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Post-Disturbance Dynamics of Branching Corals and their Predators

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Post-Disturbance Dynamics of Branching Corals and their Predators

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Environmental Science and Management

by

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June 2023

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Speare, K. E., Adam, T. C., Winslow, E. M., Lenihan H. S., Burkepile D. E. (2022). Marine Heatwave Kills Largest and Smallest Corals, Eroding Resilience Capacity of Reefs. Global Change Biology.

Ladd., M, C., Winslow, E. M., Burkepile, D. E., and Lenihan, H. S. (2021). Corallivory Varies with Water Depth to Influence the Individual Performance and Slow Population Recovery from Disturbance of *Acropora hyacinthus*. Ecosphere. doi.org/10.1002/ecs2.3623.

Lenihan, H., Ake, H., and Winslow, E. M. (2019). MCR LTER: Coral Reef: Long-Term Coral Population and Community Dynamics: Annual Island Wide Coral Demography Survey 2011 ongoing.

Winslow, E. M., Read, E., Group, B., Ho, D., and Grant, C. (2017). Planning and Incentivizing Native Olympia Oyster Restoration in Southern California. Report of a Forum Sponsored by American Honda Motor Corporation Aquarium of the Pacific Bren School of the University of California, Santa Barbara.

ABSTRACT

Post-Disturbance Dynamics of Branching Corals and their Predators

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Coral reefs are among the most biodiverse, valuable, and impacted ecosystems on the planet. Disturbances that kill coral, the foundation species of coral reef ecosystems, are becoming more frequent and more severe, thereby threatening the persistence of global reefs which provide food, jobs, and coastal protection for over one billion people worldwide. However, even the most extreme disturbances seldom cause total mortality of corals, and the spatial variability of surviving coral has consequences for how the rest of the ecosystem responds. In my dissertation work, I sought to understand 1) how and where branching corals evaded mortality during a severe marine heatwave, 2) the extent to which coral predators can amplify the impact of disturbance on coral through species interactions, and 3) whether and how the effects disturbance-driven mortality of branching coral cascaded through the ecosystem and impacted coral predators that vary in their dependency on coral as a food source. To answer these questions, I utilized and performed a combination of field experiments, *in situ* surveys, and statistical model. My work provides insight into the complex and nuanced relationship between coral and coral predators and improves our ability to understand and predict both how different disturbances impact coral reef ecosystem dynamics.

CHAPTER 1. Corals survive severe bleaching event in refuges related to taxa, colony size, and water depth

1.1 ABSTRACT

Marine heatwaves are increasing in frequency and duration, threatening tropical reef ecosystems through intensified coral bleaching events. However, there is variability in bleaching response across small spatial scales during most warming events. Corals can exhibit size- or taxa-dependent bleaching patterns, certain morphologies are more bleaching resistant, and corals in deeper water generally bleach less. Gaining a better understanding of which corals evade bleaching during a heatwave is of paramount importance for reef management and conservation. Following a marine heatwave in 2019, we surveyed ~5,100 coral colonies on both shallow and mid-depth reefs (10 and 17 m depth) around Moorea, French Polynesia. Overall, *Acropora* corals bleached more severely than *Pocillopora* corals. However, *Acropora* exhibited less bleaching at deeper sites compared to shallower sites and smaller colonies bleached less than larger colonies. Large *Pocillopora* corals bleached at the lowest observed levels of heat stress and disproportionately more than smaller colonies. Our findings indicate that the impacts of thermal stress are complicated and whether or not a coral bleaches depends on complex interactions between taxa, depth, and colony size.

1.2 INTRODUCTION

Human-induced climate change is increasing the frequency and intensity of marine heatwaves that can cause extreme ecological changes in marine communities, especially in tropical latitudes (Holbrook et al., 2019). Of major concern is the impact of sustained, elevated seawater temperature on reef-building corals (Webster et al., 2017). Coral bleaching is a stress response of corals to warm water in which the coral host expels the endosymbiotic dinoflagellate microalgae (Symbiodiniaceae) (Brown, 1997) from its tissues, resulting in the loss of coloration in coral colonies. The mutualism between corals and Symbiodiniaceae is sensitive to small changes in temperature, such that an increase of only 1-2°C can trigger bleaching (Heron et al., 2016; Hughes et al., 2018). In some instances, bleached corals can recover from thermal stress by re-establishing endosymbionts in their tissue (Lewis and Coffroth, 2004) but bleaching often leads to coral mortality. As such, extreme warming events have led to massive pan-tropical coral bleaching and mortality in 1998, 2010, and 2015-2016 (Heron et al., 2016; Hughes et al., 2018, 2017). Climate projections forecast that bleaching will become more frequent and more severe as the climate continues to warm, thereby threatening corals and coral reef communities at a global scale (Donner, 2009; Souter et al., 2020).

Although bleaching is a major threat to corals worldwide, bleaching does not impact all corals uniformly across a reefscape, even during the most severe marine heatwaves (Hughes et al., 2017; Loya et al., 2001). Spatial variation in bleaching can be partially related to local levels of heating, solar irradiance, and differences in physical conditions among microhabitats (Lenihan et al., 2008), many of which vary across depth. Corals at shallower depths are exposed to higher solar irradiance where light can act synergistically with temperature to initiate coral bleaching (Loya et al., 2001; Riegl and Piller, 2003). Deeper water can serve as a refuge from bleaching through the attenuation of light and general cooling of water with depth (Baird et al., 2018; Muir et al., 2017). In addition to reprieve from light and warmer surface water, deeper reef habitats experience more intense internal waves (Leichter et al., 2012, 2006) that can originate near shelf breaks, travel hundreds of kilometers, and transport cool, nutrient rich water onto the reef (Leichter et al., 2012; Roder et al., 2010). Waves and currents can also buffer reefs from the thermal stress associated with high surface temperatures (Bak et al., 2005), as water movement facilitates gas exchange that reduces the buildup of oxygen radicals (Nakamura et al., 2005, 2003; Nakamura and Woesik, 2001).

Different coral genera and associated endosymbionts vary widely in their susceptibility to bleaching, and thus taxonomic composition of the coral community can drive spatial and temporal patterns of bleaching and mortality (Obura, 2005). Massive and encrusting coral taxa are generally more resistant to bleaching and bleaching-induced mortality in the short term and are therefore considered "winners", while branching and tabular species are usually more susceptible to heat stress and are often classified as "losers" during bleaching events (Loya et al., 2001). Variation in bleaching susceptibility also exists within a given taxa as a function of colony size (Speare et al., 2022; van Woesik et al., 2012). For example, larger colonies of *Pocillopora* and *Acropora* sometimes exhibit higher bleaching prevalence, severity, and bleaching-induced mortality (Brandt, 2009; Shenkar et al., 2005; Speare et al., 2022) than smaller conspecifics. Additionally, *Pocillopora* species may also differ in their susceptibility to thermal stress, and size-dependent bleaching and mortality may be driven, in part, by the disproportionate representation of thermally-sensitive cryptic species across the size spectrum (Burgess et al., 2021).

Here, we examined how corals on shallow and mid-depth tropical reefs responded to a prolonged marine heatwave that impacted Moorea, French Polynesia from November 2018 to July 2019 to further understand the context that drives variation in the bleaching response in corals (Figure 1). Using *in situ* temperature measurements, we quantified how accumulated heat stress (AHS, an integral measure in °C-weeks) and the mean daily temperature fluctuation (MDTF, measured in °C) varied across small spatial scales around the island. We also conducted an extensive survey two months after the peak of the marine heatwave that focused on the two most abundant genera of corals on the outer reef in Moorea, *Pocillopora* and *Acropora*. We assessed how heat stress influenced bleaching patterns in concert with coral taxonomy, colony size, and depth around Moorea. We hypothesized that above a threshold of heat stress, coral bleaching would increase with colony size but decrease with water depth. The results of this study provide evidence that refugia exist for many corals impacted by a marine heatwave and the pattern of survivorship is driven by taxonomic identity, water depth, colony size, and the interaction of *in situ* heat stress with colony size.

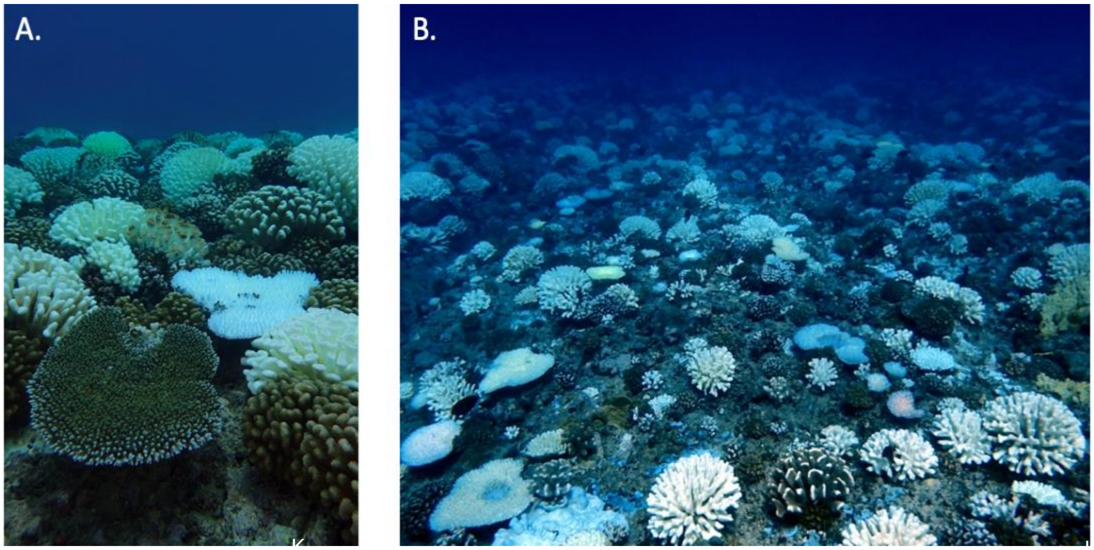


Figure 1. Bleaching across the reefscape in May 2019, two months after bleaching began on A) the north shore (LTER 1) and B) the west shore (LTER 5). Photo credit: Kelly Speare.

1.3 RESULTS

Seawater temperature

During the prolonged marine heatwave from November 2018 to July 2019, seawater temperatures (measured *in situ*) were consistently above the previous long-term mean ocean temperature by at least one standard deviation at both 10 and 17 m water depths (Figure 2). Seawater temperatures were above 29.0°C from 14 December 2018 until 1 May 2019 at both 10 and 17 m, which is the threshold above which corals in Moorea begin experiencing thermal stress (Pratchett et al., 2013), and bleaching was first reported in Moorea in March 2019. Mean daily seawater temperature was marginally higher at 10 m (29.31 ± 0.06°C, mean ± SD) than 17 m (29.22 ± 0.05°C) pooled across forereef sampling sites (see Figure A1 for sites; $t_6 = 2.03$, $p = 0.08$, 95% CI [-0.017, 0.184]; Fig. 2). The maximum mean daily seawater temperature at 10 and 17 m sites was 30.30°C and 30.27°C respectively.

Accumulated heat stress (AHS) is a measure of the magnitude and duration of warming that corals experience (Pratchett et al., 2013), and is defined as the number of weeks over a threshold temperature (29°C in Moorea) in a 12-week running sum with units of °C-weeks (see Materials and Methods). Prior work in Moorea found that maximum AHS above 4.0 resulted in bleaching in 1991, 1994, 2002, 2003, and 2007 (Pratchett et al., 2013). During the bleaching year, 1 August 2018 to 31 July 2019, maximum AHS across sites was not significantly higher at 10 m depth (5.32 ± 0.61 °C-weeks, mean ± SD) than 17 m (4.71 ± 0.46 °C-weeks) ($t_6 = 1.60$, $p = 0.16$, 95% CI [-0.327, 1.553]). However, the maximum AHS observed at any 10 m site was 6.06 °C-weeks as compared with a maximum value of 5.24 °C-weeks at 17 m. The northwestern most site (LTER 1) experienced the highest level of AHS at both 10 and 17 m and the southeastern site (LTER 4) was the coolest at both depths

(Table 1; Figure 2). For each site where continuous measurements were collected at both 10 and 17 m, the deeper site experienced lower AHS (Figure 2).

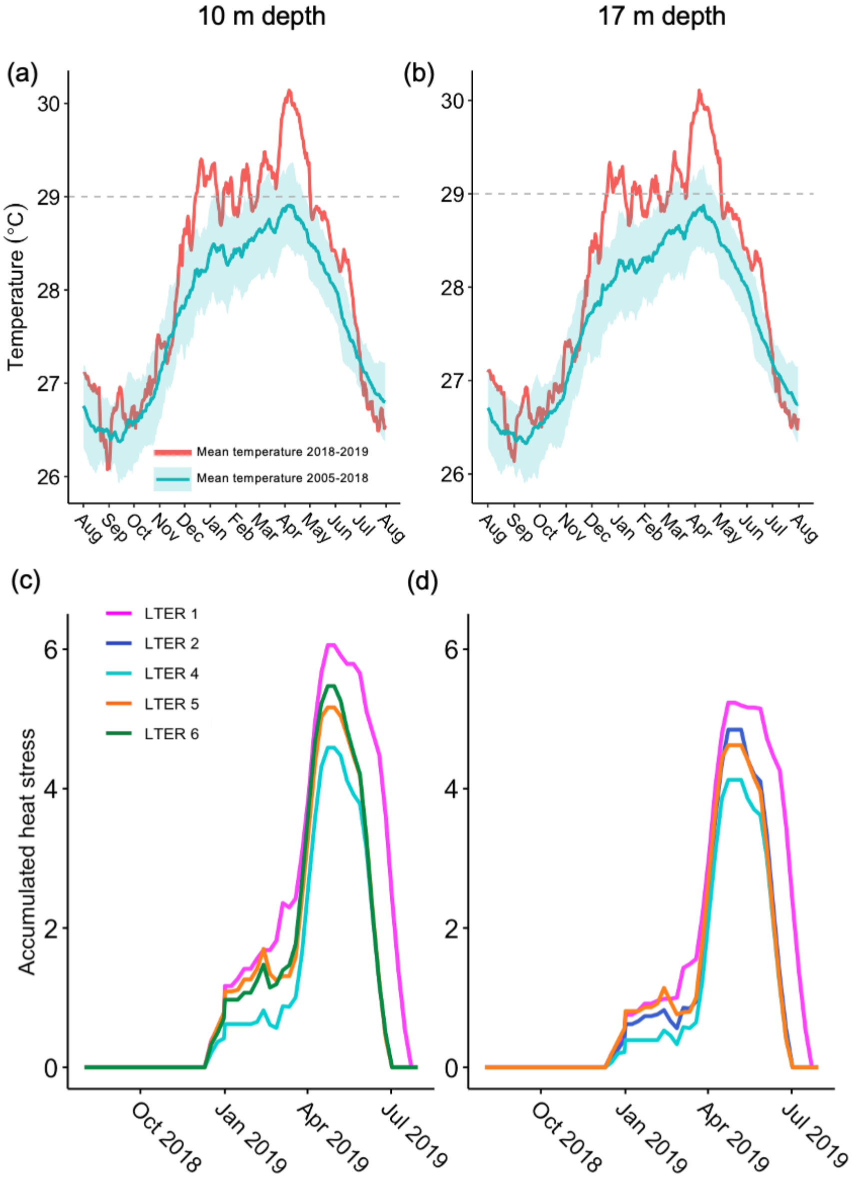


Figure 2: Mean temperature (blue line) ± 95% confidence interval (blue shading) across days from 2005 to 2018, and mean temperature (red line) of the bleaching year from 1 August 2018 to 31 July 2019 at **A)** 10 m, and **B)** 17 m. Dotted horizontal line represents the 29°C threshold temperature at which corals begin accumulating thermal stress. Accumulated heat stress (°C-weeks) at **C**) 10 m depths and **D**) 17 m depths from 1 August 2018 to 31 July 2019 at the sites used in our study.

