PORIFERAN ABUNDANCE IS NEGATIVELY ASSOCIATED WITH CORAL HEALTH IN THE MESOAMERICAN REEF

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Abstract.–The Mesoamerican Reef is the second largest coral reef in the world and has experienced a 50% loss of coral coverage in recent decades. Due to the high biodiversity of marine life that depend on the Mesoamerican Reef, identifying drivers of coral loss is crucial. This study was designed to assess the relationship between the presence of yellow band disease (YBD) and white plague type-II (WPII) on stony corals with environmental (water depth) and biological stressors (abundance of sponges in close proximity) in the reef surrounding the Bay Islands, Honduras. Both radial and parallel transect survey techniques were used to quantify the abundance of seven sponge species within a one-meter radius of *Orbicella* species and *Montastraea cavernsoa*. The strongest predictor of coral health was the abundance of *Callyspongia plicifera*, followed by *Svenzea zeai*, in close proximity to diseased coral. A weak, but positive, correlation between poriferan abundance and the presence of disease lesions on coral was observed. However, no significant relationship of disease prevalence with water depth was observed. Additionally, no differences in the prevalence of disease lesions between four species of native stony corals were observed. These findings suggest coral species are equally susceptible to bacterial pathogens, but that close association with poriferans may increase the transmission and persistence of harmful bacteria in coral reef ecosystems.

The Mesoamerican Reef is the second largest coral reef in the world, extending from the northern tip of the Yucatan Peninsula to the Honduran Bay Islands, and is only second in size to the Great Barrier Reef of Australia (Gerholdt 2016). However, in recent decades, the abundance and distribution of coral reefs has been shrinking rapidly across the globe; Great Barrier Reef coral coverage has declined by 50% from 1985 to 2012 (Sweatman 2017), and an 80% loss of coral reef structures has been detected in the Mesoamerican Reef over the last 20 years (AIMS 2017). Multiple stressors have been implicated in these declines. Rising ocean temperatures, ocean acidification,

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increased sediment erosion, rising sea levels, and more intense storms contribute to the decline in coral health (Hoegh-Guldberg et al. 2007).

Coral reefs support a high biodiversity, including 65 species of stony corals in the Mesoamerican Reef and 180 species of sponges within the Caribbean Sea (Charteris 2012; Rodriguez et al. 2014). Stony corals are critical to the health and persistence of the reef as their calcium carbonate skeletons create the foundation of the reef (Smith & Buddemeier 1992). Reef health is very fragile, and anthropogenic stressors such as pollution, urban and agricultural runoff, increased tourism activities (e.g., snorkeling, scuba diving), artificial beach construction, and the destruction of mangroves, can make coral more susceptible to disease (Fabricius 2005). The Australian Institute of Marine Science estimates that 6% of coral mortality is caused by disease (AIMS 2017). Stony coral is susceptible to several bacterial diseases, with yellow band disease (YBD) and white plague type-II (WPII) being two of the most common. In the Caribbean alone, WPII accounts for almost two-thirds of coral disease (Cardenas 2012). Both YBD and WPII affect the health of stony corals *Orbicella* spp. and *Montastraea cavernosa* by targeting and killing the tissue of the coral (Cervino et al. 2004).

While it is well known that coral diseases such as YBD and WPII are caused by bacteria, there is still uncertainty about environmental and biological stressors that may influence how pathogenic bacteria are transmitted between corals. The Mesoamerican Reef harbors numerous species of sponges, including the branching vase sponge (*Callyspongia vaginalis*), azure vase sponge (*Callyspongia plicifera*), giant barrel sponge (*Xestospongia muta*), row pore rope sponge (*Aplysina cauliformis*), erect rope sponge (*Amphimedon compressa),* brown tube sponge (*Agelas conifera*), dark volcano sponge (*Svenzea zeai*), and stovepipe sponge (*Aplysina archeri*) (Rutzler 2012). Poriferans play critical roles in substrate deposition and nutrient cycling in reef ecosystems (de Goeij et al. 2008). Poriferans intake microorganisms through their ostia that are captured by choanocytes and digested material is expelled through their osculum (Wehrl et al. 2007). Poriferans may act as biological stressors on stony corals by harboring

