure 4). The fewest bites were taken from sponges, zoanthids, *Antillogorgia* spp., *G. ventalina*, *E. caribaeorum*, and anemones (Appendix IV)**.**

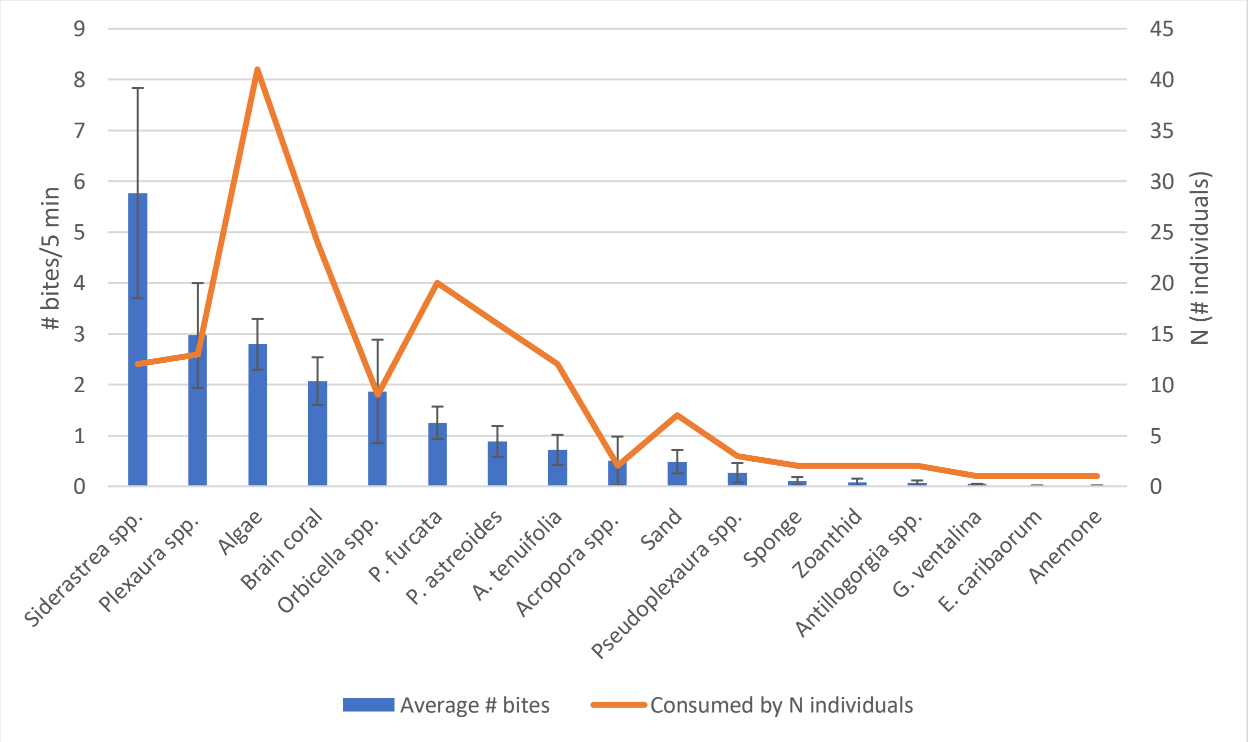

Figure 4: Average total number of bites taken from each food during a 5-minute focal follow, in comparison to the number of individuals who were observed consuming each type of food during the focal follow period. Error bars represent +/- SE. P-values listed in Appendix IV.

C. capistratus individuals took an average of 19.85 total bites from any food resource throughout the five-minute focal follow period.

Discussion

Abundance

Chaetodontids have been used as indicators of reef health, with various studies correlating Chaetodontid abundance with coral cover and diversity (Birkeland & Neudecker, 1981; Bouchon-Navaro & Bouchon, 1988). Contrary to previous research, this study found no relationship between *C. capistratus* abundance and coral cover on shallow reefs around Porvenir Island. This discrepancy could be explained by local variation in coral community composition and dietary preference. Studies on Pacific reefs reported the strongest correlations between Chaetodontid abundance and cover by *Acropora* spp., which provide food and shelter to local fish populations (Bouchon-Navaro & Bouchon, 1988; Cole et al., 2008). However, I observed low abundances of *Acropora* spp., and these species constituted a relatively small proportion of *C. capistratus* diets. The relative rarity of *Acropora* corals at the sampled locations may explain why no diet-based association with *Acropora* spp. characterized the distributions and abundances of *C. capistratus* populations in this study.

