*Environmental Effects on the Morphology of Hawaiian Rice Coral (*Montipora capitata*)*

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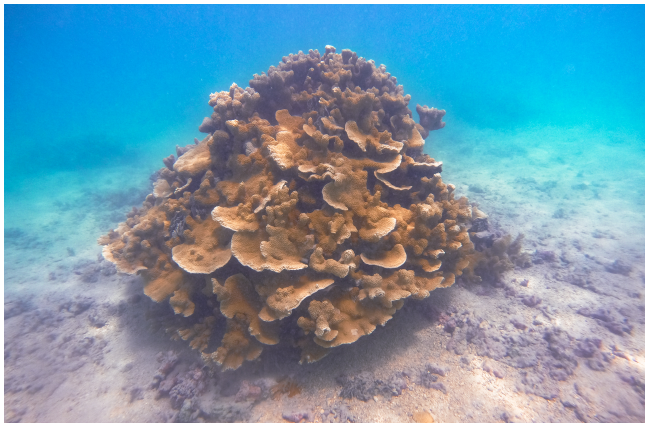

Hawaiian scleractinian corals provide diverse ecosystems that are extremely sensitive to environmental changes. O`ahu experiences rapid environmental alteration due to its human population, thus offering an ideal test region for this study. Here, the focus is identifying the relationship between the morphology of Montipora capitata corals and the environmental factors of sedimentation, effluent, sea surface temperature (SST), wave action, irradiance (PAR), and depth using a multiple logistic regression model and a generalized linear model (GLM). Environmental factor values were derived from the 2018 Ocean Tipping Points Hawai`i Study (OTP) and correlated with data from 198 coral colonies, which were collected via a comprehensive sampling campaign at 97 locations. Statistical analyses found significant relationships between M. capitata morphology and SST, sedimentation, wave action, and depth. Additionally, a visual representation of coral morphology around O`ahu provides direct insight on the prevalence of different coral growth patterns while supporting the findings of the GLM. These findings present the first documentation of this species' growth island-wide, facilitating a broader understanding of Hawaiian Montipora corals and the crucial factors influencing their growth. Such insights are instrumental in advancing conservation initiatives aimed at mitigating the adverse effects of both natural phenomena and human-induced climate change.

Over the last year and a half, I have worked on this project while underscoring my passion for the environment and the ocean. I continuously broadened my scope of the field of marine research and recognized more comprehensive trends about the coral reefs on Oʻahu. This project opened my eyes to conservation and outreach that I will incorporate into my future career.

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Introduction

Hawaiian scleractinian corals play an integral role as foundational species in maintaining marine communities throughout the island archipelago (Putnam et al., 2017). These reef-building corals provide habitats, food, and other resources for a quarter of all marine life and ensure the stability of the reef ecosystem (Putnam et al., 2017). These corals must adapt to changing environments and face challenges such as climate change and anthropogenic influences (Putnam et al., 2017). There are a variety of environmental factors that affect corals including climate patterns, ocean temperatures, circulation, and nutrient availability. Due to the plethora of disturbance opportunities, scleractinian corals are known to modify their morphology to optimize growth (Zawada et al., 2019). Thus, exploring morphologies may provide information to identify how corals react to environmental stresses, allowing for a detailed view of the seascape.

The initial historical decline of Hawaiian corals began with the local increase of Western influence, and the subsequent escalation of industrial, commercial, and military occupation on O`ahu which led to severe degradation of the surrounding reefs (Gulko et al., 2002). For years, it was believed that Hawaiian corals were immune to bleaching events that plagued other regions of the world. However, extreme coral bleaching was eventually documented in the 1990s in Kāneʻohe, Oʻahu (Gulko et al., 2002). Since then, increasing attention has been brought to the subject of maintaining coral integrity throughout the islands. Continuous data collection over time can offer insights into reef health and its response to the ongoing progression of climate change and conservation.

Causes for the different morphologies in corals arise via different pathways, including phenotypic plasticity and genetic adaptation. The variability of growth patterns, or polymorphisms, explains plastic responses to changing environments, while adaptation is based on genetics and the development of advantageous traits over time (Todd, 2008). Plastic responses are phenotypic, meaning they are not permanent and do not directly affect offspring. However, traits that arise due to morphological plasticity can become genetically advantageous then inherited as adaptations through generational natural selection.