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and filtering pathogens that cause YBD and WPII. It is still undetermined whether the sponges are removing these microbes from circulation, thus potentially decreasing disease transmission to nearby stony corals or if they are a reservoir host for these disease-causing bacteria. For example, *Svenzea zeai* encrust on dead coral structures and are known bacteriosponges, in which they harbor unicellular photosynthetic and autotrophic microbes in nearly half of their biomass (Rutzler et al. 2003; Lee et al. 2009). Moreover, Negandhi et al. (2010) found *Xestospongia muta* harbored *Vibrio,* a bacterial pathogen potentially responsible for YBD in stony corals (Cervino et al. 2008). Furthermore, environmental stressors (e.g., temperature, salinity) can promote persistence and transmission of bacterial pathogens by increasing coral susceptibility (Bruno et al. 2007). For example, incidences of coral disease are greater in warmer waters, with water temperatures negatively associated with water depth as water depth does not always correspond with the water temperature due to thermoclines. Biological and environmental stressors have been demonstrated to have an effect on the severity of coral disease outbreaks, potentially increasing the rate of global coral reef loss (Bruno et al. 2007).

Corals are the foundation species of coral reef ecosystems; therefore, it is imperative to identify stressors that promote disease spread among corals to ensure reef health. The purpose of this study was to identify possible effects of environmental and biological stressors on the health of stony corals in the Mesoamerican Reef. Specifically, it was aimed to assess the relationship between the presence of YBD and WPII on stony corals (*Orbicella* and *Montastraea*) with 1) water depth and 2) abundance of poriferan sponges in 1-meter radius. Moreover, this study will also assess differences in disease prevalence between four species of stony corals, *Orbicella annularis, Orbicella faveolata, Orbicella franksi,* and *Montastraea cavernosa*.

Materials and Methods

Study site.–The Mesoamerican Reef is located in the Caribbean Sea

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off the eastern coast of Central America, stretching nearly 900 kilometers. This study was carried out near Utila and Roatan islands off the eastern Honduran coast (Fig. 1). Both islands are popular diving destinations for national and international tourists. Four dive sites (Paraiso, Jack Neil's Point, Bando Beach, and Radar Reef) were surveyed near Utila in May 2016 and six dive sites (Tuk's Treasure, Fish Den, Bear Den, Mandy's Eel Garden, Pillar Coral, and Tomcat Channel) near Roatan in May 2017 (Fig. 1). Each site was sampled over a week-long period.

Survey methods.–Each dive site was surveyed once on two different days during the week-long period. During the first dive at a given site, searches were conducted right of the mooring line, starting at the deepest depth in which *Orbicella* and *Montastraea* coral species were found (typically 15 - 18 m). During the dive, researchers swam ten minutes in a horizontal line (parallel to the shore) in search of the target coral species away from the mooring line. In order to determine the parallelity to the shore, divers visually determined the location of the dive site to the shore before descending. After ten minutes, researchers (using their dive computers as a measuring tool) ascended 3 meters and continued the search towards the mooring line. This was repeated until a depth of 4.5 meters was reached, creating a search pattern through parallel transects (Fig. 2).

Coral health assessment.–When a coral head of *Orbicella* and *Montastraea* was identified along the survey route, the coral species was recorded, along with health status and water depth (m). Health status was categorized as: 1) healthy - no lesions were observed on the individual coral, or 2) diseased - lesions were observed. Lesions indicative of YBD are circular, with yellow coloration around the infected blotch and dead coral tissue inside the blotch (Bruckner & Bruckner 2006). White plague type-II lesions were identified by exposed coral skeleton with a bright white circular lesion (Richardson et al. 2001). During the 2016 sampling period, only diseased corals were recorded, while both diseased and healthy corals were recorded in 2017. After each initial assessment, a Radial Survey Technique (Weil et al. 2008) was conducted around each individual coral head, with the