Exposure to short-term high frequency temperature fluctuations prior to a warming event can bolster thermal tolerance in scleractinian corals and enable colonies to escape bleaching (McClanahan et al., 2005; Oliver and Palumbi, 2011; Safaie et al., 2018). Mean daily temperature fluctuation (MDTF, °C) in the 30 days prior to the onset of bleaching can have a strong mitigating effect on bleaching (Safaie et al., 2018). Bleaching was first observed in mid-March 2019 and we selected 15 March as the start of the bleaching event for our analyses. We found that our four 17 m sites experienced a higher MDTF (0.55 ± 0.12 °C, mean ± SD) than the 10 m sites (0.38°C ± 0.07°C), averaged across sites; ($t_6 = -2.47$, $p < 0.05$, 95% CI [-0.335, -0.001]; Figure A1) from 15 February to 15 March. Corals at 17 m were exposed to a maximum daily temperature range of 1.69°C compared with 0.98°C at 10 m in the month prior to the onset of bleaching. The northern sites (LTER 1 and 2) had the highest MDTF values and the western sites (LTER 5 and 6) had the lowest values (Table 1). For each site where continuous measurements were collected at both 10 and 17 m, the deeper site experienced a higher MDTF (Table 1).

Table 1: Maximum accumulated heat stress (AHS, measured in °C-weeks) and mean daily temperature fluctuation (MDTF) values for each site x depth used in the analysis. AHS values were calculated for site x depth combinations with continuous temperature data during the bleaching year, 1 August 2018 to 31 July 2019. MDTF values were calculated for the month leading up to the first signs of bleaching (15 February to 15 March 2019), averaged across days.

Site	Depth	Maximum Accumulated Heat Stress (°C-weeks)	Mean Daily Temperature Fluctuation (°C)
LTER 1	Mid (10 m)	6.06	0.45
	Deep (17 m)	5.24	0.59
LTER 2	Deep (17 m)	4.85	0.67
LTER 4	Mid (10 m)	4.59	0.41
	Deep (17 m)	4.13	0.56
LTER 5	Mid (10 m)	5.17	0.29

	Deep (17 m)	4.62	0.39
LTER 6	Mid (10 m)	5.47	0.39

Bleaching Patterns

In our survey of 5,101 corals around the island and across depth, we found that *Acropora* corals bleached more severely than *Pocillopora* corals (Figure 3). There was a distinct pattern of size-dependent bleaching at most sites around the island for *Pocillopora* corals, especially at 10 m, where larger corals bleached more severely than smaller corals (Figure 3). *Pocillopora* corals bleached less at 17 m where this pattern of size-dependent mortality was weaker. Overall, most *Acropora* corals bleached severely on the north and southwest sides of the island (Figure 3). On the east side of the island (LTER 3 and 4), observed patterns in *Acropora* bleaching were more size-dependent than at other sites, where almost all *Acropora* corals bleached severely (Figure 3). *Pocillopora* corals also bleached less severely on the east side of the island with very little bleaching of any size classes observed at 17 m (Fig. 3). While *Acropora* corals bleached more than *Pocillopora* corals everywhere, the *Acropora* appear to have experienced a slight depth refuge at 17 m compared with 10 m (Figure 3).

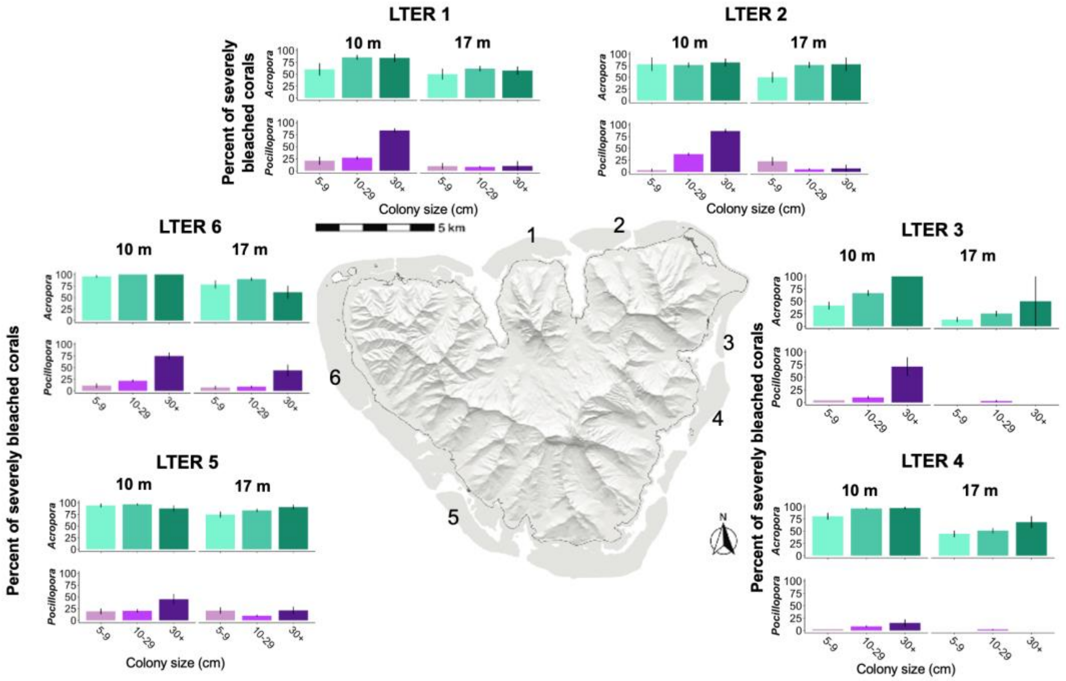


Figure 3: Percent of individuals severely bleached (≥75% of colony bleached and/or dead) in July 2019 across depth at the six permanent LTER sites around the island for both *Acropora* and *Pocillopora* corals. Green hues represent *Acropora* corals in 5-9 cm, 10-29 cm, and large ≥ 30 cm size classes. Purple hues represent *Pocillopora* in 5-9 cm, 10-29 cm, and large ≥ 30 cm size classes. Error bars represent standard error.

Drivers of severe bleaching in Acropora corals

We defined severely bleached corals as colonies that were ≥75% bleached and/or dead at the time of our surveys in July 2019. Severe bleaching in *Acropora* corals was significantly related to depth (Depth effect: $\chi^2(1) = 11.24$, $p = 0.014$; table A1) and size (Size effect: $\chi^2(2) = 6.32$, $p = 0.011$; table A1), but not AHS (AHS effect: $\chi^2(1) = 0.41$, $p = 0.558$; table A1), nor the interaction between size and AHS (Size x AHS effect: $\chi^2(2) = 0.65$, $p = 0.535$; table A1). *Acropora* corals at 10 m bleached more severely than those at 17 m (pairwise comparison of marginal means, p = 0.014; Figure 4; table A1). Small *Acropora* corals (5-9 cm) bleached less severely than both mid-size (10-29 cm) and large colonies (≥ 30) (pairwise comparison of marginal means, $p = 0.031$ and $p = 0.015$ respectively; Figure 4; table A1), regardless of depth. The effect of AHS was not significant for *Acropora* corals, but this observation was probably driven by *Acropora* corals bleaching severely at even the lowest observed levels of AHS.

Drivers of severe bleaching in Pocillopora corals

There was no significant effect of water depth on severe bleaching of *Pocillopora* corals (Depth effect: $\chi^2(1) = 1.61$, $p = 0.238$; table A2) or AHS on severe bleaching (AHS effect: $\chi^2(1) =9.60$, $p = 0.10$; table A2). Patterns of bleaching in *Pocillopora* corals differed from *Acropora* corals in that there was as significant interaction between size and AHS driving bleaching in *Pocillopora* (Size × AHS effect: $\chi^2(2) = 8.60$, $p = 0.004$; table A2). This interaction was significant because large (≥ 30 cm) *Pocillopora* colonies were more sensitive to AHS than mid-size (10-29 cm) and small-(5-9 cm) colonies (pairwise comparison of marginal means, $p = 0.010$ and $p = 0.011$ respectively; Figure 4; table A2) and showed more severe bleaching at similar values of AHS.

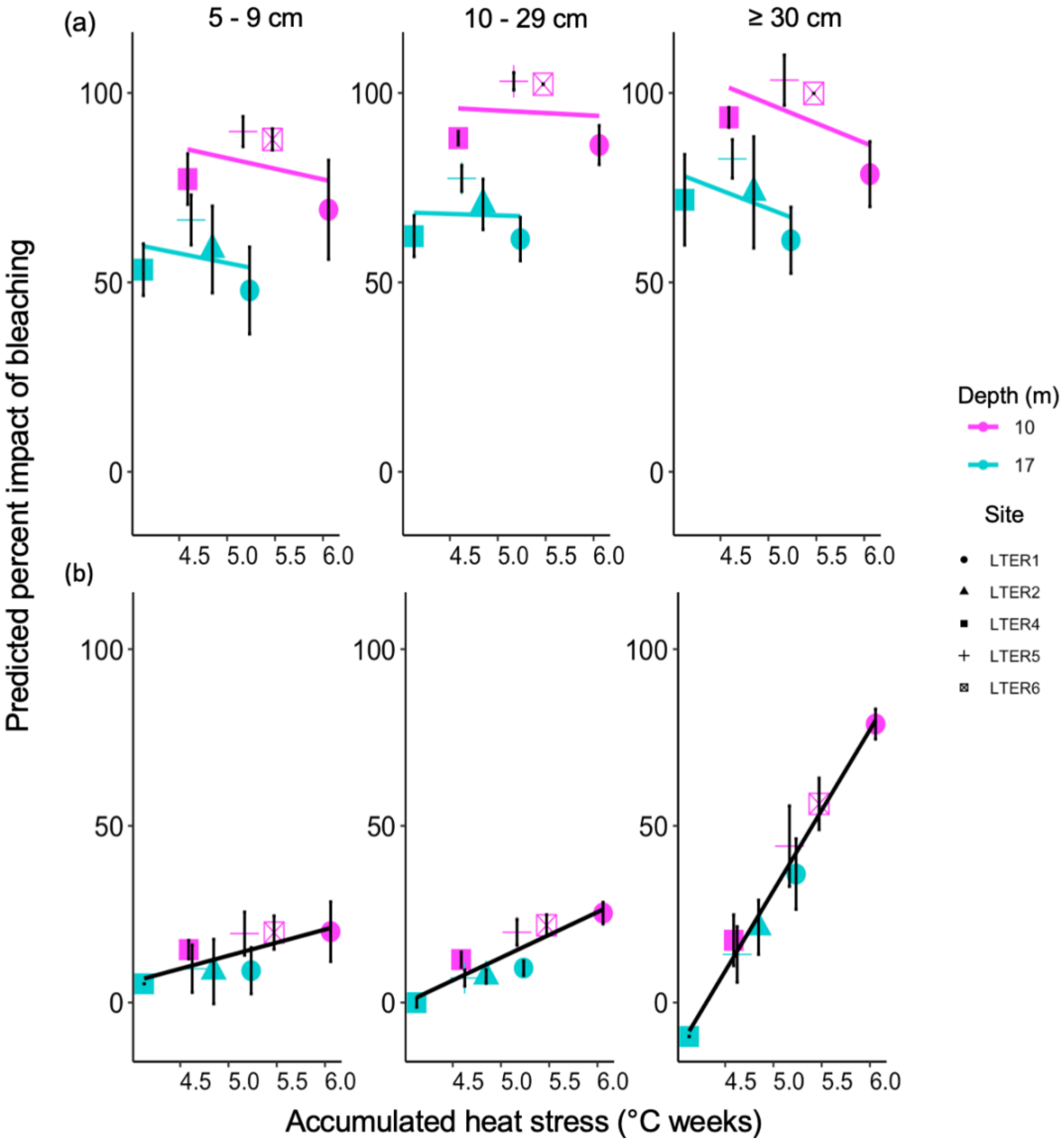


Figure 4. Linear mixed model outputs of the predicted mean percent of severely bleached corals at each site and depth for colonies 5-9 cm, 10-29, and ≥ 30 in diameter for **A)** *Acropora* corals, and **B)** *Pocillopora* corals across measured accumulated heat stress (AHS, measured in °C-weeks) values. Pink represents model outputs for 10 m depth and teal represents model outputs for 17 m depth and shapes represent the different sites. Error bars represent standard error.

1.4 DISCUSSION

As marine heatwaves increase globally in frequency and duration, the severity and prevalence of coral bleaching is projected to increase (Donner, 2009; Heron et al., 2016).

However, even in extreme warming events, bleaching can be heterogeneous across taxa and spatially across the reefscape (Hughes et al., 2017). The idea that certain coral taxa or functional groups are winners or losers in a bleaching event is well-documented (Loya et al., 2001). In many systems, *Acropora* is generally considered a losing genus as it typically bleaches at lower levels of heat stress than other genera (Adjeroud et al., 2009; Burkepile et al., 2020). Our data support this idea and expand upon it by showing that *Pocillopora* and *Acropora*, the two dominant branching coral taxa in Moorea, bleached extensively around the island during the 2019 marine heatwave. However, there were instances around the island where *Acropora* and *Pocillopora* did not bleach. Our work highlights where each coral taxa avoided bleaching and disentangles some of the factors ameliorating bleaching. Understanding the nuanced differences in bleaching across space, colony size, thermal stress, and water depth for different taxa is key to predicting the ultimate impacts of marine heatwaves.

Thermal stress is the major driver of large-scale bleaching events (Hughes et al., 2017) and is most often quantified using remotely sensed sea surface temperature (SST) data. The availability of remotely recorded SST has served as a useful and accessible tool for predicting bleaching events across regional and global spatial scales (McCarthy and Intergovernmental Panel on Climate Change, 2001). For example, Donovan et al. (Donovan et al., 2021). demonstrated that high levels of bleaching from 2006-2016 matched high levels of heat stress across 223 sites across the globe. Recent work in the Caribbean related levels of localized coral bleaching to thermal stress across 5 x 5 km^2 pixels of sea surface temperature (Banon et al., 2018). However, remotely sensed data may be less useful for detecting sub-regional differences in water temperatures, including locations at different depths around an island. Our study utilized temperature data recorded *in situ* at each site and water depth that revealed considerable differences in heat stress around the island and across depth. Consequently, we found that the variation in heat stress across spatial scales of < 5 km partially explained the bleaching variation in *Pocillopora* corals.

Our work is one of a growing number of studies to focus on smaller-scale variation in temperature measured *in situ* to explain variation in bleaching across space (Donovan et al., 2020; Thomas et al., 2018). Using *in situ* water temperature measurements has an advantage over remotely sensed SST data because water temperature often varies with depth, and therefore remotely sensed SST data may not faithfully estimate water temperatures on deeper reefs. Previous studies have assessed the variation in bleaching across depth (Baird et al., 2018) but the use of a single satellite-derived temperature value for all observed depths may obscure important trends in the relationship between temperature and bleaching across depths. We found the maximum AHS values between 10 m and 17 m depths at any given site varied by a minimum of 0.46 and maximum of 0.82 °C-weeks above 29.0°C, which could have major biological implications.

The hypothesis that bleaching severity declines with depth is based on the attenuation of light (Lesser et al., 2009) and temperature with depth. Corals at shallower depths are exposed to higher levels of solar irradiance where the excess solar energy is absorbed by symbionts (Jones et al., 1998). Excess solar energy contributes to higher rates of photoinactivation, which inhibits symbiont photosynthesis (Skirving et al., 2018), and once symbionts are no longer nutritionally contributing to the symbiosis, the coral host expels them from its tissues (Skirving et al., 2018). Corals in deeper water do not experience the same level of solar irradiance as corals located at shallower depths because the attenuation of light acts as natural shading for corals at depth (Mumby et al., 2001). Anomalously warm water can also interact with solar irradiance to exacerbate bleaching, as photosynthesis is a temperature dependent process where photosynthetic rates can drop drastically with warmer temperature[1], making shallow water corals vulnerable to bleaching. Yet, the level of refuge from bleaching that corals experience at deeper depths has differed temporally and across the globe over the last half century (Baird et al., 2018; Smith et al., 2016). In Moorea, higher levels of bleaching were observed at deeper depths during two previous bleaching events in 1994 (Hoegh-Guldberg and Salvat, 1995) and 2002 (Penin et al., 2007). However, those results focused on bleaching only, not mortality as a result of bleaching, and the overall level of heat stress was less extreme than in the 2019 bleaching event (Hoegh-Guldberg and Salvat, 1995; Penin et al., 2007). Baird et. al (Baird et al., 2018) found that both *Acropora* and *Pocillopora* bleached less with depth during the 2016 bleaching event in the Great Barrier Reef and depth refugia effect was stronger for *Acropora* corals.