One key environmental factor that alters coral growth responses is the depth at which they live. With increasing depth, sunlight is differentially absorbed in the water and is therefore less available to photosynthetic organisms. Corals have a critical symbiotic relationship with Symbiodiniaceae, a photosynthetic algae that presents the coral with fixed carbon energy in exchange for shelter and nutrients (Stambler, 2011; Frankowiak et al., 2016). When a colony resides deeper in the ocean, there is less light and it often alters its morphology in order to maximize the surface area available for light capture (Stanley, 2006). Specifically, it has been documented that optimal coral shape is related to the local light intensity (Muko et al., 2000). Typically, scleractinian corals tend to develop branching structures in high-light conditions, while adopting a plating morphology in poorly lit areas (Muko et al., 2000). Based on these findings, it is clear that depth as a function of light absorption has an effect on *Montipora capitata* morphology.

Irradiance plays a role in coral growth in a manner similar to depth. Photosynthetic available radiation (PAR) is used to measure irradiance by assessing light intensity at reefs. Available sunlight leads to photosynthesis in these areas, which stimulates high reef productivity and increased health (Wedding et al., 2018). Though, conditions of irradiance are sometimes different at the same depths because turbidity and other methods of shading limit the sunlight's ability to penetrate to the seafloor.

Sea surface temperature (SST) also affects photosynthesis, production, and growth in aquatic communities (Carricart-Ganivet, 2004). SST can vary depending on the geographical location and factors such as atmospheric and oceanic circulation and other climate interactions (Deser et al., 2010). O`ahu experiences patterns of El Niño Southern Oscillation, which alters the transport of warm and cool water through the Pacific (Lu et al., 2020). Plus, the topography of the seafloor and reef formations limits circulation of O`ahu's coastal waters, leaving some areas less susceptible to mixing and therefore allowing for solar heating (Jokiel, 1977). Following typical trends, windward O`ahu has lower SST due to its exposure to wind and rain which cause upwelling and mixing, whereas leeward O`ahu experiences less weather and higher temperatures. However, waters along east O`ahu maintain some of the warmest temperatures on the island due to protection by barrier reefs that reduce mixing (Bahr et al., 2015). The heating and cooling patterns of SST indirectly affect coral growth, as they directly modify the photosynthetic capabilities of the symbionts that live within them.

A similar trend is found between corals and the nutrients in the water. Algal symbiont photosynthesis requires nutrients, water and sunlight, but an excess of nutrients can be detrimental to efficacy and energy production. Chlorophyll-*a* is one such component of seawater that is also a great indicator of eutrophication, which is often harmful to photosynthetic organisms (Bell et al., 2014). Chlorophyll-a concentrations are frequently employed as indicators of phytoplankton biomass among coral reefs. These natural signals can present information regarding the status of reefs based solely on how much primary production is occurring, and therefore is a useful metric in discussing coral growth patterns in regions of varying productivity (Wedding et al., 2018).

Another influential factor is sedimentation. Specific regions

of the ocean have different water flow rates that allow sediment deposition and transport. For reef-building corals, the amount of sediment in the water can physically affect their growth (Duckworth et al., 2017). Some sediments in the water smother corals when making contact with their external surfaces, often resulting in bleaching and sometimes in coral death (Duckworth et al., 2017). Still, some morphologies are more effective in facilitating cleanliness of coral surfaces. Particularly, arborescent growth is optimal in areas with high sedimentation, as this form limits the horizontal surface area of the coral in order to restrict particle settlement (Duckworth et al., 2017). Likewise, plating species are not optimal in those same areas because they would be smothered by the sediments and face growth inhibition (Duckworth et al., 2017). Advantageous shapes such as arborescent forms may be more prevalent in areas with higher sedimentation rates in order to ensure effective coral growth and survival.