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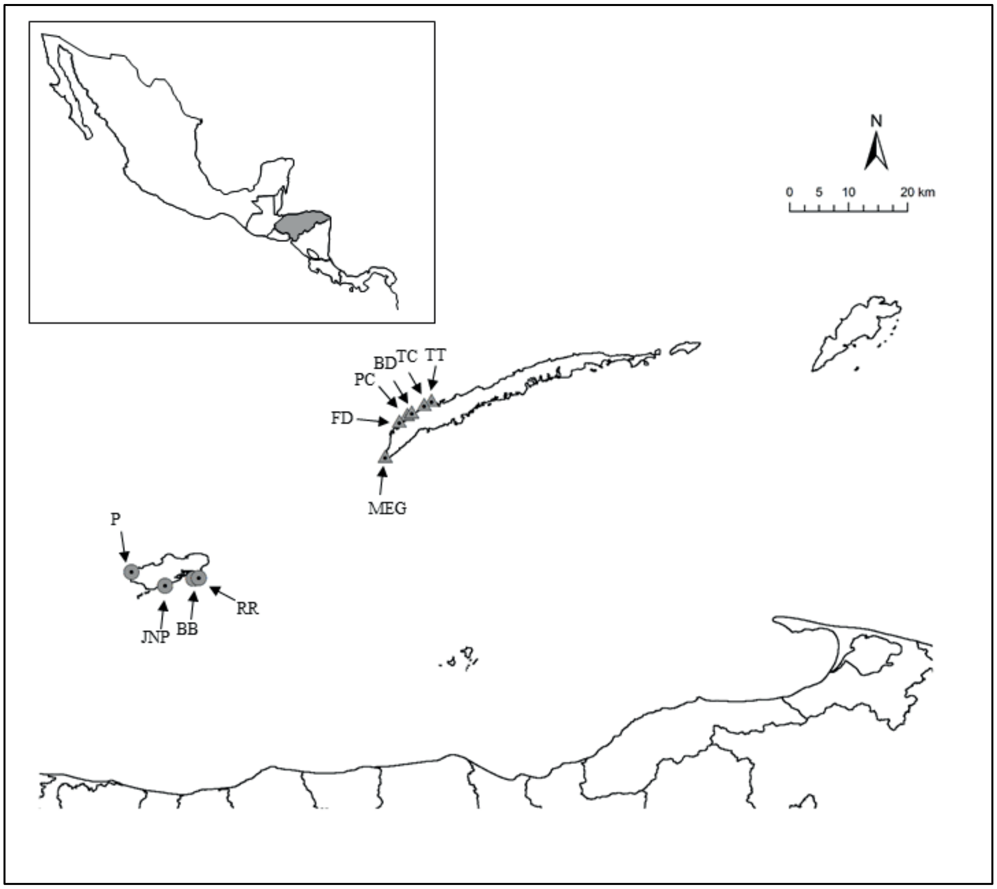

Figure. 1. Study sites in the Mesoamerican Reef off the eastern coast of Honduras (shaded grey inset). Circles represent dive sites surveyed in 2016 near Utila: Paraiso (P), Jack Neil's Point (JNP), Bando Beach (BB), and Radar Reef (RR). Triangles represent dive sites surveyed in 2017 near Roatan: Mandy's Eel Garden (MEG), Fish Den (FD), Pillar Coral (PC), Bear's Den (BD), Tomcat Channel (TC) and Tuk's Treasure (TT).