In our study, *Acropora* bleached less at the deeper sites, but this pattern was not explained by differences in AHS, implying that differences in solar irradiance may be an important predictor as has been suggested previously. While we did not measure solar irradiance in our study, Coelho et al (Coelho et al., 2017). found that shaded *Acropora* colonies bleached less than those exposed to direct sunlight after only 2-degree heating weeks (DHW). Shaded *Pocillopora* corals only experienced bleaching reprieve after 7 DWH (Coelho et al., 2017), thus indicating that reductions in light appear to have a greater impact on the bleaching response in *Acropora* compared with *Pocillopora* corals. Temperature fluctuation leading up to the bleaching event also may have driven the *Acropora* depth refuge by acclimating colonies and endosymbionts to mild temperature stress (Palumbi et al., 2014; Safaie et al., 2018). Deep internal waves in Moorea deliver cool water to relatively shallow depths (Leichter et al., 2012; Roder et al., 2010) and the associated temperature fluctuation has been observed to mitigate the effects of bleaching (Wyatt et al., 2020).

Biotic refuges can also provide shelter from disturbance for individuals with traits that enable them to evade the effects of a given perturbation (Davis et al., 2013). Corals experience biotic refuge from bleaching through size, morphology, and genetic lineage, amongst other factors (Burgess et al., 2021; Loya et al., 2001; Woesik et al., 2011). Our previous work shows *Pocillopora* and *Acropora* corals exhibit size-dependent bleaching at 10 m in Moorea (Speare et al., 2022), specifically that larger corals bleached disproportionately more than smaller corals. Here, we expand upon this result to show that size was a more important predictor of bleaching than depth for *Pocillopora*. Pooled across all sites and depths, 52% of large *Pocillopora* corals (≥30 cm) were severely bleached or dead compared with 13% of small (5-9 cm) individuals and 14% of mid-size (10-29 cm) individuals. Large *Pocillopora* colonies were more sensitive to AHS and bleached disproportionately more than small and mid-size colonies for the same level of AHS. Similarly, our statistical model highlighted that small (5-9 cm) *Acropora* colonies bleached substantially less than mid-size (10-29 cm) and large individuals (≥30 cm) across site and depth.

Several mechanisms may contribute to the strong size-dependency of bleaching experienced by corals. Larger corals have a low surface area to volume ratio relative to smaller colonies and are less successful in exchanging compounds with the surrounding seawater (Lesser et al., 1990), a potential explanation as to why larger corals of both genera bleached more severely than small corals across depth around the island. It is also possible that large *Pocillopora* corals were disproportionately represented by a more thermally sensitive cryptic species in Moorea (Burgess et al., 2021), which may have contributed to the size-dependent bleaching pattern we observed. However, size-dependent bleaching has been observed for other coral genera (Pisapia et al., 2019; Shenkar et al., 2005), and it is likely that multiple mechanisms contributed to the size-dependent bleaching of *Pocillopora* corals around Moorea.

As extreme thermal anomalies increase in time and space in our changing climate, sensitive coral species in shallow reefs will continue to suffer extreme rates of mortality. The loss of live corals at shallow and mid-depths from bleaching will likely decrease the diversity and abundance of reef fish (Bargahi et al., 2020) and other invertebrates (Salas-Moya et al., 2021) that rely on corals for habitat and food, resulting in unpredictable outcomes for tropical marine ecosystems. Existing literature suggests that deep, mesophotic reefs (≥ 30 m) have the potential to sustain coral populations through partial escape from the impacts of warming (Bongaerts et al., 2010; Bridge et al., 2013; Glynn, 1996). Our work suggests a shallower (17 m) bleaching reprieve may exist for *Acropora* corals, and although depth did not explain bleaching patterns in *Pocillopora*, larger colonies may find reprieve at depth through the attenuation of temperature. The loss of the largest *Pocillopora* and *Acropora* will likely have unforeseen impacts on reef ecosystems by reshaping the size-structure of populations (Speare et al., 2022). This study highlights that reefs do not necessarily experience the wholesale loss of corals even during extreme heatwaves, and that corals have the capacity to escape bleaching and persist into the future. Our work contributes to understanding the intertwined mechanisms whereby corals experience refuge from thermal events, and by disentangling the complex biological and physical factors that drive individual corals to bleach, we are better able to understand the dynamics of bleaching events.

1.5 MATERIALS AND METHODS

Study site

Moorea, French Polynesia is a high volcanic island (17°30°S, 149°50°W) within the Society Island Archipelago that is characterized by shallow fringing reefs (2-4 m water depth), relatively deep bays (10-35 m), and outer reefs with steeply descending slopes. Our study was conducted on the outer reefs of Moorea which, at the time of the bleaching event, were recovering from a 2007-2009 crown-of-thorn seastar (COTS), *Acanthaster plancii*, outbreak and cyclone in 2010 (Adam et al., 2011; Adjeroud et al., 2009; Kayal et al., 2012). The coral community on the outer reef has historically been a resilient system as it has recovered relatively quickly from other multiple disturbances over the past several decades (Holbrook et al., 2018; Kayal et al., 2018). Bleaching events in Moorea have also been documented in 1991, 1994, 2002, 2008, 2016, and 2017 (Hédouin et al., 2020; Hoegh-Guldberg and Salvat, 1995; Penin et al., 2007), several of which were characterized by high levels of spatial variation in coral mortality around the island and across depths. Prior to the 2019 thermal stress event, live coral cover ranged from 13-80% (mean 47%) at 10 m water depth and from 12-36% (mean 26%) at 17 m depth (Moorea Coral Reef LTER and Edmunds, 2020).

Ocean temperature

Ocean temperature was recorded continuously around the island on the outer reef as part of the MCR LTER project from 2005-2019. We used measurements recorded at two water depths, 10 and 20 m, at six permanent sites (LTER 1-6) (Figure A3). Each site-depth combination contained a bottom-mounted thermistor (SeaBird Electronics SBE 39 or SBE56) that recorded water temperature every 20 min during the 14-year time series. Four of the twelve thermistors failed to collect continuous temperature data throughout the duration of the bleaching year analyzed (1 August 2018 to 31 July 2019), therefore we omitted them from our temperature analysis. Due to this instrument failure, we excluded both 10 and 17 m at LTER 3; 17 m at LTER 6; and 10 m at LTER 2 (see Figure A3 for the specific depth × site locations utilized). To determine whether seawater temperature was warmer at 10 m than 17 m during the warming event (25 November 2018 – 19 May 2019), we calculated the daily mean seawater temperature at each site-depth combination and performed a Welch two-sided t-test across the 10 m and 17 m sites with continuous temperature data throughout the bleaching year.

<u>Accumulated Heat Stress</u>: To quantify the effect of temperature on bleaching severity in Moorea, we used seawater temperature data to calculate accumulated heat stress (AHS) in °C-weeks, the number of weeks in a 12-week running sum above a maximum monthly mean temperature (°C). The maximum monthly mean temperature in Moorea is 29°C, which is the temperature threshold at which corals begin experiencing thermal stress (Pratchett et al., 2013). We calculated the AHS as a 12-week running sum of mean weekly temperatures exceeding the MMM (29.0°C) by at least 0.1°C at each site × depth combination (Liu et al., 2003; Pratchett et al., 2013). To test whether maximum AHS was higher at 10 m compared with 17 m during the bleaching year, 1 August 2018 to 31 July 2019, we extracted the

maximum AHS value at each site × depth and performed a Welch two-sided t test across 10 m and 17 m sites. We also utilized maximum AHS values in our linear mixed model analyses.

<u>*Mean Daily Temperature Fluctuation*</u>: The mean daily temperature fluctuation (MDTF, measured in °C) is the mean daily range in temperature over a given period of time. The MDTF in the 30 days leading up to the start of bleaching can have a strong mitigating effect on bleaching (Safaie et al., 2018). Bleaching was first observed in Moorea in mid-March and used 15 March as the beginning of the bleaching event in our analyses. We calculated the temperature fluctuation for each day from 15 February 2019 to 15 March 2019, the month leading up to the start of the bleaching event, at each site × depth combination, took the mean at each site × depth, and used a Welch two-sided t test to test whether MDTF was significantly different between 10 and 17 m depths. Due to co-linearity with AHS, we were unable to include MDTF in our linear mixed models.

Coral bleaching surveys

To assess whether bleaching severity differed around the island and with water depth, two SCUBA divers conducted benthic surveys along 10 and 17 m isobaths at each of the permanent MCR LTER outer reef sites (LTER 1-6) from 9-15 July 2019, approximately two months following the peak in thermal stress (Figure A1). The bleaching and mortality surveys were executed along two belt transects (each 50-m long x 1-m wide) at each depth × site to assess how the marine heatwave impacted coral populations across depth and space. We recorded data on colony-level bleaching and mortality for a total of 5,101 colonies of the two dominant coral taxa, *Pocillopora* (n = 3,227) and *Acropora* (n = 1,874) across 16 transects (two at each depth × site), recording the percent of each individual colony that was healthy, bleached, or recently dead. We defined recently dead as any portion of an individual coral colonized with filamentous turf algae but not yet colonized by macroalgae (Figure 2). The maximum diameter of each colony was estimated visually and assigned a categorical size bin to represent corals of 5-9 cm, 10-29 cm, or ≥ 30 cm in diameter.

We applied a slightly different survey methodology for each genus to account for the greater abundance of *Pocillopora* corals than *Acropora* corals on the outer reef. Each genus was surveyed along a 50 m transect at each site × depth, but only *Pocillopora* colonies that intersected the transect were recorded. Because *Acropora* colonies were less abundant than *Pocillopora*, divers recorded every *Acropora* colony within a 1-m swath along the transect. *Pocillopora* corals cannot reliably be classified to species based on size, color, or morphology (Marti-Puig et al., 2014) and were therefore identified to genus in our surveys. We acknowledge that there are several cryptic species exist within the *Pocillopora* genus that have different bleaching responses (Burgess et al., 2021). Some of the most common *Acropora* corals on the outer reef of Moorea prior to the bleaching event were *Acropora lutkeni*, *A. globiceps*, *A. retusa*, and *A. hyacinthus* (Carroll et al., 2006). We identified *Acropora* colonies to genus as we could not distinguish between most species when bleached or dead. We also acknowledge that species-level differences in bleaching and mortality are possible, however, it is common to pool data by genus for landscape- and regional-scale ecological studies, including those that investigate size-specific or depth-specific impacts of disturbances on corals (Dietzel et al., 2020).

Statistical Analyses

For each site × depth × size class (24 total) combination we calculated the percent of corals that were severely bleached for each genus. Severely bleached corals were individuals that were at least 75% bleached and/or dead at the time of our July surveys. We selected the 75% threshold to consider only individuals that suffered the most extreme impacts of the heatwave. We used a linear mixed model (LMM) for each taxon to evaluate how the percent of severely bleached *Pocillopora* and *Acropora* corals was related to accumulated heat stress (AHS), water depth (10 and 17 m), colony size (an ordinal variable in which 5-9 cm < 11-29 cm < ≥30 cm), and the interaction between AHS and colony size. Water depth, AHS, and colony size were fixed effects in our LMM models, and site was included as a random effect. We excluded sites from our analysis that did not have continuous temperature data from the bleaching year, therefore, our analysis included data from four sites at 10 m and four sites at 17 m sites (see Figure A3 for specific site × depth combinations used). Each taxa-specific model was fit by Maximum Likelihood using Laplace Approximations (Bolker et al., 2009; Raudenbush et al., 2000), and we ran a Wald Chi-Squared Test with Kenward-Roger degrees of freedom approximations on our model to quantify the relative importance each interaction and main effect had in influencing severe bleaching in corals. Post-hoc pairwise tests were performed with the emmeans package using a Tukey adjustment for approximating p values (Lenth, 2022). All data visualization was performed in ggplot2 (Wickham, 2016) and model plots through the sjPlot package (Lüdecke et al., 2023).

CHAPTER 2. The differential response of butterflyfishes to coral decline and recovery in Moorea, French Polynesia

2.1 ABSTRACT

Coral reefs are experiencing growing threats around the world, and the impacts do not stop with declines in coral. The damage and loss of coral habitat can have major cascading consequences for a wide range of reef-dwelling organisms. Most notably, species that are highly dependent on coral for food or habitat are particularly at risk. Since the impact of disturbance on coral can cascade through tropical food webs, unraveling the broader ecosystem-wide consequences of major coral reef stressors is thus challenging. The island of Moorea, French Polynesia, has experienced a range of major reef disturbances over the last two decades and provides an opportunity to characterize and quantify some of the complexities of these broader ecosystem-wide effects. The percent cover of branching coral (*Acropora* and *Pocillopora* species) fluctuated between 1% and 38% over the period from 2006 to 2021 in response to multiple disturbances on the island of Moorea (an outbreak of the Crown of Thorns seastar, a category 4 cyclone, and a major bleaching event). We assessed the extent to which the declines and increases in butterflyfish abundance were correlated with the declines and increases in coral cover during periods of decline and recovery. Changes in butterflyfish populations were associated with broad changes in branching coral cover that reflected differential fish species connections to coral as prey. The magnitude of increase in obligate corallivores did not match the recovery of branching corals and marginally tracked the decline in coral abundance following a predator outbreak

and following major bleaching event. Butterflyfish that were facultative corallivores or non-coral feeders inconsiderably increased or decreased, or did not change at all in response to the complex coral dynamics across sites and years. Changes within this diverse guild of butterflyfish highlight that disturbances to basal reef species can have differential impacts on butterflyfish with diverse dependencies on branching coral for food, can vary greatly across space, and such consequences may extend further up reef food webs.

2.2 INTRODUCTION

The loss and modification of habitat strongly influences and shapes communities in diverse habitats (Menge and Sutherland, 1987). In coral reef ecosystems, the loss of coral can have major implications for reef-dwelling organisms that depend on coral for parts of their life history (Booth and Beretta, 2002; Munday, 2004). Corallivorous fish, fish that consume corals, are among species with the greatest reliance on coral (Pratchett et al., 2006a; Price et al., 2021). Fishes in the *Chaetodon* genus (family: Chaetodontidae; commonly referred to as butterflyfishes) comprise over half of the known corallivorous fishes and are highly dependent on corals as direct or indirect food sources (Cox, 1994; Pratchett, 2013). Thus, the presence of butterflyfish is highly correlated with live coral cover (Syms and Jones, 2000), and they are considered indicators of healthy reef communities (Emslie et al., 2011; Graham et al., 2009).

Disturbances do not uniformly impact corals (Adjeroud et al., 2009; Loya et al., 2001), and the extent to which corals are affected is related to the type and magnitude of disturbance (Adam et al., 2014). Physical disturbances such as tropical storms (e.g., cyclones, typhoons, hurricanes) have the capacity to abruptly remove physical coral structure from reef habitats (Adam et al., 2014; Emslie et al., 2011). The wholesale loss of coral structure following tropical storms has been documented across many reefs (Adam et al., 2011; Fabricius et al., 2008; Roff et al., 2015). Coral bleaching and coral predator outbreaks can be classified as biological disturbances that kill the coral tissue but leave the hard carbonate skeletal structure intact (Cheroske et al., 2000; Emslie et al., 2011). While such biological disturbances can induce widespread mortality of coral on a reef, the coral structure remains, which can still support butterflyfish that consume algae or other non-coral prey (Sano, 1987; Sano, 2004). The short-term impacts of biological and physical disturbances may differ, as butterflyfish rely on the structural complexity of corals even devoid of live tissue to varying extents (Graham et al., 2009; Wilson et al., 2008). For example, Emslie et al. (2011) assessed the response of butterflyfish to various disturbances in the Great Barrier Reef and found the wholesale loss of butterflyfish only occurred when the structural complexity of the entire reef was lost through breakage of branching coral through physical disturbance (Emslie et al., 2011). Instead, typically only a subset of corals die during both physical and biological disturbances, and the proportion of loss is related to the magnitude of disturbance (Hughes et al., 2017; Nyström et al., 2000). Because branching corals serve as both food and habitat to many butterflyfish species (Emslie et al., 2011; Jones and Syms, 1998; Pratchett et al., 2008), disturbance events causing the mass mortality of coral threatens the persistence of butterflyfish species.