The last environmental factor considered in this study is wave action. The prevalence of wave activity on a reef is responsible for a number of effects, such as the physical stress of water movement causing erosion, or specific conditions encouraging niche organisms to inhabit the areas. Herbivorous fishes, for example, have unique preferences for wave and tidal conditions depending on the species and the state of the reef (Bejarano et al., 2017). Wave action also affects coral larvae recruitment. Specifically, certain algae species flourish in high wave activity zones, and this stimulates algal overgrowth. This overgrowth reduces the availability of substrate cover, which is essential for coral settlement (Becerro et al., 2006). Additionally, wave energy directly impacts coral shape by dictating the vertical complexity at which they can grow. Colonies with more hydrodynamically satisfactory morphology tend to experience less damage in areas of high wave energy to avoid breaking of fragile branch-like structures (Graus et al., 1977).

To account for the anthropogenic influences on coral health, the land-based stressor of nutrient effluent is included. In Hawai`i, onsite waste disposal systems (OSDS) present a critical concern for coral reefs due to the state's disproportionately high number of OSDSs in nearshore areas compared to other regions of the country (Wedding et al., 2018). Moreover, the risk of pollution and nutrient over-enrichment in coastal marine ecosystems is greatly increased by OSDSs, due to their leaching of contaminants into Hawai'i's groundwater systems. Chronic nutrient enrichment has been demonstrated to impact growth, symbiont density and host-symbiont nutrient exchange in Hawaiian corals, and such processes may influence morphology in areas with chronic nutrient subsidies (Fox et al., 2021).

Overall, the ways in which corals demonstrate phenotypic and genotypic responses to environmental variables are especially important to consider, as topics surrounding ocean degradation dominate marine health concerns. This study aims to compare the morphologies of the Hawaiian stony coral *Montipora capitata* at different depths around the coast of Oʻahu. The sites were selected through stratified random sampling of environmental rasters as part of the seascape genomics project of Samantha Shedd, a PhD student in the School of Life Sciences. Based on previous knowledge of corals and their growth patterns, it is expected that there will be a significant difference in growth morphology of *M. capitata* at different depths, SSTs, and sedimentation rates. These results will be useful in comprehending environmental trends that could answer questions regarding these organisms' responses to their environment, such as their susceptibility to being harmed by changing conditions, and how we can be more effective in monitoring anthropogenic influences on such conditions. Since *M. capitata* is an extremely resilient species of coral with a large spatial range around O`ahu, knowing how the reefs form with respect to their conditions can inform us on how they will continue to supply ecosystem services (Williams et al., 2021). Ultimately, this knowledge can be applied to predictions about coral resistance to climate change and other environmental threats, and provide information about how to preserve and manage these critical ecosystems.

Methods and Materials

Objectives

This project focused on identifying colonies of Montipora capitata and obtaining visual assessments of their physical morphology. The SST and sedimentation were acquired based on the findings of the 2018 Ocean Tipping Points Hawai`i Study and the depth was documented in situ upon identification of the species in the field. The photos were categorized by morphology and these data were tested for correlation through a generalized linear model RStudio (version 4.3.1).

Study Areas

O`ahu maintains climates that differ seasonally and are often subject to change. This study contains samples from a majority of the regions around the island; however, the spread of sites is not evenly distributed around its perimeter. Many samples come from the windward side of the island, within Kāne`ohe Bay. The climate of Kāneʻohe remains constant for most of the year, with a 24% chance of rain daily during the wet season of November to March (NOAA, 2022). The south side of Oʻahu experiences variable conditions betw-een the wet and the dry season, with a large increase in wave and wind swell from May to September. During this time, the opposite side of the island has very light wave

action. However, the winter brings consistent swells of 20-60 foot waves to O`ahu's North Shore. The west side of O`ahu experiences the least amount of rain and wind, receiving anywhere from 9 to 15 inches per year (NOAA 2024). The northern end of the west side also encounters increased wave swell during the winter around the same times as the North Shore.

Sample Collection

Following protocols for the seascape genetics project, 400 GPS sites were selected around O`ahu. 97 sites were visited for this study with searches for *Montipora capitat*a colonies within 100 meters of the coordinates. The sites were accessed via snorkeling from the shore or taking a boat organized by the seascape project. Once a colony of *M. capitata* was identified, videos were taken to document the physiology. Sample sizes varied by site, as some locations had more colonies than others. The goal was to document three colonies at each site, but one to four colonies per site were sampled, for a total of 198 morphology identifications between October 2022 to February 2024.