Additional studies found positive correlations between *C. capistratus* abundance and total coral cover in the U.S. Virgin Islands (Birkeland & Neudecker, 1981). These patterns were supported by the classification of *C. capistratus* as an anthozoan specialist, and thus its spatial distribution the product of a restricted diet. *C. capistratus* around Porvenir Island were observed to have more varied diets than previously reported; individuals foraged on algal and sand substrates, and non-coral prey comprised 17% of the observed diet. This finding suggests that populations around Porvenir Island may occupy a wider dietary niche compared to previously studied populations. Therefore, this dietary flexibility may allow *C. capistratus* to exploit not only areas with considerable coral cover, but also sandy flats and algae dominated reefs.

Finally, most previous studies on Chaetodontid abundance and behavior used SCUBA methods and therefore conducted surveys across greater depths (Birkeland & Neudecker, 1981; Noonan & Childress, 2020; Bouchon-Navaro & Bouchon, 1988; Cole et al., 2008). This study used snorkeling methods, and therefore sampling was restricted to reefs at depths less than 3 m. This methodological difference could impact the observed coral community composition and therefore food availability based on species-specific depth distributions (Clifton et al., 1997), which may account for discrepancies in correlating *C. capistratus* abundance with coral cover.

Dietary composition and preference

Degree of dietary specialization varies widely across *Chaetodontidae* species. I report that the diets of *C. capistratus* populations around Porvenir Island are comprised of a diverse array of food resources, however the dietary proportions of each food suggest that foraging and prey choice are not random behaviors.

C. capistratus individuals were observed to feed less than expected on the most common scleractinian corals at the sampled reefs, *P. furcata, P. astreoides,* and *Agaricia* spp. In contrast, less abundant species including *Acropora* spp., *Orbicella* spp., brain coral (genera *Pseudodiploria*, *Colpophyllia,* and *Favia*), *Siderastrea* spp., and octocorals comprised larger proportions of *C. capistratus’* diet than was expected based on availability. These results corroborate the findings of Birkeland and Neudecker (1981) which characterize *C. capistratus* as an active generalist. As an active generalist, *C. capistratus* forages for evenness among prey items, feeding less than expected on common resources and more than expected on rarer resources. However, this research also suggests that some resources are too rare for *C. capistratus* individuals to preferentially exploit. Previously reported prey categories including *M. cavernosa*, *S. intercepta, E. caribaeorum,* anemones, zoanthids, and tunicates (Birkeland &

Neudecker, 1981; Gore, 1984; Lasker, 1985) each represented less than 1% of the benthic area surveyed in this study, and were foraged on very rarely, if at all. Therefore, it seems that *C. capistratus'* even diet is constrained to common and semi-common species, with the rare prey representing irregular, opportunistic foraging events.

The preferentially diverse diet of *C. capistratus* may be driven by the nutritional value of different coral species and their contributions to *C. capistratus* physiological processes. Westoby (1974) proposed nutrient composition as the optimal mode of diet selection. Therefore, the observed preferences for foods of varying abundance and commonality may suggest that each prey offers unique and necessary nutrients. However, previous studies (e.g., Tricas, 1985, Keesing, 1990; Pratchett, 1995) have failed to find correlations between feeding preferences and nutritional or caloric values of different corals. Other studies have suggested that preference relates to the taste of given coral's mucous membrane, the number and strength of nematocysts, the presence of toxic chemical defenses, or the carbon and nitrogen ratios of tissues (Gore, 1984, Reese, 1977). However, no consensus has been reached on the molecular or cellular factors driving prey choice among Chaetodontids. Additionally, there is a lack of studies that compare tissue composition among Caribbean corals, or investigate Caribbean Chaetodontid diets through a nutritional lens. Therefore, future research should focus on Caribbean species and explore foraging behavior in the context of the energetic tradeoffs associated with different prey types.