Butterflyfish, however, vary greatly among species in their dependence upon corals for food and can broadly be categorized as either: obligate coral feeders that feed exclusively on corals, facultative coral feeders that feed on corals and other types of food, or non-coral feeders that do not feed on corals but consume motile invertebrates, algae, sponges, and other small prey that are often associated with live coral (Cole and Pratchett, 2014; Harmelin-Vivien and Bouchon-Navaro, 1983; Tricas, 1989; Wilson et al., 2008). Butterflyfish also vary in their preference and adaptation to feed on different coral species, and branching corals are often preferred (Cole et al., 2008; Cole and Pratchett, 2014; Harmelin-Vivien and Bouchon-Navaro, 1983; Pratchett, 2005). Thus, the reliance of butterflyfishes on branching coral varies greatly among species and functional feeding groups based on the dietary needs of the species. The majority of butterflyfish exhibit prey preferences and consume a narrow range available prey items (Graham, 2007; Irons, 1989; Pratchett, 2005; Reese, 1981). However, when preferred prey is not readily available, many butterflyfish species have the capacity to consume less preferred corals in their diet, yet this dexterity decreases as dietary specialization increases (Cole et al., 2008).

Previous studies have documented the decline of obligate corallivore butterflyfish following disturbance and report no change in facultative corallivores and non-coral feeders (Munday, 2004; Wilson et al., 2008). For example, the only butterflyfish species to decline following the 2016 cyclone in Fiji were obligately corallivorous butterflyfish (Price et al., 2021). Following the 2002 bleaching event in the Great Barrier Reef, coral cover declined by 90% yet non-coral and facultative coral feeders were relatively unaffected while obligate coral feeders eventually declined in abundance after two years (Pratchett et al., 2006a). There are fewer studies assessing the dynamics between branching coral and corallivore recovery due to the need for multi-decadal, time series data. One study in the Philippines documented variable patterns in the recovery of butterflyfish in response to branching coral recovery, where the magnitude of recovery of corallivores matched recovery of coral in some places, but not in others (Russ and Leahy, 2017). Throughout these studies, there has been less of a focus on whether and how the dynamics of different types of butterflyfish respond to both different magnitudes of coral loss and differential rates of coral recovery following disturbances. Can patterns of coral recovery lead to predictable butterflyfish dynamics as has been documented following to declines in coral cover resulting from reef disturbances? Assessing corallivore responses to both losses and recovery of branching coral requires longer time series of consumer abundance and can provide insight to the nuanced dynamics between branching coral and corallivores.

The island of Moorea, French Polynesia has undergone multiple disturbances over the last 16 years. The island experienced a Crown of Thorns seastar (*Acanthasther planci;* a coral predator) outbreak in 2007-09 followed by a category 4 cyclone in 2010 (Adam et al., 2014; Adjeroud et al., 2009; Holbrook et al., 2018), and most recently experienced an intense marine heatwave that triggered a mass coral bleaching and mortality event in 2019 (Burgess et al., 2021; Speare et al., 2022). The intensity of each disturbance varied around the island, thus coral was differentially impacted across space and through time. In addition, the magnitude and rates of coral recovery also differed substantially over time and across sites. The variation in both disturbance history and reef recovery around the island creates a unique opportunity to test how changes in the abundance of obligate corallivore, facultative corallivore, and non-coral feeing butterflyfish scaled with both the decline and recovery in branching coral cover around the island. We were interested in understanding the relationship between the rate of change in branching coral cover and the rate of change in the number of butterflyfish during two periods of coral decline and one period of coral recovery across feeding groups of butterflyfish. We predicted that the abundance of obligate corallivores would be tightly coupled with the both the decline and increase of branching coral cover. We also hypothesized the abundance of facultative corallivores would be correlated with the recovery of branching coral due to the moderate reliance on coral for food. We did not expect facultative corallivore abundance to be correlated with the decline in branching coral cover as these species feed on taxonomic groups other than scleractinian corals. We hypothesized no relationship between non-coral feeder abundance and branching coral cover increases or declines.

2.3 METHODS

Study site

Moorea, French Polynesia, is a high volcanic island in the South Pacific. The island is triangular in shape and characterized by shallow lagoons enclosed by an offshore barrier reef (figure 1). Moorea has experienced multiple disturbances over the last 15 years including a Crown of Thorns seastar (*Acanthaster planci*, referred to as COTs) outbreak from 2007 to 2010 (Adam et al., 2014; Adjeroud et al., 2009; Kayal et al., 2012), a tropical cyclone in 2010 (Adam et al., 2014, 2011; Holbrook et al., 2018), and a major coral bleaching event in 2019 (Burgess et al., 2021; Speare et al., 2022). These disturbances impacted the different sites around the island to different magnitudes, and they also were followed by different subsequent recovery dynamics.

The data used in this study were collected by the Moorea Coral Reef Long Term Ecological Research (MCR LTER) project, established in 2004. The MCR LTER has collected biological, ecological, and physical environmental data around Moorea at six sites in three different habitats (fringing reef, lagoon reefs, and outer reefs; figure 1) since it was founded. There are two MCR LTER sites located on each island side (north, east, west). We focus on the outer reef in this study, as branching coral cover has fluctuated dramatically there during the time the MCR LTER has collected data. We use fish (Moorea Coral Reef LTER and Brooks, 2022) and coral (Moorea Coral Reef LTER and Edmunds, 2020) data collected as part of the MCR LTER core time series surveys in the following analysis to understand spatial and temporal trends in branching coral cover and the response of corallivore abundance.

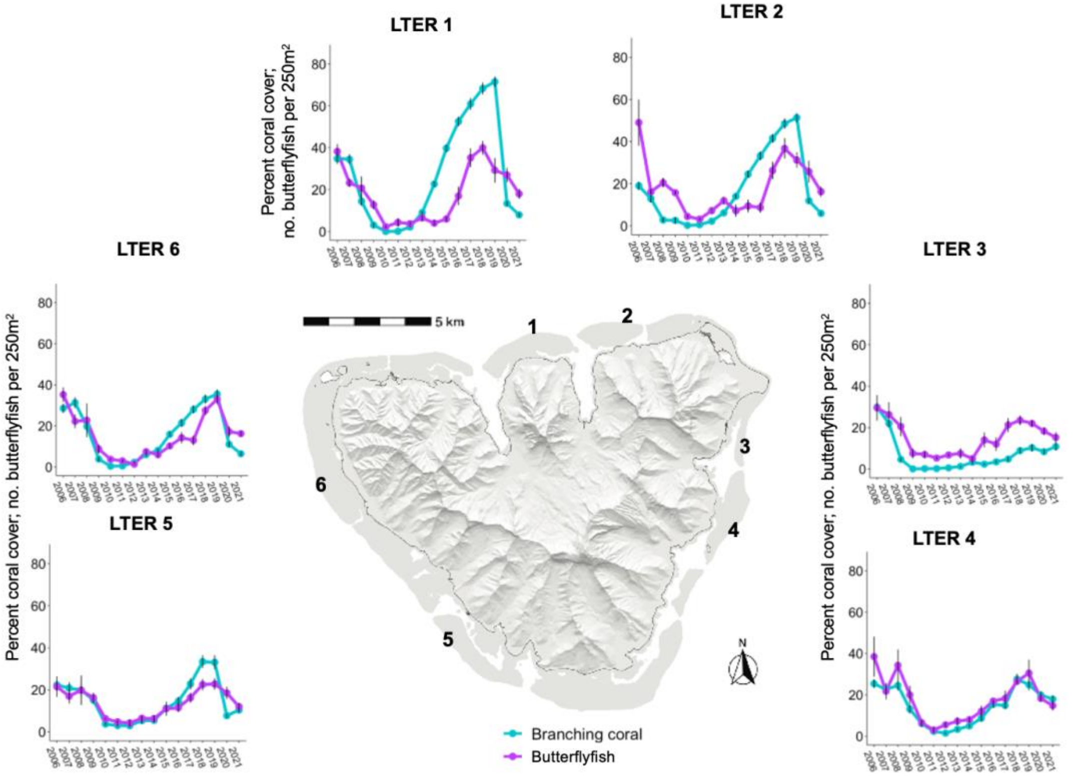


Figure 1. Changes in branching coral percent cover (blue) and butterflyfish abundance (purple) at each of the six LTER sites from 2006-2021. Branching coral species include *Pocillopora* and *Acropora*, butterflyfishes include species listed in table 1. Error bars represent standard error. Sites 1 and 2 are the north shore sites, 3 and 4 are the east, and 5 and 6 are the west.

Disturbance history

The COTS outbreak began in 2007 and reduced live coral cover from ~40% to less than 5% around the island on the outer reefs (Holbrook et al., 2018; Kayal et al., 2012). Coral cover declined rapidly from 2007 to 2008 and continued to decline for 3-4 years on around the island (Adam et al., 2014). Declines in coral cover due to COTS began in 2008 at MCR LTER 5 (the southernmost site on the west shore) and LTER 3 (the northernmost site on the east shore)(Adam et al., 2014) and by 2009, the eastern sites (LTER 3 and 4) had the highest density of COTs predation-scars (Kayal et al., 2012).

In February 2010, Moorea was hit with a category 4 tropical cyclone ("Oli"), creating powerful waves that removed all coral structure at the two north shore sites – LTER 1 and LTER 2 (Adam et al., 2014; Holbrook et al., 2018). The lesser impacted sites on the west and east sides (LTER 3-6) of the island retained large proportions of dead coral structure. By 2012, coral cover had stabilized at LTER 3, 4, and 5, and had begun to recover at LTER 1, 2, and 6 (Adam et al., 2014). Recovery of coral was influenced by robust grazing by herbivorous fish populations that controlled algal growth (Adam et al., 2011) and the rapid recruitment of branching corals (Holbrook et al., 2018). Recovery from COTS and the cyclone was most pronounced on the north shore (LTER 1 and 2) by the recruitment and recolonization of *Pocillopora* coral (Holbrook et al., 2018).

Eight years later, a marine heatwave from December 2018 - May 2019 induced an intense bleaching event beginning in March 2019 (Burgess et al., 2021; Speare et al., 2022), where branching coral was reduced from an island-wide mean of 38 % before the bleaching event to 12 % by July 2019. Corals on the north shore (especially at LTER 1) were exposed to the highest level of accumulated heat stress (up to 6.06 °C-weeks), while the east side remained the coolest with 4.59 °C-weeks (Winslow chapter 1, 2023).

The disturbance history in Moorea over the last 16 years presents a unique opportunity to observe the relationship between coral cover and butterflyfish populations around the island following different types of disturbance. Given the sites around the island were differentially impacted by disturbance over the time series, we can assess whether the rate of change in butterflyfish abundance matches the rate of change in coral cover, both declines and subsequence recoveries, and how that relationship varied between butterflyfish with varying reliance on coral for food.

Live coral cover

Sampling of coral cover has been ongoing since 2005. Outer reef coral communities are censused around the island at six different sites at 10 m (figure 1). Coral cover surveys are conducted annually in April/May at all six sites on the outer reef at 10 m depth via randomly located, permanent 0.5 x 0.5 m photo quadrats (n = 40 at each site x depth) . Photos from the quadrats are analyzed in Coral Point Count (CPCe) software (Kohler and Gill, 2006) that assigns 200 random points per quadrat, which are then identified and recorded to genus. We focused only on branching coral (*Pocillopora* and *Acropora*) in our analysis for their importance in the diet of butterflyfish. The mean coral cover and standard error during each year at each site was calculated across quadrats in order to visualize temporal changes and to use in our correlations. We only utilized data from 2006 through 2021 to match that of the fish abundance data described below.

Butterflyfish abundance

Fish surveys are conducted annually in July/August at 10-12 m depth at all six LTER sites at 10 m depth. There are four, permanent 5 x 50 m transects at each site which extend from the benthos to the surface of the water column and are surveyed on SCUBA (Moorea Coral Reef LTER and Brooks, 2022). Surveys began in 2005 where divers recorded the abundance of all known butterflyfish species in Moorea that were encountered on the transect (n = 20; table 1). Each butterflyfish species was identified as an obligate corallivore (>80% of the diet is comprised of coral (Cole et al., 2008); n = 7), facultative corallivores (corals comprise some portion of the diet; n = 9), or non-coral feeders (the species does not consume coral; n = 4). We calculated the mean abundance and standard error of each feeding group during each year at each site across transects to visualize temporal changes and to use in our correlations (described below).

Table 1. Corallivore species in the Chaetodontidae family in Moorea. List of documented species in the Chaetodontidae family in Moorea, French Polynesia.

Genus	Species	Feeding type	Reference
Chaetodon	*ornatissimus*	obligate	(Harmelin-Vivien and Bouchon-Navaro, 1983)
Chaetodon	*pelewensis*	obligate	(Harmelin-Vivien and Bouchon-Navaro, 1983)
Chaetodon	*reticulatus*	obligate	(Harmelin-Vivien and Bouchon-Navaro, 1983; Michael et al., 2004)
Chaetodon	*unimaculatus*	obligate	(Cox, 1994, 1986; Harmelin-Vivien and Bouchon-Navaro, 1983; Morgan S. Pratchett et al., 2013; Sano, 1989; Wylie and Paul, 1989)
Chaetodon	*quadrimaculatus*	facultative	(Harmelin-Vivien and Bouchon-Navaro, 1983; Hourigan et al., 1988)
Chaetodon	*lunula*	facultative	(Harmelin-Vivien and Bouchon-Navaro, 1983)

Chaetodon	*ulietensis*	facultative	(Bouchon-Navaro, 1986; Pitts, 1991; Pratchett, 2005)
Chaetodon	*lunulatus*	obligate	(Bouchon-Navaro, 1986)
Chaetodon	*auriga*	facultative	(Bouchon-Navaro, 1986)
Chaetodon	*trifascialis*	obligate	(Alwany et al., 2003; Harmelin-Vivien and Bouchon-Navaro, 1983; Irons, 1989)
Chaetodon	*ephippium*	facultative	(Harmelin-Vivien and Bouchon-Navaro, 1983)
Chaetodon	*bennetti*	obligate	(Harmelin-Vivien and Bouchon-Navaro, 1983; M, 1984; Sano, 1989)
Chaetodon	*vagabundus*	non-coral	(Harmelin-Vivien and Bouchon-Navaro, 1983; M, 1984)
Chaetodon	*trichrous*	facultative	(Reavis and Copus, 2011)
Chaetodon	*citrinellus*	facultative	(Bouchon-Navaro, 1986; Harmelin-Vivien, 1989; Pratchett, 2005)
Forcipiger	*longirostris*	non-coral	(Bouchon-Navaro, 1986)
Forcipiger	*flavissimus*	non-coral	(Bouchon-Navaro, 1986)
Heniochus	*chrysostomus*	facultative	(Bouchon-Navaro, 1986; Sano, 1989)
Hemitaurichthys	*polylepis*	non-coral	(Randall, 1985)
Chaetodon	*mertensii*	facultative	(Harmelin-Vivien, 1989)