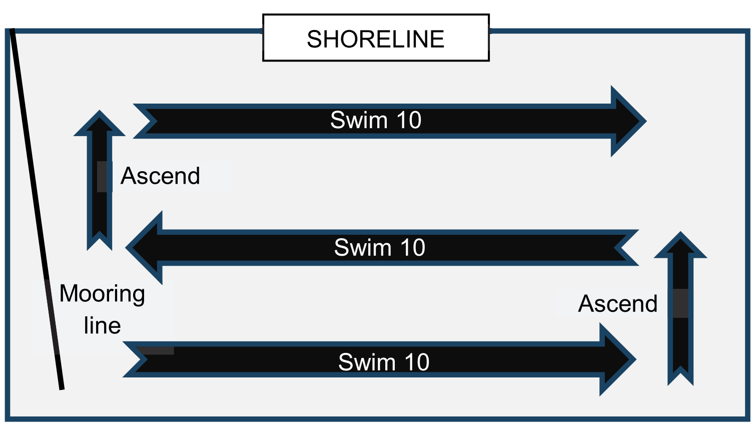

Figure 2. A depiction of the survey route used to record data during each dive.

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center of the circumference being an area with dead coral tissue or an area of substrate close to the coral head, in order not to damage the healthy coral. The center of the circumference was marked with a plumb bob (pointed weight used as a vertical reference line from the center of circumference) at the designated site near the coral head. Then a pre-measured one-meter rope was extended, as one researcher swam in a circle with the rope extended to delineate the area. The abundance (number of individuals) of vase, rope, and barrel sponges within the one-meter radius were recorded.

Statistical analyses.–A generalized linear model was used to assess the influence of biological (sponge abundance) and environmental (water depth) stressors on the presence of disease in stony corals native to the Mesoamerican Reef. A binomial regression structure was specified in the model due to the binary categories used to describe the response variable (coral health status) with the abundance of seven sponge species and water depth (m) as predictor variables. It was then followed with a *post hoc* analysis of variance to test for significant effects of each stressor on the health status of stony corals. Diagnostic plots were checked to ensure model assumptions were met. The strength of the relationship between disease status and abundance of each sponge species was tested using Pearson correlation coefficients. Chi-square tests (χ^2) were performed to assess differences in disease prevalence between the four coral species included in our study. All analyses were conducted in R ver. 3.4.1 (R Core Team, 2017).

Results

Orbicella annularis (n = 103), *O. franksi* (n = 8), *O. faveolata* (n = 24), and *Montastraea cavernosa* (n = 5) were observed during this study (Fig. 3). In 2017, overall prevalence of YBD and WPII across all coral species was 52% (54 out of 104 individuals were infected), with YBD more prevalent than WPII. Disease prevalence ranged from 33% in *O. franksi* (1/3) to 53% in *O. faveolata* (9/17) and *O. annularis* (42/80).

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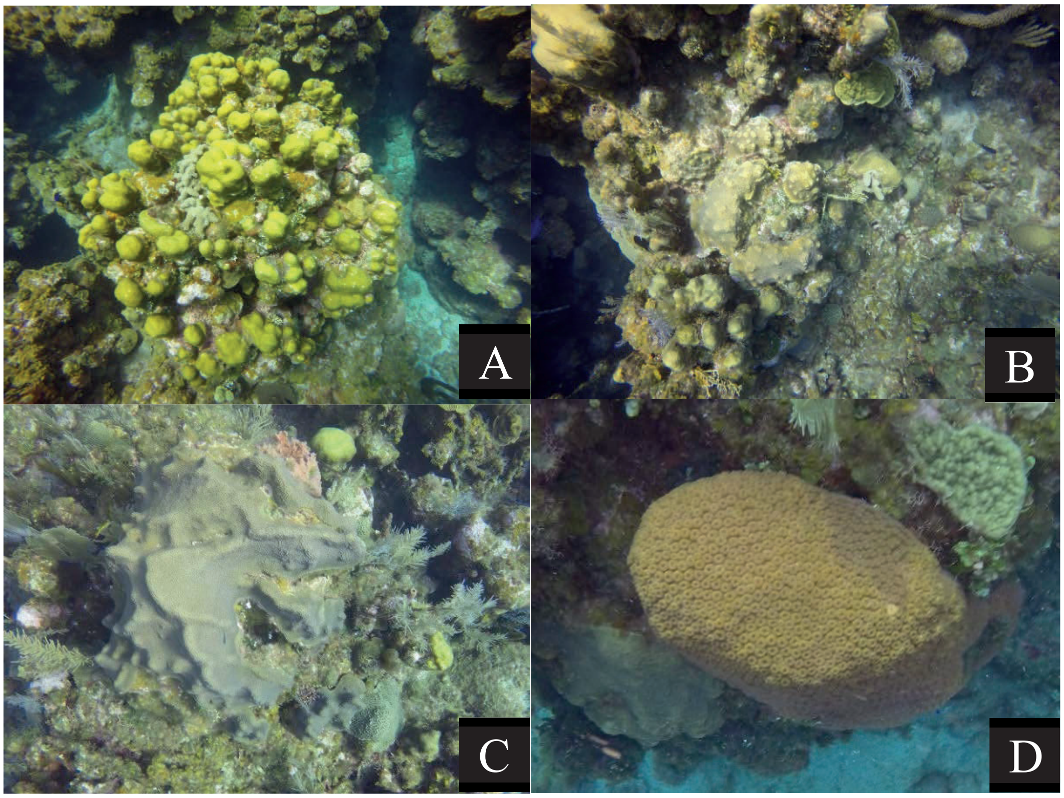