Increased handling time incurred by highly rugose coral growth forms may also contribute to the observed patterns of lower dietary contributions *P. furcata* and *Agaricia* spp. in comparison to availability. Tricas (1989) found that branching coral species elicited longer processing times compared to closely related and nutritionally similar massive coral species. These energetic costs associated with physical prey extraction could be a factor influencing the observed preferences of *C. capistratus* for various species of massive and mounding corals such as *Orbicella* spp., brain corals, and *Siderastrea* spp. However, this trend cannot explain the less-than-expected consumption of *P. astreoides* (a mounding species), nor the greater-than-expected consumption of highly complex and rugose coral species in the genera of *Acropora, Plexaura, Pseudoplexaura,* and *Gorgonia.* Therefore, additional factors to handling time must play some role in structuring the patterns of prey choice observed in this study.

Contrary to previous findings, this research suggests that *C. capistratus* is not a strict corallivore (Birkeland & Neudecker, 1981; Gore, 1984). Algae and sand were both targeted in numerous foraging events. While algae can provide some, albeit little nutritional value, the consumption of plant material by *C. capistratus* is likely incidental since the commonness of this item in the diets of Chaetodontids that preferentially feed on algae is usually substantially higher than observed here (Sano, 1989; Liedke et al., 2016). Previous studies demonstrate that algae and sand provide habitat to many small invertebrates, such as polychaetes and crustaceans, that are difficult to observe via focal follow methods (Paiva, 2006). Therefore, foraging behaviors focused on patches of algae or sand may in fact be directed towards prey items living within the substrates. Nevertheless, this study demonstrates that foraging upon non-coral substrates is not uncommon for *C. capistratus,* and therefore the classification of this species as strictly corallivorous may require reevaluation.

Foraging intensity

C. capistratus individuals were observed taking fewer consecutive bites from algae in comparison to brain corals, *Orbicella* spp., *Pseudoplexaura* spp., *Plexaura* spp., and *Siderastrea* spp. As previously suggested, this pattern could be explained by targeted foraging on cryptic invertebrates living within the algal substrate (Paiva, 2006). Discrete invertebrate prey found in sand and algae usually exhibit dispersed distributions in comparison to coral colonies, which may contain thousands of adjacent polyps. Therefore, while a foraging individual may be able to repeatedly exploit the same coral by plucking out neighboring polyps, more time must be spent searching for new prey sources between foraging events that target individual sand or algae dwelling organisms (Birkeland & Neudecker, 1981). This distribution difference could result in fewer repetitive foraging attempts directed towards non-coral prey.

Additionally, coral tissue represents an easily accessible but low-quality food source for *C. capistratus* (Birkeland & Neudecker 1981). Anthozoans generally have lower caloric value (494 cal/g wet wt, Cumminns & Wuycheck, 1971) than crustaceans and polychaetes (817 and 639 cal/g wet wt, Cumminns & Wuycheck, 1971). Previous research by Birkeland and Neudecker (1981) found that browsing Chaetodontids consistently took more bites from coral prey in comparison to sympatric predatory Chaetodontids. Therefore, *C. capistratus* individuals may take advantage of common, accessible food in the form of coral polyps, but consistently require a greater number of bites from each coral to consume sufficient nutritional and caloric content. Additionally, polychaetes and crustaceans often demonstrate predator avoidance (i.e. tubeworms) or defense mechanisms, which may deter continued foraging attempts if the first attempt is not successful (Birkeland & Neudecker, 1981). Therefore, these organisms, while potentially more rewarding to consume, may also incur more costs to find and access.

Siderastrea spp. received more consecutive bites and more total bites over the five-minute focal follow period than any other food category, including other species of massive corals. This could potentially be explained by corallite structure, and therefore tissue accessibility to browsers. *Siderastrea* spp. are characterized by large, ceroid corallites (Veron, 2000). The calices are relatively low, with the inner edges of septa shallowly sloping towards columella, resulting in a wide fossa (Cairns, 1982). This distinct morphology may leave individual coral polyps more exposed to predators, especially in comparison to corals with higher calices or more rugose corallite structures. However, further studies are needed to directly investigate how corallite morphology may impact predation levels.

Sponges received on average very few bites over the five-minute period, supporting previous findings that Chaetodontids generally do not utilize sponges as food resources. This may be explained by the specialized, tube-like mouth morphology of Chaetodontids, which is adapted to nip individual coral polyps and ill-suited to bite the smooth external surface of sponges (Bellwood et al., 2009). Additionally, the majority of Porifera species contain inner networks of calcium or silica spicules (Hartman, 1981) that are distributed throughout sponge tissues and likely to be consumed during superficial foraging attempts by *C. capistratus* (Hartman, 1981). Therefore, sponges may be energetically costly foods for *C. capistratus* individuals to process and digest, thereby representing undesirable prey.