Correlations between butterflyfish abundance and coral cover

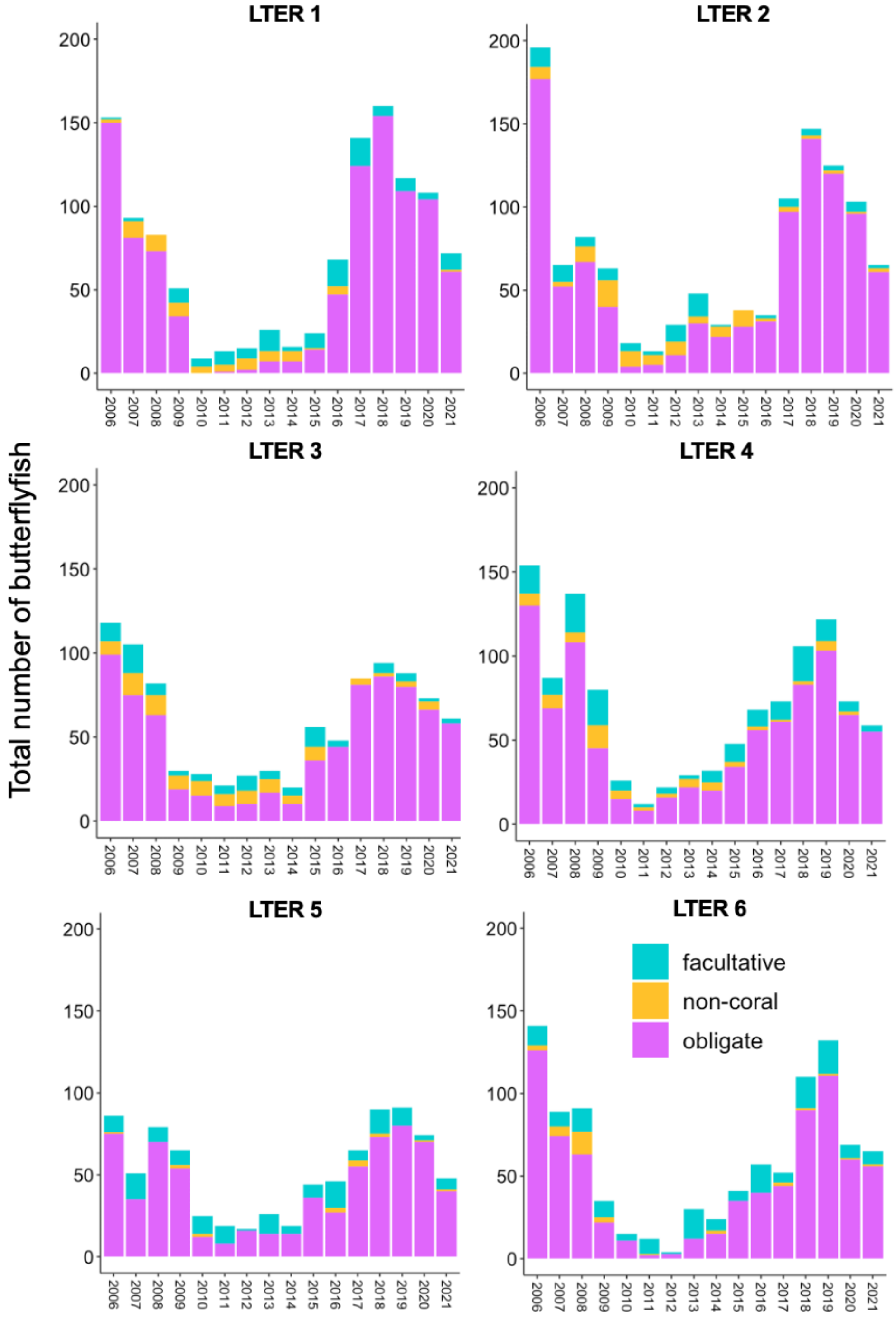
We utilized the LTER branching coral cover (*Pocillopora* and *Acropora* species) data to explore patterns of butterflyfish population response to, and recovery from disturbance across sites around the island. We broke the time series data up into three periods: 2006-2011 coral decline from COTs and cyclone ‘Oli’; 2011-2019 coral recovery; and 2019-2021 coral decline from bleaching. During each time period, we calculated the change in mean percent cover of branching coral cover between each year at each site. For example, during the period of coral decline from 2006-2011, the percent change in mean coral cover was calculated between 2006-07, 2007-08, etc. We did the same to calculate the percent change in the mean number of butterflyfish per 250 m^2 for each feeding group (obligate corallivores, facultative corallivores, and non-coral feeders). These metrics (in units of % change y^{-1} for coral or % change in number of fish per 250 m^2 y^{-1} for butterflyfish) enabled us to quantify the relationship between branching coral cover and the response of butterflyfish across feeding groups among sites using a Pearson correlation coefficient (R) and to visualize the relationships in ggplot (Wickham, 2016).

2.4 RESULTS

Temporal dynamics in coral cover and corallivore abundance

The crown-of-thorns sea stars outbreak (2007–09) followed by Cyclone Oli in 2010 drove the near complete loss of branching coral around the island (Adam et al., 2014; Holbrook et al., 2018). Prior to the beginning of the COTs outbreak, the island-wide mean coral cover was 26.6 ± 1.0 % and the mean abundance of butterflyfish was 35.3 ± 3.1 fish per 250 m^2. Both coral cover and butterflyfish abundance declined during the COTs outbreak and by 2011, just over one year following cyclone 'Oli', mean coral cover dropped to 1.1 ± 0.2 % and mean butterflyfish abundance dropped to 3.9 ± 0.4 fish per 250 m^2. Coral and butterflyfish recovered from 2011 to 2019 until the bleaching event in which island-wide mean branching coral cover peaked at 37.8 ± 1.7% and butterflyfish abundance increased to 28.1 ± 1.8 fish per 250 m^2. By 2021, the end of our time series, mean branching cover had fallen to 9.9 ± 0.6% around the island and the mean abundance of butterflyfish was reduced to 15.4 ± 0.9 fish per 250 m^2.

Obligate butterflyfish were the most dominant group throughout most of the timeseries (figure 2). Once branching coral cover dipped below 2.5% on the north shore, the number of obligate corallivores became less abundant than facultative corallivores and non-coral feeders, both of which did not really change from 2011-2014 at LTER 1 and from 2010-2012 at LTER 2 (figure 2). Obligate corallivores remained the most abundant throughout the entire time series on the east shore (LTER 3 and LTER 4) where coral cover never dipped below 5%. Obligate corallivores only became less abundant than non-coral feeders on the west shore (LTER 5 and LTER 6) in 2011 when branching coral cover was below 5% and also in 2013 at LTER 6 (figure 2). Non-coral feeders almost disappear at LTER 2 and LTER 3 during coral recovery (2011-2019). Facultative corallivores appeared to decline as coral declined at LTER 6 from 2006-2011 and never really recovered. This group was also almost non-existent at LTER 5.



2. Total number of butterflyfish feeding types at all six LTER sites across transects (1000 m^2 of reef total). Obligate corallivores are displayed in purple, facultative corallivores are in blue, and non-coral feeders are in gold.

Correlations between branching coral and butterflyfish abundance

Coral decline (2006-2011)

There were no significant relationships between site-level percent change of branching coral cover and the number of butterflyfish of any feeding type during the 2006-2011 period of coral decline (obligate corallivores: R= 0.45, p = 0.05; Facultative corallivores: 0.09, p = 0.70; non-coral feeders: R = 0.34, p = .21; figure 3).

Coral recovery (2011-2019)

There were also no significant relationships between site-level percent change of branching coral cover and the number of butterflyfish of any feeding type during the 2011-2019 period of coral recovery (obligate corallivores: R= 0.09, p = 0.64; Facultative corallivores: -0.21, p = 0.29; non-coral feeders: R = -0.21, p = 0.43; figure 3).

Coral decline (2019-2021)

There was a nearly significant positive relationship between the rate of decline in branching coral cover and the rate of decline of obligate corallivore populations (R = 0.18, p = 0.47; figure 3) following the 2019 bleaching event. There was not a significant relationship between branching coral and facultative corallivore growth rates at this time (R = 0.36, p = 0.16) and a negative, non-significant relationship between branching coral and non-coral feeder growth rates (R = 0.24, p = 0.51).

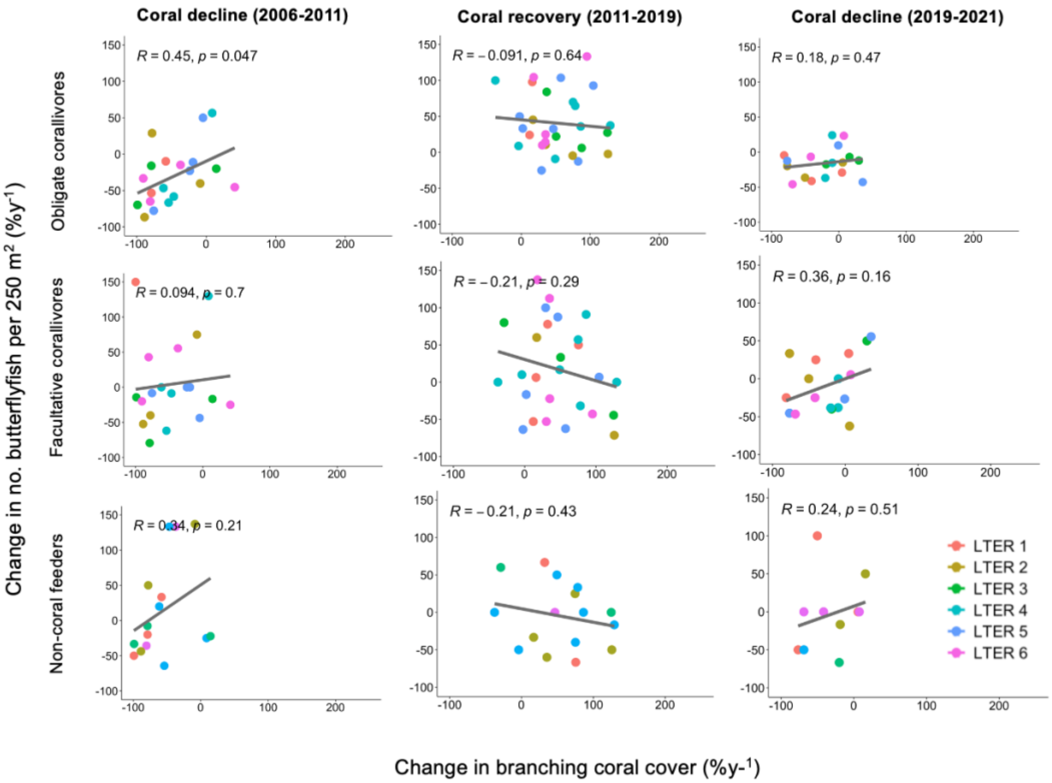


Figure 3. Relationship between the annual percent change in the number of butterflyfish per 250 m^2 and annual percent change in branching coral cover during two periods of coral decline (2006-2011 and 2019-2021) one period of coral recovery (2011-2019). Correlations at each site are represented by different colors; LTER 1 in red, LTER 2 in gold, LTER 3 in green, LTER 4 in light blue, LTER 5 in blue, and LTER 6 in purple.

2.5 DISCUSSION

As disturbances increase globally in frequency and duration in a changing climate, the severity and prevalence of mass coral mortality is projected to increase (Cheal et al., 2017; Donner, 2009). Branching coral is highly sensitive to storm energy and changes in environment (Brown, 1997; Edmunds, 2019). As such, reefs often experience coral mortality during and shortly following disturbance events (Adam et al., 2014; Hughes et al., 2003; Ribas-Deulofeu et al., 2021). Butterflyfish, however, have been observed to decline more gradually following the loss of coral (Graham et al., 2009; Pratchett et al., 2006a) and have also been observed to decline in the short term (< 1 year) following the loss of coral (Emslie et al., 2011; Sano, 2004). Few studies have observed the relationship between the recovery of branching coral and butterflyfish which depend on coral for food to varying extents. The results of this study assess under which disturbance circumstances coral cover and the abundance of different butterflyfish feeding groups decline and/or increase at similar rates. We found no strong significant relationship between the annual percent change in branching coral cover and the percent change in the number of any type of butterflyfish during periods of coral decline and recovery, however, some of these relationships were stronger than others. The response of obligate butterflyfish was positively associated with the decline of branching coral following bleaching, but not other types of disturbance or in recovery. The population response of facultative corallivorous butterflyfish and non-coral feeders did not have strong associations with the rate of increase or decline in branching coral cover. Understanding the nuanced relationship between coral cover and butterflyfish populations during periods of coral decline and coral recovery is key to predicting how reefs will respond in a changing climate.

Butterflyfish have evolved to utilize a myriad of different feeding strategies ranging from feeding exclusively on one species of coral to not feeding on coral at all (Cole et al., 2008; Harmelin-Vivien and Bouchon-Navaro, 1983). Although butterflyfish are associated with coral for food and/or habitat, the level of dependence on coral is species dependent and is important to consider when assessing disturbance impacts on reefs. Because of their dependence on coral for food, obligate corallivore butterflyfish are positively associated with coral cover (Hourigan et al., 1988; M. S. Pratchett et al., 2013). The marked variation in resource use and the degree of dietary specialization among butterflyfishes dictates how reliant species are on live corals (Nagelkerken et al., 2009; Pratchett, 2007, 2005). The lack of correlation between the response of all butterflyfish populations and branching coral cover may have been due to variation between sites in addition to the sub-lethal effects of coral loss on butterflyfish (Berumen et al., 2005; Booth and Beretta, 2002; Lawton et al., 2012), which created a buffer for the population. In support of this idea, other studies have documented a lag in changes to butterflyfish populations following loss of corals (Graham, 2007; Pratchett et al., 2006; Russ and Leahy, 2017).

In line with previous studies, we found no significant relationship between changes in facultative corallivore and non-coral feeder abundance with changes in branching coral cover. Facultative corallivores are not entirely dependent on coral for food (Pratchett, 2013) and we did not expect there to be a strong, significant correlation between these fish and coral cover. Some facultative corallivore species feed on coral minimally, for example, coral comprises <10% of the diets of *Chaetodon trichrous* and *Chaetodon lunula* (Harmelin-Vivien and Bouchon-Navaro, 1983; Reavis and Copus, 2011). These species have been observed to feed on filamentous algae and small benthic invertebrates that live within corals (Hobson and Hobson, 1974). Following the cyclone, the skeletal structure of coral was removed almost entirely at some sites (LTER 1 and LTER 2), leaving bare substrate. The recovery of coral was characterized by the rapid recruitment of *Pocillopora* corals (Holbrook et al., 2018), which are small and cannot harbor as many invertebrates that some facultative corallivore species feed upon as larger colonies, possibly the reason for the lack of association between changes in facultative corallivores with increases in coral cover.

Although insignificant or weak, correlations existed between all butterflyfish feeding groups and branching coral following bleaching. The mean annual percent change in obligate corallivore populations were moderately positively associated with annual changes in branching coral cover (figure 3). The annual decline of coral from bleaching was less variable across sites whereas COTs had a greater and more variable annual impact on branching coral. This is unsurprising, given the pulse disturbance nature of bleaching where the impact was greatest in 2019 and subsided in subsequent years. The COTs outbreak occurred over multiple years and was more extreme on the northern sites compared to other sites around the island, contributing to the variation in coral decline. The negative, insignificant relationship between annual change in branching coral cover and both facultative corallivores and non-coral feeders may have resulted from an increase in non-coral prey sources following bleaching. For example, many facultative corallivore and non-coral feeding butterflyfish feed on algae (Harmelin-Vivien and Bouchon-Navaro, 1983), which increases following bleaching events (Fukunaga et al., 2022; Raj et al., 2021).

One shortcoming of this study is the timing of annual surveys. Coral cover is measured in April, and fish surveys are taken in early August. The COTS outbreak occurred over multiple years and cyclone Oli hit Moorea in January 2010, before coral and fish annual surveys. However, the 2019 bleaching event began in mid-March (Burgess et al., 2021; Speare et al., 2022) and the coral surveys were taken prior to the mass mortality of coral while fish were quantified following most of the coral mortality. Thus, the 2019 coral data likely overestimates the live coral cover during the fish surveys. While it is possible the abundance of butterflyfish began declining before the annual fish surveys were taken five months later, we would not expect such rapid change in fish abundance. Butterflyfish species can feed on bleached coral when pigmented tissue is not available and some species show no preference between the two (Cole et al., 2009; Pisapia et al., 2012). Additionally, butterflyfish can switch which species of coral they prey upon when preferred resource availability is low (Semmler et al., 2022). We also acknowledge that we only considered two non-coral butterflyfish species, which were observed in low abundance. While our analysis depicts no relationship between non-coral feeders and branching coral cover as we hypothesized, there were only four sites with non-coral feeding species data during the recovery period (2011-2019) and three sites during the decline following bleaching (2019-2021). Studies with more data may be more robust in determining the relationship between branching coral cover and non-coral feeding butterflyfish.