Upon revision of the photographic data from field observations, colony morphology was grouped according to the major categories of growth forms of scleractinian corals (Figure 1; Pratchett et al., 2015). The morphologies observed in sample species were encrusting, massive, tabular, digitate, caespitose, and arborescent.

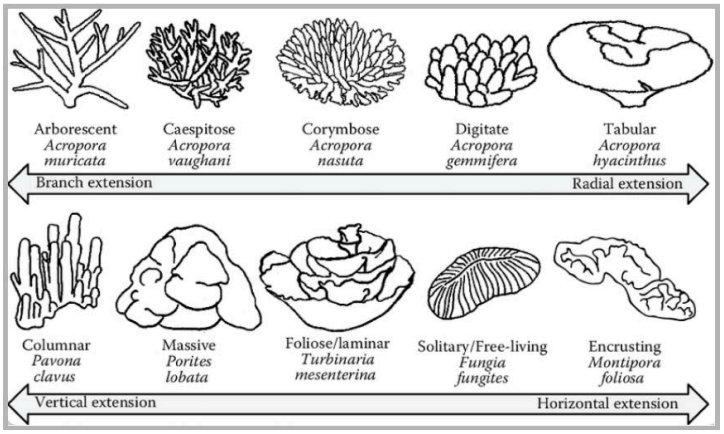

Figure 1. The major morphological categories of growth forms of scleractinian corals by their major growth axis (Pratchett et al., 2015).

Environmental Factor Data

The depths were recorded on site, and sedimentation, nutrient effluent, SST, wave action, PAR, and chlorophyll-*a* values from the OTP project were extracted. The OTP case study documented the long-term SST averages between 2000 and 2013, and sedimentation in 2005 (Wedding et al., 2018). These two factors provide evidence of the corals' generalized response to solar heat and radiation and natural ocean cycles. The same study estimated irradiance and chlorophyll-a levels through 2002-2013 from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS), and wave action from 2000-2013 from the University of Hawai`i's Simulating WAves Nearshore model (SWAN). These oceanic drivers supply data that varies naturally with seasonal climate cycles. To evaluate anthropogenic influence, nutrient flux estimates (as units of gallons of nutrients) were modeled based on catchment OSDS density between 2009 and 2014 (Wedding et al., 2018).

Statistical Analysis

A multiple logistic regression model (LRM) tested the potential for seven environmental factors to predict the morphological classes across all 198 colonies among 97 sites using the AOV package. The independent variables of environmental influences were standardized using a logarithmic transformation prior to the model to meet the assumption of normality. The resulting residuals were then plotted to assess normality of the dataset. In addition, a generalized linear model was run using the GLM package, comparing each morphology individually to the environmental factors at each site. For each model run, the presence or absence of a particular morphology at a site served as the dependent variable, while independent environmental data from the OTP survey were used as predictors. Prior to modeling, the environmental data were scaled using the 'scale()' function in R to ensure comparability across variables in the models. A binomial distribution was specified for the response variable, reflecting the binary nature of the presence-absence data. The default logit link function for the binomial family in R was utilized to model the relationship between predictors and the response variable. This analysis was conducted a total of six times, each time focusing on the presence or absence of one morphology type. It was assumed that if a morphology was not recorded during initial data collection, it was absent from the survey site. This assumption simplified the modeling process, but should be remembered when interpreting the results.

Results

A total of 198 samples of M. capitata were collected and assigned a morphology classification across 97 sites around the coast of O`ahu (Figure 2).