Figure 3. Visual representation of the four coral species monitored in this study: (A) *Orbicella annularis*; (B) *Orbicella franksi;* (C) *Orbicella faveolata*; and (D) *Montastraea cavernosa.*

Sponge species recorded within a one-meter radius surrounding corals included *Callyspongia vaginalis* (n = 75)*, C. plicifera* (n = 31)*, Xestospongia muta* (n = 25)*, Svenzea zeai* (n = 96), *Aplysina archeri* (n = 63), and *Amphimedon compressa* (n = 45) in this study (Fig. 4). Sponge abundance is influential on stony coral health, specifically the abundance of *C. plicifera* and *S. zeai* explained a significant amount of variation in the prevalence of disease in all coral species ($P < 0.05$) (Table 1). Abundance of these specific sponges was positively, but weakly, correlated with coral disease, with the abundance of *C. plicifera* exhibiting the strongest correlation with disease ($r = 0.23$) followed by *S. zeai* ($r = 0.20$).

All four coral species recorded in this study are susceptible to YBD and WPII, however, only two species were found to be affected by both

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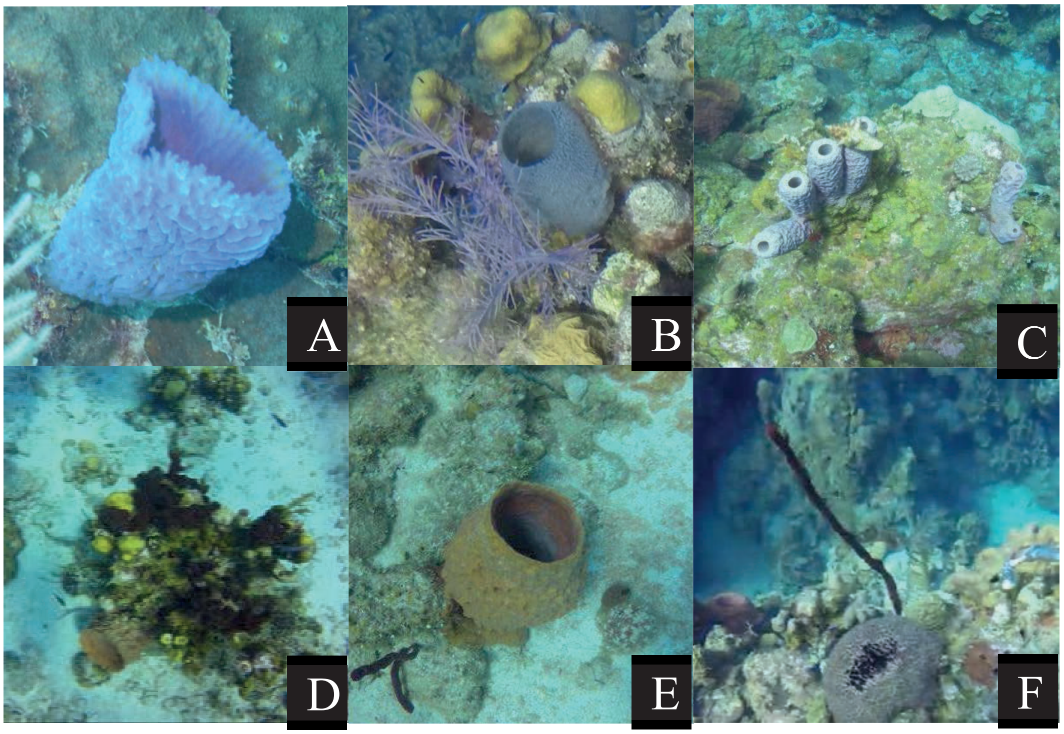