Assemblages of coral-associated fish are regulated by the diversity and abundance of scleractinian corals (Graham et al., 2009). Butterflyfishes are a specialized taxa and rely on coral for various components of their life history (Cole et al., 2008; Nagelkerken et al., 2009; Pratchett, 2007). Our work highlights how changes in coral cover can influence the abundance of butterflyfishes around an island where the physical environment and history of disturbance impact varies across space and through time, yet the extent to which butterflyfish respond is highly variable. While we did not observe strong, significant relationships between annual changes in branching coral cover and butterflyfish with different dependencies on coral for food, our work suggests that butterflyfish populations lag behind both declines and increases in coral cover. As live coral declines globally from repeated bleaching events, we may see a disappearance of butterflyfishes that are heavily reliant upon corals for food (Emslie et al., 2011; Pratchett et al., 2006b; Russ and Leahy, 2017). Unless recovery of branching corals is rapid and the time between major disturbances is great enough for fish populations to bounce back as has been the case in Moorea, extreme and frequent disturbances may compromise the persistence of butterflyfishes. However, if branching coral cover does not return and coral cover remains low following disturbance, we may see reefs dominated by facultative corallivores with minimal reliance on branching corals and non-coral feeding butterflyfish. More multi-decadal time series data are needed to assess the recovery potential of both corals and various groups of butterflyfishes to predict the composition of reefs into the future.

CHAPTER 3. Increased corallivory following coral bleaching reduces growth and increases mortality in *Acropora hyacinthus*

3.1 ABSTRACT

Thermal anomalies are increasing in time and space, thereby threatening the persistence of reef-building corals through intensifying bleaching events. However, the extent to which reefs bleach across depth varies in time and space. Corals at deeper depths often bleach less than those closer to the surface. Corals that are susceptible to bleaching are also often preferred food sources for corallivores that continuously graze colonies without causing whole-colony mortality. When coral cover is high, the impact of chronic corallivory can have limited impacts on coral populations. When bleaching events cause mass mortality of corals, however, corallivores may then have significantly greater impacts on the remaining coral individuals. The present study assesses 1) how the interaction between coral bleaching and corallivory varied across space to reduce survival of the reef-building coral, *Acropora hyacinthus,* following a marine heatwave, 2) the extent to which corallivory affected the relative growth of *A. hyacinthus* after bleaching, and 3) how these processes varied across depth (5, 10, and 17 m). We found that bleaching and corallivory reduced the abundance of *A. hyacinthus* across depth, especially in the shallows. Prior to the bleaching event, corallivory did not impact the growth of *A. hyacinthus* at depth. However, following the bleaching event and the reduction in live *A. hyacinthus*, corallivores then negatively impacted coral growth. Our findings indicate that the interaction of bleaching and corallivory is nuanced, where the vulnerability of *A. hyacinthus* colonies to bleaching mortality is high at shallow depths and corallivory exacerbates mortality. In contrast, colonies at depth have a greater chance of survival from bleaching but their post-bleaching success is reduced by exposure to corallivory.

3.2 INTRODUCTION

Reef-building corals are in rapid decline as a result of anthropogenic stressors (Hughes et al., 2017a). One of the most prominent threats to coral is exposure to elevated and sustained seawater temperature (Couch et al., 2017; Leggat et al., 2019). Corals that endure elevated seawater for extended periods of time expel the symbiotic dinoflagellates (Symbiodiniaceae) that live within their tissues as a stress response (Brown, 1997). Corals devoid of their Symbiodiniaceae appear white or pale in color, hence the term coral bleaching. Bleaching often results in mortality (McClanahan, 2004) as endosymbionts provide the coral host with carbon through photosynthesis (Brown, 1997). In their absence, corals are forced to rely on energy reserves that would otherwise be used to meet other metabolic requirements (Grottoli et al. , 2006), thus compromising a coral's ability to survive, grow, and reproduce (Douglas, 2003; Hoegh-Guldberg, 1999). However, bleached corals have the capacity to recover from thermal stress when the endosymbiont community is re-established (Grottoli et al., 2006). Although recovery is highly variable, 20-60% of bleached coral colonies recovered following recent marine warming events around the globe following recent bleaching events (Sakai et al., 2019; Thinesh et al., 2019).

Bleaching is not uniform across a reefscape and spatial variation can be partially related to local levels of thermal stress (Chou et al., 2016; Lenihan et al., 2008), many of which vary across depth. As such, reefs at shallower depths typically experience higher levels of bleaching compared with those at deeper depths (Baird et al., 2018). Corals at shallower depths are exposed to higher solar irradiance where light can act synergistically with temperature to initiate coral bleaching (Loya et al., 2001; Riegl and Piller, 2003). Deeper water can serve as a refuge from bleaching through the attenuation of light and general cooling of water with depth (Baird et al., 2018; Muir et al., 2017). In addition, deeper reef habitats experience more intense internal waves (Leichter et al., 2012, 2006) that can originate near shelf breaks and transport cool, nutrient rich water onto the reef (Leichter et al., 2012; Roder et al., 2010). Waves and currents can also buffer reefs from the thermal stress associated with high surface temperatures (Bak et al., 2005), as water movement facilitates gas exchange that reduces the buildup of oxygen radicals (Nakamura et al., 2005, 2003; Nakamura and Woesik, 2001). In addition to providing a refuge from bleaching, the physical environment at depth may provide more favorable conditions for the recovery of corals that do bleach.

For corals that survive bleaching events, the added stress and metabolic costs of bleaching may make surviving corals more susceptible to other stressors that would otherwise be less harmful. Post-bleaching mortality of coral has been linked to the density of coral predators, where corals with the densest aggregations of corallivorous snails were more likely to die after bleaching than colonies with fewer snails (Shaver et al., 2018). Additionally, the reduction in live corals after bleaching events may increase corallivory on the surviving corals. When coral cover is high, the impact of predation on corals can be minimal (Cole, 2011), as most coral predators take a few bites from any given colony before moving on to the next and thus, rarely cause whole-colony mortality (Cole, 2011; Cole and Pratchett, 2011). However, unlike corals, many reef fish are relatively unaffected by thermal anomalies in the short term (within one year) (Pratchett et al., 2006; Price et al., 2021). Generally, the abundance of corallivores, fish that consume live coral tissue for up to 100% of their diet (Cole et al., 2008), does not immediately change following bleaching (Munday, 2004; Pratchett et al., 2006; Price et al., 2021). As a result, if there are fewer available corals to consume after a bleaching event, then an unchanged population of predators will likely concentrate predation on the remaining corals. Previous studies have documented that per capita coral mortality depends on the surrounding coral abundance. For example in the Caribbean, corals on reefs with lower coral cover were preyed upon more frequently and intensely by corallivorous parrotfish compared to corals on reefs with higher coral cover and similar numbers of corallivores (Burkepile, 2012). A similar pattern was observed in Hawaii, where *Porites compressa* corals experimentally placed in areas of high coral cover experienced very little impact from corallivory, but those in low coral cover areas were preyed upon heavily (Jayewardene et al., 2009). Thus, reefs that experience major bleaching events may experience further post-bleaching mortality via increased predation pressure on the remaining coral colonies.

Bleaching related mortality reduces the overall number of corals, but the interaction of bleaching and corallivory may further dampen a colony's capacity to perform regular metabolic processes, and thus, survive. Corals allocate a portion of their energy to growth, however, following bleaching, energy stores can become exhausted from recovering from bleaching (Grottoli et al., 2006). Corals also are forced to allocate energy to heal from predation (Edmunds and Lenihan, 2010; Henry, 2005), thus corals that recover from bleaching and are exposed to corallivory may have less energy to devote to growth. Therefore, impacts negative of corallivory on coral may increase following bleaching even if the rate of corallivory were to remain unchanged.

There is a growing body of literature documenting interactions between bleaching and corallivory impacting coral growth and mortality on reefs following marine heat waves (Cole and Pratchett, 2012; Rice et al., 2019; Shaver et al., 2018). However, few studies assess the extent to which these interactions between corallivory and bleaching impact reef dynamics and across areas with different habitat characteristics, such as depth zones. Previous studies have shown that corallivory does not impact growth of coral at depth compared to shallower reef environments (Ladd et al., 2021), and other studies have demonstrated that corals generally bleach less at deeper depths where temperature extremes are dampened (Baird et al., 2018). We were interested in understanding how depth related changes in bleaching and corallivory altered the species interactions between coral and corallivores? Here, we used the 2019 bleaching event in Moorea, French Polynesia to understand whether and how bleaching and subsequent corallivory acted synergistically to influence the differential recovery or mortality of corals across reefs at different depths. Simplistically, one could hypothesize that lower heat stress and lower pressure from corallivory would facilitate survival from bleaching at depth. However, corallivores are not restricted to maintaining a constant depth distribution or other behaviors following a bleaching event. Thus, the details of corallivore responses could significantly affect these simple predictions. The results of this study suggest that high levels of corallivory cause mortality of recovering corals that might otherwise recover regardless of depth, but despite a greater impact of corallivory in deep habitats following bleaching, the shallow corals we observed experienced total mortality whereas there were more survivors at depth.

3.3 METHODS

Study site

Moorea, French Polynesia is a high volcanic island within the Society Island Archipelago in the South Pacific. We focused our study on the outer reef of the north shore, which has experienced various disturbances over the last 16 years including a Crown of Thorns (COTs) outbreak from 2007 to 2011 (Adam et al., 2014; Kayal et al., 2012) that reduced coral cover from ~40 to <5 % at 10 m depth on average around the island, and a tropical cyclone that removed virtually all coral structure on the north shore in 2010 (Adam et al., 2014; Holbrook et al., 2018). Coral cover recovered rapidly on the north shore and was characterized by rapid recruitment of branching corals (Holbrook et al., 2018), such that the mean island-wide coral cover was ~50 % at 10m by 2019. The 2019 bleaching event began with anomalously warm (>29°C) seawater temperatures in December 2018 that extended to May 2019 (Burgess et al., 2021; Speare et al., 2022). The first signs of bleaching occurred in mid-March 2019, and most corals had either recovered or died by October 2019. *Acropora* corals experienced extreme bleaching, 80% of the genus bleached severely (≥75% of a colony was bleached or dead) across depth (Winslow, Chapter 1).

Study species

<u>*Acropora hyacinthus*</u>

Corals in the *Acropora* genus are dominant in provisioning habitat and are a preferred food source for many corallivores (Cole et al., 2008; Kayal et al., 2011). Yet, *Acropora* corals are highly sensitive to thermal stress and are thus declining in abundance on tropical reefs worldwide due to their susceptibility to bleaching (Clark et al., 2017; Hughes et al., 2018). We focused on *Acropora hyacinthus* as it is abundant on the outer reef of Moorea and is easily identifiable due to its tabular morphology. Prior to the bleaching event, *A. hyacinthus* was more abundant at 5m than at 10 and 17m on the north shore of Moorea, but there was no difference between abundance at 10 and 17 m (Ladd et al., 2021).

Excavating corallivores

We focused on teleost corallivores that remove portions of coral skeleton along with live coral tissue (Rotjan and Lewis, 2008), often leaving visible bite scars on corals. Our fish censuses included fish that are known corallivores in Moorea (Cole et al., 2008; Moorea Coral Reef LTER and Brooks, 2022; Rotjan and Lewis, 2008) (table A1). We acknowledge that non-excavating corallivores, coral predators that remove live tissue without damaging coral skeleton (Rotjan et al., 2006) such as fish in the family Chaetodontidae, also likely played a role in the dynamics of *A. hyacinthus* recovery. However, we focus here on excavators that leave physical damage that can be quantified *in situ*, because their visible impact was overwhelming in the period after the bleaching event (see below).

Coral and fish surveys

Bleaching patterns in *Acropora hyacinthus*

To quantify how bleaching and bleaching related mortality varied across depth,

we conducted bleaching surveys on the north shore of Moorea at two permanent sites that are part of the Moorea Coral Reef Long Term Ecological Research (MCR LTER) project (LTER 1 and LTER 2), as conducted for Winslow Ch1 and Speare et al. 2022 (Speare et al., 2022). Two SCUBA divers swam along a 50 x 1 m transect at 5, 10, and 17 m isobaths at each site on 11-12 July 2019, approximately two months following the peak in thermal stress. On each transect we recorded each colony of *Acropora hyacinthus,* the size of the colony (5-10 cm, 11-29 cm, or ≥ 30 cm in diameter), and the percentage of each individual colony that was healthy, bleached, or recently dead was recorded. Recently dead was defined as any portion of a colony colonized with filamentous turf algae but not yet colonized by macroalgae (Speare et al., 2022), thus indicating mortality during the previous weeks or months since the thermal stress event. Only colonies ≥ 5cm were considered in our surveys.

Abundance of excavating corallivores

Surveys of corallivorous fishes were conducted in October 2018 (pre-bleaching event) and August 2019 (post-bleaching event). Five, surveys were conducted at each depth at the GB1 site (between the LTER 1 and LTER 2 moorings), where a diver slowly swam the length of the 25m transect and recorded the number of known obligate and facultative corallivorous fish within a 5 m swath (table A1). Transects were chosen haphazardly and were oriented parallel to the reef crest along the same depth contour. Corallivores within our surveys were classified to family. We did not estimate sizes of each fish. To determine whether there were differences in the number of corallivores between depths and between years, we performed an ANOVA with an interaction between depth and year (before or after bleaching). We used a Tukey HSD test to test whether there were significant differences between significant predictors.

To supplement our surveys with species-level data on corallivorous fishes, we utilized the MCR LTER annual fish surveys. MCR LTER fish surveys are conducted annually in July/August at 10-12 m depth around the island (Moorea Coral Reef LTER and Brooks, 2022). This dataset does not quantify differences across depth, but we used it to assess whether there were differences in the abundance and biomass of excavator species before and after the bleaching event, as the surveys across depth only considered corallivores at the family level. For these surveys, divers swim along four permanent 5 x 50 m transects at each site that extend from the benthos to the surface of the water column. Total counts by species and the size (total length in cm) of each fish encountered on the transect is recorded. Biomass (body weight in g) was estimated using the formula $w = aL^b$ where L is the fish fork length in cm and parameters a and b depend on species (Kulbicki et al., 2005), which were obtained primarily using FishBase.

To test whether the bleaching event impacted excavating corallivore populations at 10 m, we quantified corallivore abundance (number of individuals per 250 m^2) and biomass ($g/250m^2$) at each transect (LTER 1 and LTER 2) from 2018-2020, 2018 representing the pre-bleaching community and 2019-2020 representing the post-bleaching community. The annual fish surveys are conducted across six sites and record all reef species. As such, we filtered the time series data for known corallivore species (table A1) at LTER 1 and LTER 2. We then performed two linear mixed models in the lme4 package (Bates et al., 2014), one with fish abundance as the response variable and one with biomass. In both models, year was a fixed effect and transect nested within site was a random effect. We selected this date range to assess whether the bleaching event altered corallivore populations during the bleaching event (changes between 2018 and 2019) and whether they changed following bleaching (changes between 2019 and 2020).

Predation impact

Excavating corallivores leave distinctive bite scars on their coral prey (Bonaldo and Bellwood, 2011; Burkepile, 2012; Ladd et al., 2021; Rotjan and Lewis, 2008). To assess the level of predation by excavating corallivores on individual *A. hyacinthus* colonies before and after bleaching, we quantified bites on *A. hyacinthus* colonies using two different datasets. Pre-bleaching predation was quantified by conducting *in situ* surveys in October 2018 across depth at the GB1 site where divers swam along four, nonoverlapping 25 x 1 m transects haphazardly placed at each depth to survey colonies (n = 71 at 5m, n = 62 at 10m, and n = 22 at 17 m) of *A. hyacinthus* which had at least 50% of their surface area within the transect. For each colony we encountered, we recorded the length and width of the colony to the nearest cm and later calculated the surface area (cm^2) of each colony as ellipses; surface area = pi*a*b, where a represents the longest diameter of the tabular coral and b represents the perpendicular measurement to the longest diameter. We also recorded the number of bite scars on each colony on each transect at each depth to quantify the mean number of bites per 100 cm^2 of surface area (bite density) of live *A. hyacinthus* colony area. We performed a linear mixed model with bite density as the response variable, depth as a fixed effect, and transect as a random effect in order to detect any differences across depth prior to bleaching. We then performed a Tukey HSD post-hoc test in the emmeans package following the mixed model to quantify any differences across depth (Lenth, 2022).