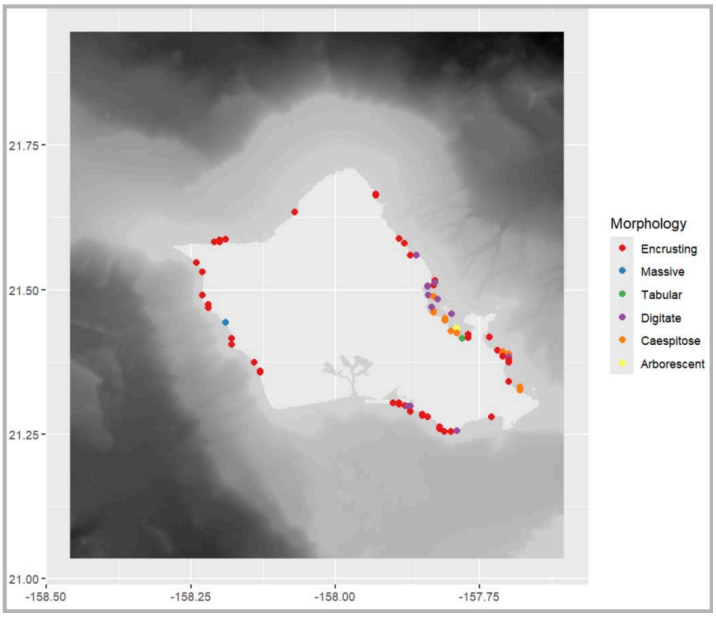

Figure 2. *M. capitata* morphologies present around O`ahu based on coordinates of the collection sites. Figure created with RStudio version 4.3.1.

Massive and tabular morphologies each accounted for 1.01% of growth types, arborescent colonies were 1.5% of samples, while 17.7% of samples consisted of digitate colonies, 19.2% were caespitose, and the remaining 59% of corals were encrusting (Figure 3).

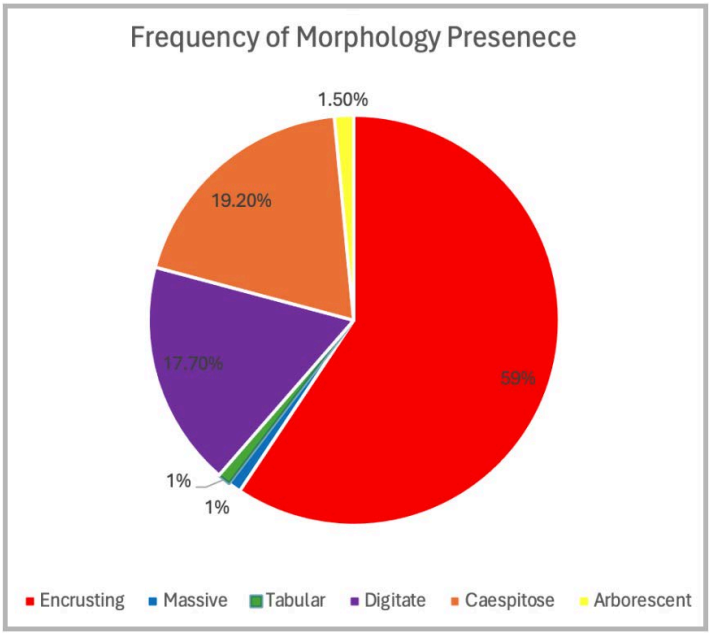

Figure 3. The frequency of each growth type among the 97 sites sampled. Data collected via photographic samples of 97 sites around O`ahu, Hawai`i. Figure created with Microsoft Excel.

Linear Regression

After running the LRM a Q-Q plot was created to confirm normality of the residuals. This model found significance with an alpha less than 0.05 (P<0.05), indicating that sedimentation, SST, and wave action had a significant effect on morphology (Table 1). Wave action had the strongest positive effect on coral morphology (P=3.31-16), followed by SST (P=2.20-11) and sedimentation (P=4.23-6). Depth was marginally significant (P=0.0588).

Env. Factor	P-Value
Sedimentation	4.23x10^-6
Effluent waste	0.9433
SST	2.20x10^-11
Wave action	3.31x10^-16
PAR	0.7031
Chlorophyll-a	0.2389
Depth	0.0588

Table 1. Results from logistic regression models, stating the environmental factor and its corresponding P-value. Color indicates significance with P < 0.05.

Generalized Linear Model

	Number of samples	Sedimentation	Effluent waste	SST	Wave action	PAR	Chlorophyll-a	Depth
Encrusting	118	0.142308	0.557009	0.000517	0.001449	0.814774	0.009169	0.002464
Digitate	35	0.121557	0.06254	0.30668	0.00463	0.23744	0.73231	0.81942
Caespitose	38	0.319125	0.195058	1.91e-05	0.474991	0.352910	0.231264	0.000735

Table 2. Resulting p-values from the GLM demon-strating correlation between the three most common morphologies and environmental factors. Color indicates significance with P < 0.05.