Figure 4. Visual representation of the sponge species recorded during this study: (A) Azure vase sponge (*Callyspongia plicifera*); (B) Branching vase sponge (*Callyspongia vaginalis*); (C) Stove pipe sponge (*Aplysina archeri*); (D) Dark volcano sponge (*Svenzea zeai*); (E) Giant barrel sponge (*Xestospongia muta*); and (F) Erect rope sponge (*Amphimedon compressa*).

Table 1. Results of analysis of variance testing the significance of predictor variables (i.e., sponge abundance and water depth) on the health status of stony corals. Abundance of sponge species is based on untransformed counts of sponges within a 1-meter radius surrounding an individual coral. Deviance explains the relative contribution of each predictor variable for explaining variation in the health status of stony corals, with predictor variables that significantly influence coral health in bold.

Predictor variable	Deviance	*P*-value
Svenzea zeai	7.51	**< 0.01**
Xestospongia muta	0.01	0.75
Callyspongia plicifera	13.15	**< 0.01**
C. vaginalis	1.89	0.17
Aplysina archeri	1.38	0.24
Amphimedon compressa	0.23	0.63
Water depth (m)	1.02	0.31

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diseases (*Orbicella annularis* and *O. faveolata*) (Fig. 5). Conversely, *O. franksi* and *Montastraea cavernosa* were only infected by YBD.

Lesions indicative of YBD and WPII were observed on coral in water depths ranging from 3 to 19 m, which is the entire depth range included in our study. There was no indication that water depth played a significant role in increasing disease prevalence in four stony coral species (P = 0.31) (Table 1). Moreover, no significant difference in disease prevalence was observed between coral species (χ^2 = 22.05, P = 0.99).

Discussion

The relationship between environmental and biological stressors on the health of stony corals (*Orbicella* and *Montastraea*) in the Mesoamerican Reef was explored. A significant effect of environmental stress, based on water depth, on the prevalence of YBD and WPII disease was not detected. However, it is demonstrated that biological stressors, specifically poriferan abundance in close proximity (one-meter radius of coral head), have a negative effect on coral health. Specifically, a positive correlation was found between the abundance of two sponge species, *Callyspongia plicifera* and *Svenzea zeai*, and the presence of disease lesions indicative of YBD and WPII on coral reefs. Lastly, there was no evidence of species-specific susceptibility to bacterial pathogens in the Mesoamerican Reef.

Few studies have explored the relationship between sponges and bacteria. Vacelet & Donadey (1977) revealed that most demosponges and calcareous sponges host microflora, some of which can be pathogenic to coral reefs. In a comprehensive study, Gloeckner et al. (2014) quantified the microbial abundance in 56 species of sponges, 41 of which are native to the Caribbean Sea. Of these, over half were identified as having high microbial abundance, including three sponges included in this study (*Svenzea zeai, Aplysina archeri, Xestospongia muta*) (Gloeckner 2014). *Svenzea zeai* is a known bacteriosponge, allowing the sponge to harbor and ferment bacterial organisms that are the causative agents of coral diseases such as YBD and WPII.