To quantify the bite density on *A. hyacinthus* tissue following the bleaching event, we tagged ~50 bleached *A. hyacinthus* colonies at 5, 10, and 17 m in July 2019 across approximately 500 m^2 of reef (more specific methodologies described below) to track their recovery. At this time, virtually all *A. hyacinthus* were bleached at all three depths. We revisited and resampled these tagged colonies until October 2020 but for the purposes of comparing bite density post-bleaching to pre-bleaching, we considered the number of bites on each colony in October 2019 (one year following pre-bleaching bite surveys) to calculate the mean number of bites per 100 cm^2 of live *A. hyacinthus* tissue at each depth, using the same ellipses calculation for surface area as above. We standardized our metric (bites per 100 cm2 of A. hyacinthus) in order to compare the prevalence of corallivory before and after bleaching. Because the survey methodologies were different, we were not able to perform a two-way ANOVA to determine whether there was a difference in bites/cm^2 between years and depth. Instead, we performed a one-way ANOVA on the post-bleaching data to determine whether there was a difference in bites/cm^2 across depth using coral as a replicate, as this dataset did not have transects. To determine differences across depth, we performed a Tukey HSD post-hoc test in the emmeans package following the ANOVA (Lenth, 2022).

Corallivory and recovery from bleaching

To understand whether and how bleached corals recovered from bleaching across depth, we tagged bleached *A. hyacinthus* colonies at 5m (n = 51), 10m (n = 52), and 17m (n = 43) depths between July 11 and July 20, 2019, at the GB1 site. Once divers identified a 100% bleached colony, it was photographed with a ruler to calculate colony size, and we fastened a numbered cattle tag to the substrate nearby to identify and resample the colony in subsequent surveys at each depth (Figure A1). Three subsequent surveys (#2: between 12 and 13 August 2019; #3: 23 October 2019; and #4: between 25 October and 8 November 2020; see table A2 for specific dates for each depth) were conducted at each depth (table A2) to assess overall coral health (bleached, recovered, or dead) and the number of bites on each colony. Some of the initially tagged corals could not be relocated on subsequent surveys. Thus, we only considered *A. hyacinthus* colonies that we observed throughout the entire survey period (n = 138 colonies total: n = 51 at 5m, n = 51 at 10m, and n=36 at 17). To understand whether the bite density (measured as the number of bites per 100 cm^2 of live tissue) varied across depth and through time, we conducted a liner mixed model with bite density (number of bites per 100 cm^2) as the response variable, the interaction of survey number and depth as fixed effects, and colony number as a random effect to account for resampling. We then ran an ANOVA followed by a Tukey HSD test in the emmeans package (Lenth, 2022) to identify pairwise differences between fixed effects.

To understand whether corals were more or less likely to die as a function of depth (5, 10, or 17m), maximum bite intensity (the maximum number of bites per 100 cm^2 of coral tissue during the time series for each colony), and size (surface area in cm^2), we utilized a generalized linear model (GLM). The binary response variable indicated whether a colony died (represented with a 1) or survived (recovered, indicated with a 0) at the end of the time series, October 2020. We tested three, two-way interactions between the independent variables: maximum bite density (number of bites per 100 cm^2), depth (5, 10, or 17m), and size (surface area of colony cm^2). To assess pairwise differences between significant effects, we performed a Tukey HSD test in the emmeans package (Lenth, 2022).

Corallivory impacts on coral growth pre and post bleaching event

Corallivory comes at an energetic cost to corals without causing whole colony mortality (Cole, 2011; Cole et al., 2008; Cole and Pratchett, 2011) and corals are forced to allocate energy towards healing from predation instead of prioritizing other metabolic processes such as growth. Corals that have recently recovered from bleaching have reduced energy stores and if preyed upon, have even less metabolic energy to allocate towards growth (Henry, 2005; Rice et al., 2019). We wanted to test for potential differences in the impact of corallivory on healthy corals pre- and post-bleaching. Thus, we hypothesized that corallivory would inhibit the growth of recently recovered corals post-bleaching compared to corals before the bleaching event. To test and understand this hypothesis and whether it varied across depth, we conducted an *in situ* growth experiment on *A. hyacinthus* before and after bleaching. We selected our growth metric as percent change in mass (g/day) relative to the initial starting mass of the nubbin to remove any potential confounding effects of initial coral size on growth rates. Experimental methodologies are described below.

Pre-bleaching experiment

On August 9th, 2018, we collected *A. hyacinthus* nubbins from the north shore of Moorea between LTER 1 and LTER 2 (GB 2, ~ 500 m northwest of GB 1) (n = 8 colonies per depth; 24 colonies total). From each colony we collected six branches (hereby referred to as nubbins) that were ~10 cm in length to use in our experiment. Each nubbin was placed into a labeled plastic bag and placed in a cooler filled with fresh seawater during transportation to water tables at Gump Research Station. Onshore, each branch was placed into the base of a cut, 50-mL Falcon tube using ZSPAR. All nubbins were labeled and buoyant weighed following Spencer Davies (1989) (Spencer Davies, 1989). Within 24 hours, nubbins were returned to the reef and were randomly assigned to a depth, treatment, and replicate without stratification by origin. Treatments consisted of: (1) without predation (full predator exclusion; controls), or (2) with predation (no predator exclusion; exposed). Predator exclusions were full cages, protecting each nubbin from corallivory. Corals in the exposed treatment had no protection from corallivory.

Twenty-four experimental tables were deployed at each depth for a total of 144 *A. hyacinthus* nubbins in the experiment. Coral nubbins at 10 m were deployed for 74 days (collected on 4 November 2018) and for 75 days at 5 and 17 m depths (collected on 5 November 2018). All nubbins were re-weighed for a final buoyant weight once they were collected at the end of the experiment. Percent change in mass (g/day) was calculated the for each coral by Δ mass = $((w_f - w_i)/w_i)$, where w_i is the initial mass of a coral at the beginning of the experiment and w_f is the final mass of a coral at the end of the experiment. Each value was then divided by the number of days elapsed under experimental treatment (89 days for 5 and 17 m corals, 88 days for 10 m corals).

Post-bleaching experiment

The post-bleaching experiment was initiated on August 6th, 2019, ~3.5 months following peak thermal stress at 5 m, 10 m, and 17 m on the same reef. At this time 52% of our tagged *A. hyacinthus* had died following the bleaching event (74.5, 50.0, and 32.5% of colonies at 5, 10, and 17m respectively) and we were interested in understanding how the reduction in available prey may have changed the impact of corallivory on remaining healthy corals at each depth. The same experimental methodology was implemented as in the pre-bleaching experiment except all coral nubbins (n = 60) came from a single healthy colony at 10 m, as many *A. hyacinthus* colonies were dead or still bleached at this time. Ten experimental tables were deployed at each depth (n=10 nubbins for each depth x caging combination) and nubbins at each depth were deployed for 76 days. The daily percent change in mass (g) was calculated using the same methodology used in the post-bleaching experiment.

Corallivory and its impact on growth before and after bleaching

To understand whether and how the impact of corallivory on growth of *A. hyacinthus* changed across depth following bleaching, we quantified the percent change in mass for each individual control nubbin (predator exclusion) and each individual exposed nubbin (with predation) on each experimental plate at each depth during each year. We then calculated the mean difference in growth between the two treatments at each depth and year.

Because the experiments were conducted with slightly different methodologies, we performed an ANOVA for each year (pre-bleaching and post-bleaching) separately to determine whether there were differences in the impact of corallivory on growth of *A. hyacinthus* across depth.

3.4 RESULTS

Bleaching trends across depth

The bleaching event impacted *A. hyacinthus* colonies differently across depth (figure 1). Over 50% of *A. hyacinthus* colonies were killed at 5 and 10 m compared to less than 30% at 17 m in July 2019, three months following the peak in thermal stress. Most colonies were still bleached at 17 m at this time, 50.1% of colonies compared to 22.7 and 25.5% of colonies at 5 and 10 m respectively. The number of small (5-9 cm in diameter) colonies we surveyed consisted of 25, 113, and 74 individuals at 5, 10, and 17 m respectively. We surveyed 46, 180, and 78 mid-size (10-29 cm in diameter) colonies and 37, 96, and 26 large (≥ 30 cm in diameter) colonies at 5, 10, and 17 m respectively. Overall, smaller colonies (5-9 cm in diameter) more commonly evaded bleaching, with 13.7, 17.3, and 33.4% of small colonies unbleached at 5, 10, and 17 m compared to only 3.2, 5.7, and 7.8 % of unbleached large colonies (≥ 30 cm in diameter) at each depth respectively.

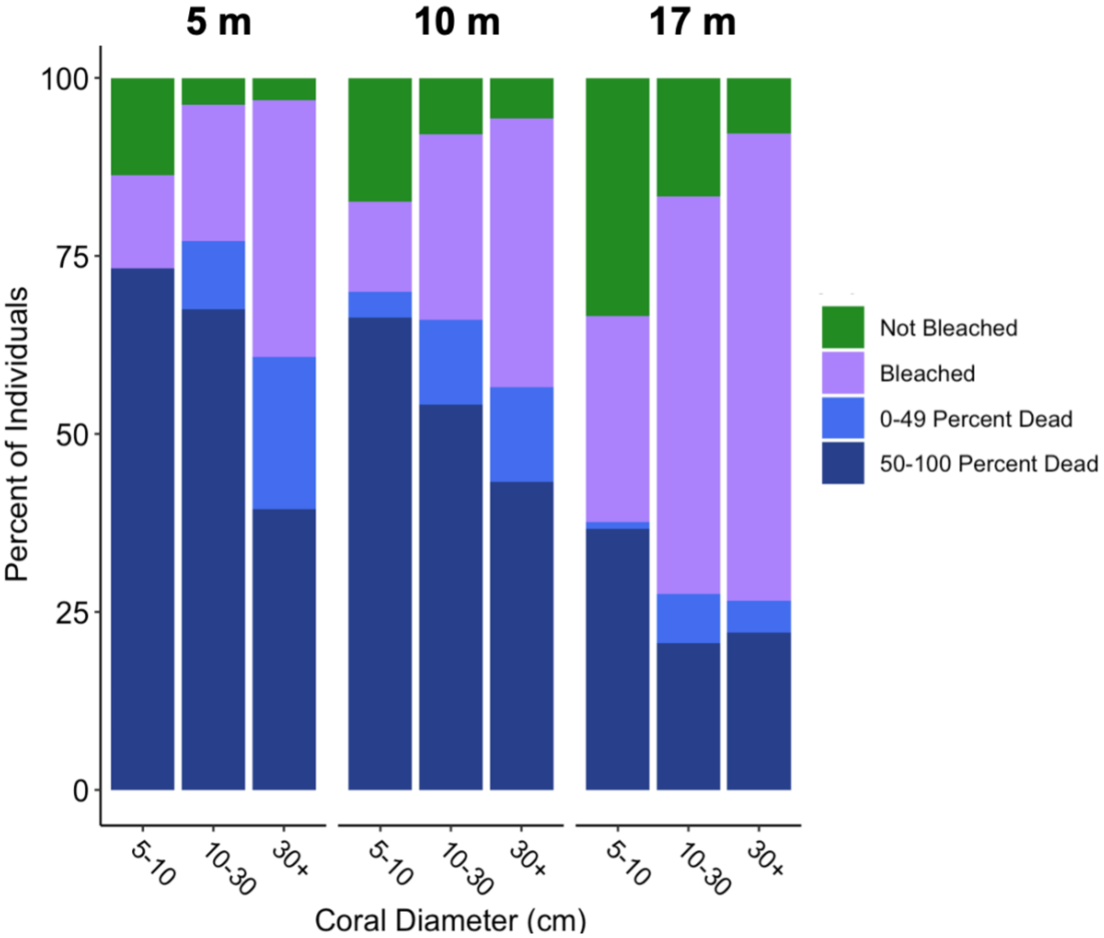


Figure 1. Percent of individual *Acropora hyacinthus* colonies that were not bleached (green), completely bleached (purple), experienced <50% mortality (light blue) or had at least 50% mortality (dark blue) during July 2019 at 5, 10, and 17 m across different size categories on the north shore of Moorea.

Number of corallivores

The bleaching event did not meaningfully impact corallivore abundance. The number of excavating corallivores was marginally different across depth at the family level (depth effect; p = 0.06; table A3), where there were slightly higher abundances at 10 m prior to bleaching. There was also only marginal evidence for changes across depth following bleaching at the family level (depth*year effect; p = 0.07; table A3; figure 2A. At the species level, there was no difference in the abundance of excavating corallivore species at 10 m depth between before and after bleaching (year effect, p = 0.49; table A4). There was also no change in corallivore biomass at 10m depth at these sites before and after bleaching (year effect, p = 0.63; table A5).

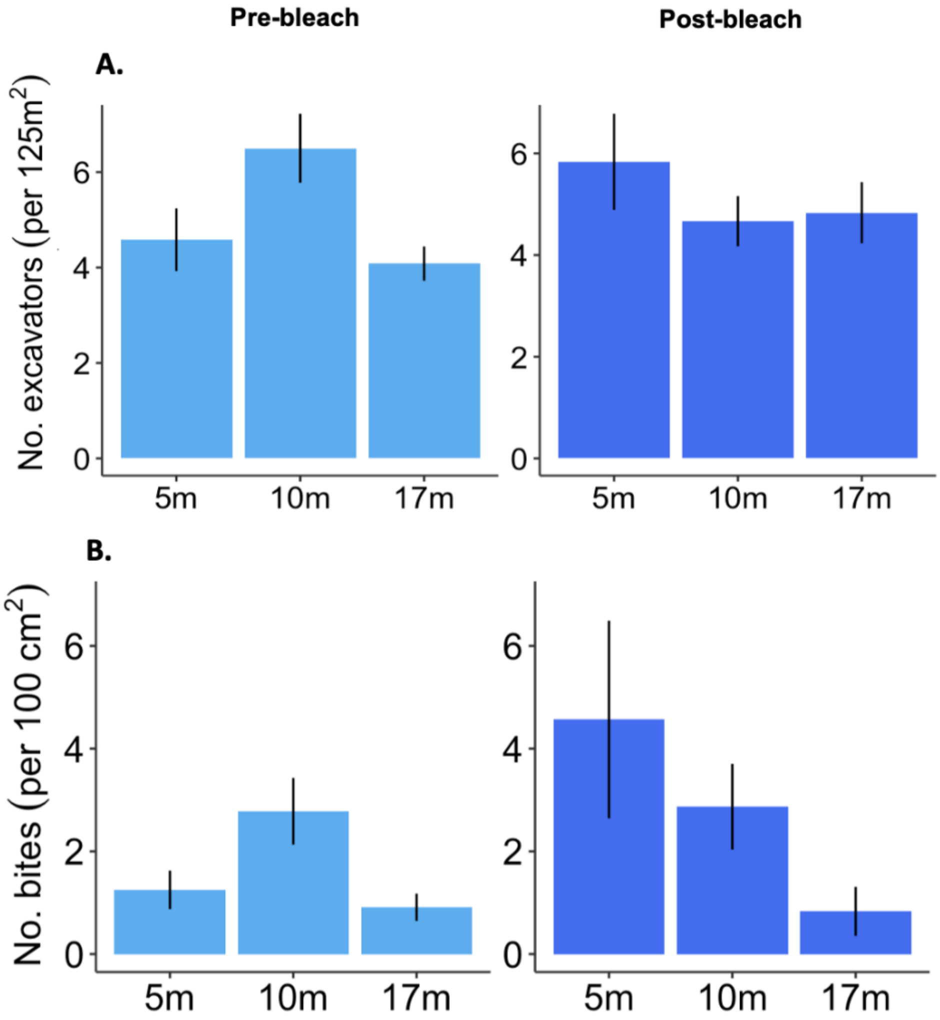


Figure 2. Patterns in A) the number of corallivores per 125m^2, for the full list of included species, see table A1, and B) the number of bites per 100 cm^2 of healthy *Acropora hyacinthus* tissue. Error bars represent standard error.