A GLM was used for the three most common morphologies observed around O`ahu (Table 2). The other three morphologies were not included due to the small sample size (<2%; Figure 1). The GLM shows significance for the individual relationships between encrusting corals and SST, wave action, chlorophyll-*a*, and depth (Table 2). Upon closer examination, the slopes of the model indicate that encrusting corals more frequently inhabit areas of higher wave disturbance and increasing depth. The opposite pattern is true

when evaluating the influence of SST and chlorophyll-a; encrusting corals are less prevalent with increasing temperature and chlorophyll-a concentrations (Figure 4).

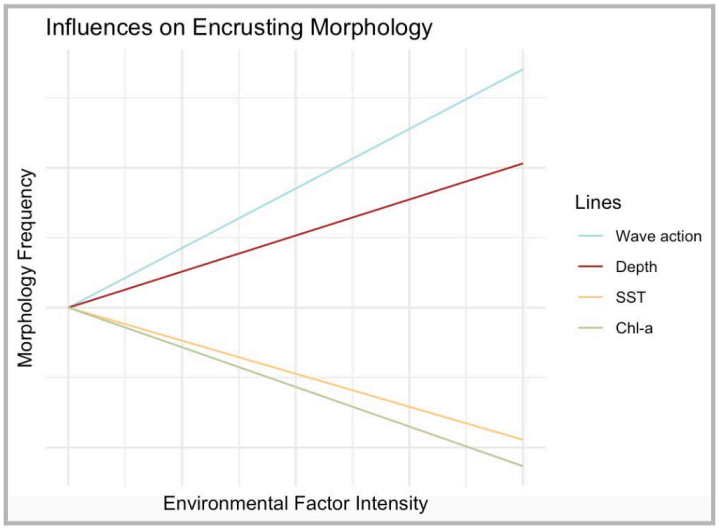

Figure 4. Slopes from the GLM on encrusting morphology show trends in colony preference with each significant environmental factor (Wave action = 1.70; Depth = 1.03; SST = -0.94; Chl-*a* = -1.13344). Figure created with RStudio version 4.3.1

Discussion

Through this visual and environmental factor-focused research around O`ahu I compared *Montipora capitata* morphology with recorded environmental conditions as a way to regionally predict growth forms of coral colonies. To access sedimentation, effluent waste, SST, wave action, PAR, and chlorophyll-a data at each coordinate, results of a study on environmental drivers of coral reefs by Wedding et al. (2018) were utilized. Extensive field sampling from November 2022 through February 2024 allowed for collection of 198 samples of *M. capitata* of varying morphological characteristics. These data were categorized by their dominant growth form then tested against the environmental data to find correlation and offer a means of predicting morphologies with prior knowledge of the environment.

These recordings suggest that encrusting forms of *M. capitata* largely dominate the coastal reefs of O`ahu, which suggests that it is the most adaptable to the island's varying conditions. Due to the lack of complexity in growth form, encrusting corals can maximize their growth through horizontal extension, creating optimal conditions for symbiont photosynthesis and development.

The LRM also provided important conclusions regarding the connections between morphology and the combination of environmental factors. There was a significant relationship between morphology and SST, wave action, and sedimentation at a site. Furthermore, the GLM suggests that the independent factors of SST, wave action, chlorophyll-a concentrations, and depth have significant impacts depending on the morphology.

The three variables of SST, wave action, and sedimentation were expected to heavily influence coral morphology, as some colonies are more fragile and unable to withstand these extreme environmental conditions. Wave intensity has a highly positive relationship with morphology according to the LRM, indicating that *M. capitata* is sensitive to wave action. According to the GLM, encrusting colonies were found more commonly in areas with high rather than low wave action. Encrusting growth is more resistant to disturbances than other forms, since this morphology is extremely vertically compressed and entirely anchored to the substrate. More complex morphologies such as arborescent contain branching structures with less integrity due to their vertical extension into the water column. Therefore, complex growth patterns are less likely to be found in areas of high wave disturbance, as branches are more susceptible to breaking (Storlazzi et al., 2002). In fact, digitate and caespitose colonies assessed in this study were found most commonly at sheltered sites with little waves, where they may grow fragile branches with less risk of damage.