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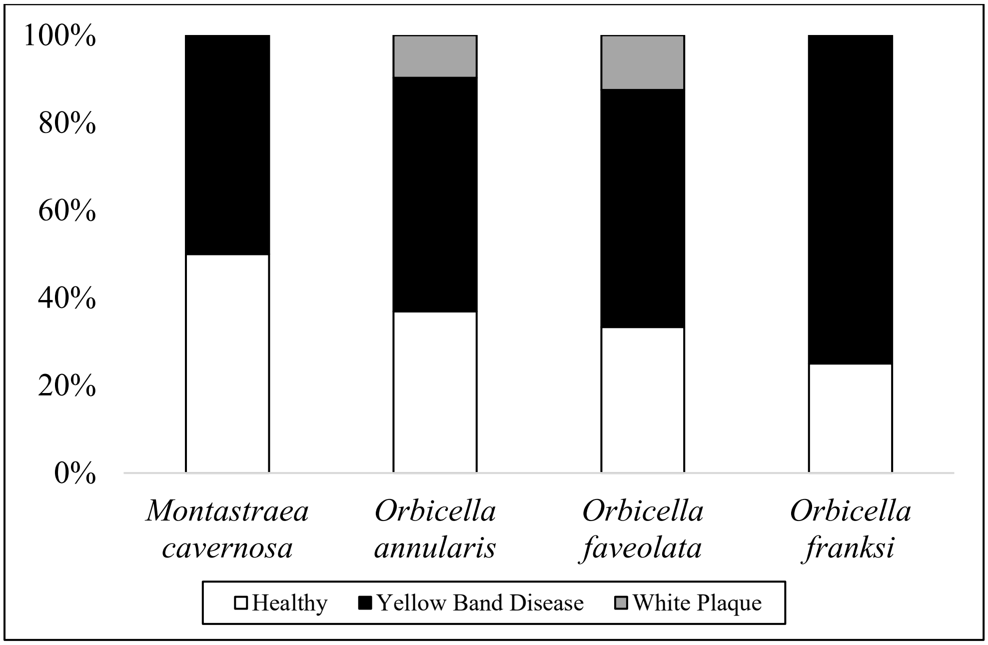

Figure 5. Proportion of individuals of each coral species that were identified as healthy (absence of disease lesions) or infected with yellow band disease (YBD) or white plague type-II (WPII).

Moreover, *S. zeai* also encrusts and grows over dead coral structures, thereby competing with coral for space in the reef (Rutzler et al. 2003; Lee et al. 2009). *Aplysina* sp. is known to host a high microbial abundance as well as have symbiont microorganisms and cyanobacteria within their tissues (Erwin & Thacker 2008; Gloeckner et al. 2014).

Although no correlation between water depth and coral disease prevalence was observed, studies have shown that water depth, along with other environmental stressors, can play a role in disease dynamics of stony corals. Bacteria communities vary based on water depth, as Klaus et al. (2007) found in their study of coral microbial communities. In the study, Klaus et al. (2007) found a variance in microbial communities within coral tissue, depending on the depth and influence of pollution. As depth becomes shallower, corals have a higher presence and stronger susceptibility to anthropogenic stressors.

Water temperature is a well-documented driver of the global loss of coral reefs, as just a few degrees increase in ocean temperatures can wreak havoc on marine ecosystems (Hoegh-Guldberg & Bruno 2010).

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Maynard et al. (2015) concluded that increasing water temperature plays a role in disease susceptibility, increasing host susceptibility and pathogen abundance. With the increasing temperature of the ocean, water quality declines and corals become stressed, making them more susceptible to disease.

Future studies that examine drivers of coral disease should consider sponge abundance and other biological stressors as well as environmental stressors, such as water quality and water temperature. In addition to the sponge species recorded in this study, encrusting sponges should also be examined in order to evaluate the association of coral disease between all sponge species. Marulanda-Gomez et al. (2017) conducted a short- and long-term analyses within a Caribbean reef and found that encrusting sponges did grow and take over substrate from live coral. Due to a limited amount of space within reef communities, encrusting sponges have a greater chance of competing with the coral for space, increasing the stress level of coral species, so those sponge species could add to coral disease susceptibility.

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