Few bites were also taken from zoanthids, *Antillogorgia* spp., *G. ventalina*, *E. caribaeorum,* and anemones. While previous studies have observed *C. capistratus* foraging attempts on each of these organisms (Birkeland & Neudecker, 1981; Gore, 1984; Lasker, 1985), they occurred at very low frequencies in the sampled sites of this study (all <1% of benthic survey). Therefore, while *C. capistratus* may forage opportunistically on these prey resources when available, these organisms are not likely to comprise significant amounts of *C. capistratus* diets in the reefs surrounding Porvenir Island due to low availability.

Foraging levels

Previous studies investigating the foraging levels of Chaetodontids have found much inter- and intraspecific variation, with scleractinian specialists generally taking more bites than non-coral browsers because of nutritional differences (Birkeland & Neudecker, 1981). The foraging levels for *C. capistratus* calculated from this study (19.85 bites/5 min) fell below previously recorded range for *C. capistratus* (29.4 - 67.33 bites/5 min) but above the recorded rates for Caribbean non-coral browsers (*C. striatus:* 8 bites/5 min; *Prognathodes aculeatus*: 12.2 bites/5 min) (Birkeland & Neudecker, 1981; Lasker, 1985; Bonaldo et al., 2005; Randall, 1967; Motta, 1989). This finding may be explained by the varied diet of the studied population of *C. capistratus,* which includes both anthozoan and non-coral prey. However, the foraging ecology of *C. capistratus,* and more generally Chaetodontids, differ profoundly from area to area (Randall, 1967), and therefore further studies are needed before attempting to draw any overarching consensuses about foraging levels and behaviors of Caribbean Chaetodontids.

Implications for stony coral tissue loss disease

The wide dietary niche observed for *C. capistratus* in reefs surrounding Porvenir Island provides insight on the potential resilience of the species in the face of SCTLD. This finding is supported by recent research on *C. capistratus* foraging behaviors on diseased reefs in Roatán, Honduras, where individuals on reefs with higher disease prevalence foraged significantly more on non-coral prey than individuals on reefs with lower disease prevalence, but there was no difference in overall foraging levels across reef sites (Casement, 2021). Noonan and Childress (2020) also reported *C. capistratus* in the Florida Reef Tract demonstrated resilience to decreased coral cover and showed no signs of declines in population numbers nor foraging levels in response to SCTLD. Despite some evidence of dietary plasticity, the most preferred species of coral in this study (*Siderastrea* spp., brain corals, and *Orbicella* spp.) are among the most susceptible species of coral to SCTLD (Weil et al., 2019). Contrastingly, the less-preferred species such as *Agaricia* spp., *P. furcata,* and *P. astreoides* have demonstrated a higher degree of resilience to the disease. Therefore, while *C. capistratus* individuals may exhibit a wide dietary niche that allows them to persist in the face SCTLD, it is likely that their ability to evenly forage will be impacted by changes in coral diversity.

Limitations to focal follows

While focal follow studies provide valuable knowledge of the behaviors associated with foraging events, constraints on human vision and following capabilities can reduce the accuracy of prey identification and therefore diet predictions. This limitation was evident in this study, as it was impossible to determine the targeted prey during foraging attempts on algal and sand substrates. Additionally, it is often difficult determine if bitten foods are actually consumed. Previous research by Castro et al. (2010) observed frequent foraging on octocorals in the field, but later found no presence of octocorals in stomach contents analyses. Similarly, a study investigating stomach contents in Florianópolis found high quantities of anthozoans, which were not recorded at all during observational studies of foraging behavior (Liedke et al., 2016). Therefore, future studies should complement field observations of feeding activities with laboratory-based stomach content analyses to gain a complete understanding of the behavioral and nutritional aspects of Chaetodontid foraging.

Conclusions

Recent and relevant research investigating the ecology and population dynamics of reef fish are of high importance, especially in the face of the innumerable stressors currently impacting coral reef ecosystems. SCTLD represents the foremost threat to Caribbean coral communities and subsequently Chaetodontids (Precht et al., 2016; Bellwood et al., 2009). Baseline studies on Chaetodontid populations and behaviors are needed in order to directly quantify species responses to SCTLD in both ecological and conservation contexts.