Likewise, SST has a significant effect on coral morphology. Specifically, encrusting corals more often populated waters with lower temperatures whereas caespitose colonies were more frequently in warmer waters. Due to the direct correlation between SST and primary production, it is assumed that complex morphologies exist in areas with higher productivity. Simple growing corals like encrusting corals do not require the same amount of product yield since their forms lack the complexity seen in other colonies, and therefore are able to grow effectively even in conditions that are less conducive to complicated growth.

The LRM also indicates that sedimentation is significantly related to morphology. However, when viewing the results of the GLM, sedimentation does not show a significant correlation with the specific morphologies tested. Alternatively, the LRM did not find depth to be a significant factor in coral growth, yet the GLM shows that encrusting and caespitose corals are significantly affected by depth. This suggests that although the individual morphologies were not altered by depth or sedimentation as single factors of influence, reviewing growth by environmental conditions indicated that these variables play significant roles in morphological determination. Essentially, predicting the morphology of a coral colony based solely on depth or sedimentation may be not feasible; however, with additional environmental data, such predictions are possible using regression modeling.

Various limitations and possibilities for error were present in this study. Unequal sample size may have led to skewed data when assessing the frequency of morphologies at

the sites. Some regions provided only one sample while others sustained up to four, which may have increased the weight of samples from certain sites. Another factor was the randomness of sample selection. The sites were selected randomly, but despite best efforts to sample colonies randomly, the lack of a mathematical method to guarantee randomness within each site introduced bias. Moreover, the depths of all samples were recorded with the same dive computer, though tide changes may account for slight variations in depth depending on the date and time of sampling. This was a short-term study that occurred over 18 months, and therefore does not consider seasonal growth, tide patterns, or community composition.

Finally, a critical flaw emerges from the underlying assumptions inherent in GLM processing. This model operates on the binary premise of the presence or absence of the morphology, presuming that if a characteristic was not documented at a particular site, it equates to its non-existence. However, coral populations exhibit non-uniform growth patterns. Merely documenting three digitate colonies at one site does not negate the possibility of other morphologies being present, unlike what the model assumes. Conversely, the absence of recorded digitate growth does not imply its absence in reality. Encrusting species are likely ubiquitous across all study sites, yet instances of their oversight or non-recording due to sample bias cannot be discounted.

Ultimately, acknowledging that *M. capitata* species demonstrate markedly different morphologies in different environmental conditions offers valuable information about the current state of the marine ecosystem in O`ahu. Climate change has been an extreme concern in the last decade, and this data emphasizes that marine organisms do grow in response to natural factors. Although differences in morphology among colonies and locations does not indicate health, reef structures provide unique ecosystem services that may decline if conditions worsen. Specifically, Hawai`i's coral reefs contribute $360 million annually to society and the economy (Wedding et al., 2018).

Ecotourism and recreation are closely tied to the health of marine ecosystems; more complex reefs yield greater aesthetic value, enhancing experiences for visitors. Additionally, these intricate scleractinian reefs generate habitats for marine organisms, which promotes biodiversity and local species availability for recreational fishing (Woodhead et al., 2019). The interest in how changes in corals affect the community structure of ecosystems offers ample opportunities for viewing the interactions between corals and other marine species. The variability of these interactions is critical in assessing how coral and other marine species differ in response to environmental discrepancies. Moreover, complex morphologies of *M. capitata* are critical in bestowing O`ahu with coastal protection from storms and extreme wave action to resist coastal erosion and degradation.

These factors underscore the legitimacy of worries about climate change's effects on reefs. It would be advantageous to expand assessments on the impact of morphology in other native species, while considering additional factors like algal cover and proximity to different coral species. Future research should focus on analyzing genetic content to understand how corals of the same species can manifest physical plasticity like *M. capitata*. Replication on other Hawaiian islands may reveal trends in morphology that are unique to the location of the colony relative to the land. Core factors in these experiments may incorporate environmental-DNA technologies as they continue to improve and support more accessible science. In uncovering the intricate interplay between environmental factors and the morphology of *Montipora capitata,* this study not only details the vulnerability of Hawaiian scleractinian corals but also underscores the urgency of informed conservation strategies essential for protecting these precious ecosystems amidst the escalating challenges of climate change.

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