This study provides data on the abundances, foraging behaviors, and dietary preferences of *C. capistratus* on healthy reefs surrounding Porvenir Island in the Guna Yala Comarca of Panamá. This paper finds that *C. capistratus* occupies a wide dietary niche and can exploit a diverse array of food resources. However, the dietary proportions of each food resource demonstrate that prey choice is not a random behavior. Additionally, *C. capistratus* may rely less heavily on coral resources than previously believed, and readily forages on algal and sand substrates to find alternative sources of prey. These findings suggest that *C. capistratus* may exhibit behavioral and dietary plasticity that allows local populations to exploit to reefs with varying levels of coral abundance and diversity.

SCTLD is not the first, nor the last disease to dramatically alter coral reef ecosystems, and the majority of its impacts on fish communities are yet to be determined. While SCTLD has not yet been observed on Panamá's reefs, it is expected to reach the region within several years. The generalist foraging behaviors of *C. capistratus* described here demonstrate potential resilience of local populations to the impending degradation of Panamanian coral reefs as the result of SCTLD. This research represents the first step in determining the proximate and long-term effects of SCTLD on Caribbean *Chaetodontidae* populations. Future studies should continue to evaluate the population health and behaviors of reef fish across sites with varying levels of disease in order to gain an ecosystem-wide view of the current changes unfolding on Caribbean reefs.

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Appendix I

Table 1: GPS Coordinates of the seven sampled reef sites. Coordinates were taken using Garmin GPSMAP 64S.

Reef	Coordinates
Porvenir South Reef	(9°33’28.4” N, 78°56’41.3” W)
Lemon Cays Reef	(9°33’28.9” N, 78°56’50.8” W)
Smithsonian Reef	(9°33’9.2” N, 78°57’15.4” W)
Aguadargana Reef Complex	(9°33’5.6” N, 78°56’45.8” W)
Barrier Reef	(9°34’13.3” N, 78°57’41.6” W)
Perro Chico South Reef	(9°33’25.9” N, 78°52’32.5” W)
Nalunega Reef	(9°33’7.8” N, 78°57’18.7” W)

Appendix II

Table 2: Observed vs expected dietary proportions of different food resources available to *C. capistratus*. Expected values were calculated based on a benthic survey. Observed values were calculated based on bite counts during focal follows. $X^2 = 9160.9$, df = 19, $p < 0.0001$.

	Algae	**Sand**	**Sponge**	**Acropora spp.**	**Agaricia spp.**	**P. astreoides**	**P. furcata**	**Orbicella spp.**	**Brain coral**	**Siderastrea spp.**	**M. cavernosa**
expected	0.3800	0.1135	0.0259	0.0201	0.1133	0.1131	0.1291	0.0254	0.0190	0.0179	0.0014
observed	0.1385	0.0243	0.0050	0.0252	0.0361	0.0445	0.0630	0.0940	0.1041	0.2905	0.0000

	S. intercepta	**E. caribaeorum**	**G. ventalina**	**Plexaura spp.**	**Eunicea spp.**	**Pseudoplexaura spp.**	**Anemone**	**Zoanthid**	**Tunicate**
expected	0.0008	0.0061	0.0010	0.0081	0.0005	0.0095	0.0034	0.0114	0.0004
observed	0.0000	0.0008	0.0025	0.1528	0.0000	0.0134	0.0008	0.0042	0.0000

Appendix III

Table 3: P-values from a pairwise Wilconxon rank sum test with continuity correction comparing the number of bites taken in a row from each food resource. Bold values indicate significance (<0.05).

	Algae	Anemone	*Antillogorgia* spp.	*Acropora* spp.	*Agaricia* spp.	Brain coral	*E. caribaeorum*	*G. ventalina*	*Orbicella* spp.	*P. astreoides*	*P. furcata*	*Plexaura* spp.	*Pseudoplexaura* spp.	Sand	*Siderastraea* spp.	Sponge
Anemone	NS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Antillogorgia spp.	NS	NS	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acropora spp.	NS	NS	NS	-	-	-	-	-	-	-	-	-	-	-	-	-
Agaricia spp.	NS	NS	NS	NS	-	-	-	-	-	-	-	-	-	-	-	-
Brain coral	**<0.01**	NS	NS	NS	NS	-	-	-	-	-	-	-	-	-	-	-
E. caribaeorum	NS	NS	NS	NS	NS	NS	-	-	-	-	-	-	-	-	-	-
G. ventalina	NS	NS	NS	NS	NS	NS	NS	-	-	-	-	-	-	-	-	-
Orbicella spp.	**<0.01**	NS	NS	NS	NS	NS	NS	NS	-	-	-	-	-	-	-	-
P. astreoides	NS	NS	NS	NS	NS	NS	NS	NS	NS	-	-	-	-	-	-	-
P. furcata	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-	-	-	-	-	-
Plexaura spp.	**<0.001**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-	-	-	-	-
Pseudoplexaura spp.	**<0.05**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-	-	-	-
Sand	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-	-	-
Siderastraea spp.	**<0.001**	NS	NS	NS	**<0.001**	**<0.001**	NS	NS	0.057	**<0.01**	**<0.001**	**<0.01**	NS	**<0.001**	-	-
Sponge	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.057	-
Zoanthid	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Appendix IV

Table 4: P-values from a pairwise Wilconxon rank sum test with continuity correction comparing the total number of bites taken over 5 minutes from each food resource. Bold values indicate significance (<0.05).

	Algae	Anemone	*Antillogorgia* spp.	*Acropora* spp.	*Agaricia* spp.	Brain coral	*E. caribaeorum*	*G. ventalina*	*Orbicella* spp.	*P. astreoides*	*P. furcata*	*Plexaura* spp.	*Pseudoplexaura* spp.	Sand	*Siderastraea* spp.	Sponge
Anemone	**<0.001**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Antillogorgia spp.	**<0.001**	NS	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acropora spp.	**<0.001**	NS	NS	-	-	-	-	-	-	-	-	-	-	-	-	-
Agaricia spp.	**<0.001**	**<0.01**	**<0.05**	**<0.05**	-	-	-	-	-	-	-	-	-	-	-	-
Brain coral	**<0.05**	**<0.001**	**<0.001**	**<0.001**	**<0.05**	-	-	-	-	-	-	-	-	-	-	-
E. caribaeorum	**<0.001**	NS	NS	NS	**<0.01**	**<0.001**	-	-	-	-	-	-	-	-	-	-
G. ventalina	**<0.001**	NS	NS	NS	**<0.01**	**<0.001**	NS	-	-	-	-	-	-	-	-	-
Orbicella spp.	**<0.001**	**<0.05**	**<0.05**	**<0.05**	NS	**<0.01**	**<0.05**	**<0.05**	-	-	-	-	-	-	-	-
P. astreoides	**<0.001**	**<0.001**	**<0.001**	**<0.001**	NS	NS	**<0.001**	**<0.001**	**<0.05**	-	-	-	-	-	-	-
P. furcata	**<0.01**	**<0.001**	**<0.001**	**<0.001**	NS	NS	**<0.001**	**<0.001**	**<0.05**	NS	-	-	-	-	-	-
Plexaura spp.	**<0.001**	**<0.01**	**<0.01**	**<0.01**	NS	NS	**<0.01**	**<0.01**	NS	NS	NS	-	-	-	-	-
Pseudoplexaura spp.	**<0.001**	NS	NS	NS	**<0.05**	**<0.001**	NS	NS	NS	**<0.001**	**<0.001**	**<0.05**	-	-	-	-
Sand	**<0.001**	**<0.05**	NS	NS	NS	**<0.01**	**<0.05**	**<0.05**	NS	**<0.01**	**<0.05**	NS	NS	-	-	-
Siderastraea spp.	**<0.001**	**<0.01**	**<0.01**	**<0.01**	NS	NS	**<0.01**	**<0.01**	NS	NS	NS	NS	**<0.05**	NS	-	-
Sponge	**<0.001**	NS	NS	NS	**<0.05**	**<0.001**	NS	NS	**<0.05**	**<0.001**	**<0.001**	**<0.01**	NS	NS	**<0.01**	-
Zoanthid	**<0.001**	NS	NS	NS	**<0.05**	**<0.001**	NS	NS	**<0.05**	**<0.001**	**<0.001**	**<0.01**	NS	NS	**<0.01**	NS