Bite density before and after bleaching

Before the bleaching event, there were no differences in the density of bites on *A. hyacinthus* across depth (depth effect, $p = 0.5$; figure 2B; table A6). Following bleaching, bite density (bites per 100cm^2 of live tissue) declined significantly with depth (figure 2B, depth effect; = 0.03; table A7). The post-hoc test revealed that there was a higher density of bites on *A. hyacinthus* at 5 m compared to 17 m (pairwise comparison; $p = 0.03$; table A7).

Corallivory and recovery from bleaching

Of the colonies we successfully followed through October 2020, 0%, 11.8%, and 43.2% of corals recovered and survived at 5, 10, and 17 m respectively (figure 3), and the overall trends in recovery from bleaching varied through time amongst the tagged colonies at each depth. As tagged corals began to die or recover, the bite density (number of bites per 100 cm^2) on live *A. hyacinthus* increased (figure 3), and this pattern differed across depth through time (depth x survey number: $p < 0.001$; table A8; figure 3). At 5m, bite density had increased slightly by August and dramatically increased by October 2019, at which time 90% of the tagged corals had died and predation was concentrated on only a few colonies. By October 2020, one year later, none of our tagged colonies had survived at 5 m and bite density thus fell to zero bites per 100 cm^2. Bite density increased at 10 m by August 2019 and remained relatively constant until October 2020 whereas bite density did not dramatically increase at 17 m until October 2019 and did not change even a year later in 2020 (figure 3).

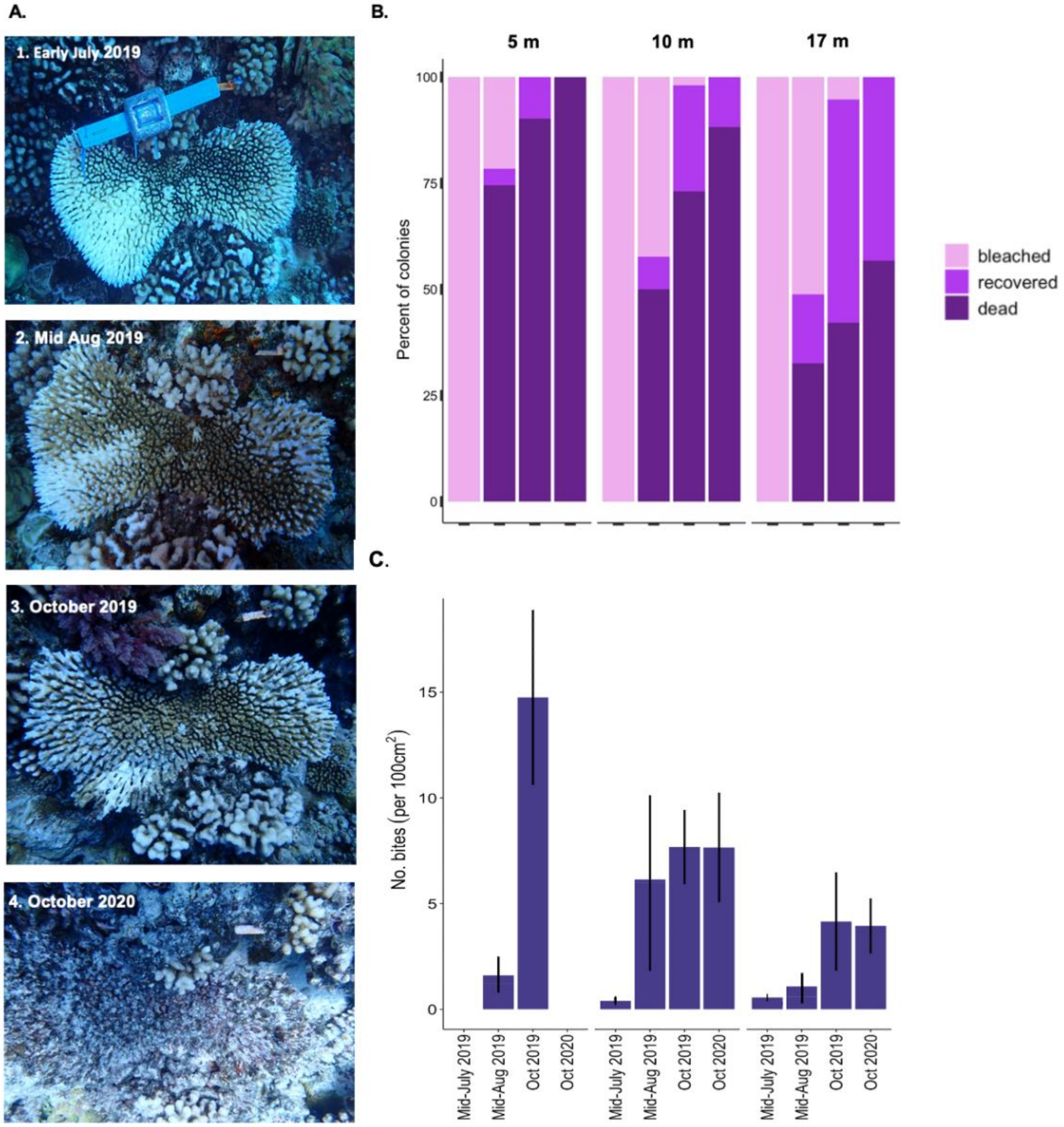


Figure 3. A) Tagged *Acropora hyacinthus* colony at 10 m depth at each survey time point that shows the intensity of predation through time until the colony is eventually found dead in October 2020. B) Percent of tagged colonies that were bleached, recovered, and dead during each survey. C) Number of bites per 100 cm^2 of bleached and recovered *A. hyacinthus* tissue at each time point, bleached bites comprise < 5% of total observed bites; error bars represent standard error.

The GLM revealed that there were no significant interactions between maximum bite density and depth ($\chi2(2) = 2.25$, $p = 0.32$; table A9), depth and surface area ($\chi2(2) = 1.63$, p

= 0.44; table A9), and maximum bite density and surface area ($\chi2(1) = 0.11$, $p = 0.73$; table A9). However, there were significant effects of maximum bite density ($\beta = -15.21$; $\chi2(1) = 6.00$, $p = 0.01$; table A9) and depth ($\chi2(2) = 22.00$, $p< 0.001$; table A9) on whether a colony died or recovered from bleaching. The pattern of recovery from bleaching varied across depth (figure 3), where more corals recovered at 17 m than at 10 and 5 m (figure 3). Our model revealed that corals at 17 m were less likely to die than corals at 5 and 10 m regardless of surface area and bite density (pairwise comparison of means, table A9) but there was no difference in predicted mortality between corals at 5 and 10 m (pairwise comparison of means, table A9). Although the surface area of corals varied from 69.5 to 2045.7 cm^2, size was not a significant predictor ($\chi2(1) = 0.11$, $p = 0.74$; table A9).

Corallivory and coral growth inhibition

Prior to bleaching, there strong depth-dependent effect of corallivory on *A. hyacinthus* (figure 4; table A10; depth effect: $p = 0.008$) where growth of corals at 5m was more negatively impacted by corallivory than at 10 and 17m (pairwise comparison of estimated means, $p = 0.05$ and $p = 0.007$ respectively; table A10). Importantly, corallivory had no significant effect on growth (impact was no different than zero) at 10m and 17m prior to the bleaching event. Although we were not able to statistically test whether there was a greater effect of corallivory on *A. hyacinthus* growth after bleaching, corallivory suppressed growth at all depths after the bleaching event (figure 4). Further, there was no statistically significant difference in the impact of corallivory on *A. hyacinthus* growth between the three depths following bleaching (figure 4; table A11; depth effect: $p = 0.22$), meaning corallivory impacted the growth of *A. hyacinthus* similarly across depth.

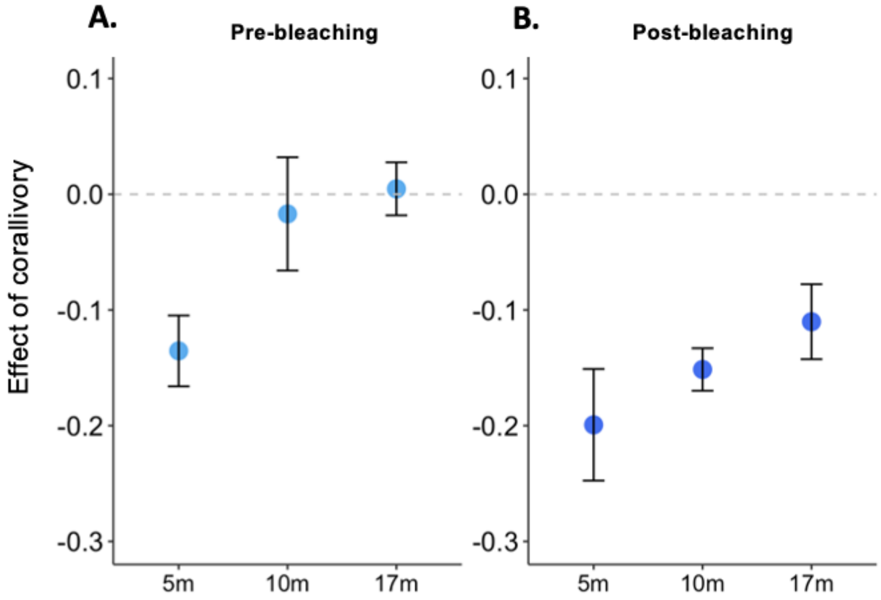


Figure 4. The effect of corallivory on the growth of corals (measured as the daily percent change in mass) of *A. hyacinthus* colonies exposed to corallivory relative to colonies that did not experience corallivory A) before bleaching, and B) following bleaching across depth. Error bars represent standard error.

3.5 DISCUSSION

Warming events that cause mass bleaching are projected to increase globally as the climate continues to change (Donner, 2009; Heron et al., 2016). How these warming events impact key coral species is important to consider for not only understanding how live coral habitat might change during subsequent warming, but also how reef species that depend upon coral for prey might respond. Generally, corals bleach less at deeper depths due to the attenuation of light and temperature (Muir et al., 2017). We found that patterns of bleaching in *Acropora hyacinthus* supported this concept, where colonies bleached at lower rates at 17 m than at shallower depths. We also expanded upon this idea and found that bleached *A. hyacinthus* colonies recovered from bleaching in higher numbers at deeper depths compared to the shallows, which has not yet been shown in the literature to our knowledge. However, the interaction between depth and corallivory is nuanced, and can exacerbate or mitigate bleaching mortality at all depths. Together, these results highlight that corallivory plays a role in the recovery of *A. hyacinthus* across depth following bleaching, and has the capacity to intensify the impacts of bleaching on corals that initially survive.

The bleaching event reduced the number of live *A. hyacinthus* colonies and the overall number of corallivores did not change across depth. As has been observed with other coral species, mortality of *A. hyacinthus* resulting from bleaching was higher in shallower water (Baird et al., 2018; Bridge et al., 2013; Smith et al., 2014). Given the pattern of *A. hyacinthus* mortality across depth, the pressure from corallivory also scaled with depth and where colonies in shallower water experienced a higher levels of corallivory relative to colonies at 17m. Our study contributes to a body of literature demonstrating that when coral is abundant, the impact of corallivory on colony survival is minimal, however, when coral cover declines rapidly, corallivory can induce subsequent mortality, in which we observed the strength of this mortality pattern across depth.

The complete mortality of tagged *A. hyacinthus* at 5m suggests that corals in shallower water are not only more susceptible to bleaching, but they also have a reduced capacity to recover compared to other depths, especially in the face of elevated per capita corallivory. A total of 40% of tagged colonies survived at 17 m, which was 4 times greater than survival 10 m. No tagged corals survived at 5 m, where bite density was highest. In addition to higher predation in shallow water compared to deeper water, physical differences (solar irradiance, temperature, movement of seawater) exist across depths (Leichter et al., 2012; Muir et al., 2017; Smith et al., 2014) that may have contributed to the difference in *A. hyacinthus* recovery. Our model revealed that the singular effect of depth was a significant predictor of whether a colony died or recovered from bleaching, as has been observed in predicting whether corals bleach (Winslow Chapter 1). This may be because corals at deeper depths typically experience cooler, darker conditions (Muir et al., 2017; Prasetia et al., 2016; Smith et al., 2014) and are exposed to higher fluctuations in temperature (Leichter et al., 2012; Wyatt et al., 2020), which can mitigate bleaching (Safaie et al., 2018). It is possible that these conditions not only dampen the impact of marine heatwaves on corals, but they also might facilitate the recovery of corals from bleaching, which has not been observed to our knowledge. One potential limitation of our recovery analyses is that we only considered the maximum bite density experienced by tagged corals in our study over the entire time series. This approach does not allow us to assess the potential impacts of repeated instances of corallivory. Moving forward in future studies, one possible way to disentangle more diverse impacts of corallivory on individual colony survival would be through use of a multi-state transition model.

In addition to directly reducing the abundance of coral, the interaction of bleaching and corallivory can also dampen the metabolic processes (e.g. biomass production/growth (Henry, 2005; Kayal et al., 2012) and reproduction (Henry, 2005)) of corals that survive bleaching (Rotjan et al., 2006). Thus, the chronic removal of coral tissue comes at a substantial energetic cost to corals such that corallivory may be important for regulating the abundance and distribution of species (Cole et al., 2008; Cox, 1986). Tabular *Acropora* corals are a preferred food source for corallivores in the Indo-Pacific (Cole and Pratchett, 2012; Pratchett, 2005) and corallivores remove a substantial portion of available tabular coral biomass annually (Cole et al., 2012). Energy reserves in bleached or recently recovered corals are already low or depleted (Fisch et al., 2019; Grottoli et al., 2006;

Leuzinger et al., 2012), and the colony may not have sufficient energy to allocate to healing from predation. In Moorea, the negative impact of corallivory on *A. hyacinthus* growth was 3.75 times greater after bleaching across depths, which could have major implications for not only the growth, but the survival and reproduction of the species. However, it is important to note that our growth analysis was conducted on a single, recovered *A. hyacinthus* colony from a single depth, which does not necessarily represent the *A. hyacinthus* population at large. Prior to bleaching, corallivory only significantly reduced the mass of *A. hyacinthus* at 5 m whereas there was a negative effect of corallivory on *A. hyacinthus* at all three depths following bleaching. As such, the effect of corallivores on coral nubbins at all three depths was negative following bleaching. We would expect the impact of corallivory to scale with the bleaching related mortality where corallivory would have the greatest impact on growth at 5m and the lowest impact would be observed at 17 m where more *A. hyacinthus* colonies survived. Although that was the trend, it was not statistically significant, likely due to a low sample size (n=10 at each depth). As mentioned above, the single *A. hyacinthus* colony we used out of necessity in our post-bleaching experiment may not be representative of *A. hyacinthus* corals at large, given it survived and recovered from bleaching and went through a strong selective filter to be used in our experiment. Thus, extrapolating results is more challenging although the patterns we observed were quite clear.

As extreme bleaching events occur more regularly, diverse reefs with high abundances of thermally sensitive species will become less common through bleaching related mortality. Thermally sensitive species that are important food sources for other reef animals are even more imperiled. The loss of *A. hyacinthus*, may have major implications for other reef species, as it is a coveted food source amongst corallivores (Cole et al., 2008), provides a unique and important habitat for reef fish (Kerry and Bellwood, 2015, 2012), and we may see a decline in specialist corallivores that have a less diverse diet. Our work contributes to a growing body of literature that evaluates the impact of corallivory on a reduced supply of preferred prey, *A. hyacinthus*. We found that bleaching and corallivory can act synergistically to 1) reduce the overall abundance of *A. hyacinthus*, and 2) negatively impact the growth of *A. hyacinthus* colonies that survive and recover from bleaching. Moreover, the extent to which *A. hyacinthus* is impacted by these processes varies across depth. Our work demonstrates that thermally sensitive coral species that survive bleaching can be vulnerable to subsequent increases in predation-related mortality. This may have major implications for the recovery of the species at the population level by reducing the capacity for *A. hyacinthus* to grow, reproduce, and thus survive subsequent disturbance events.

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APPENDICES

CHAPTER 1 APPENDIX

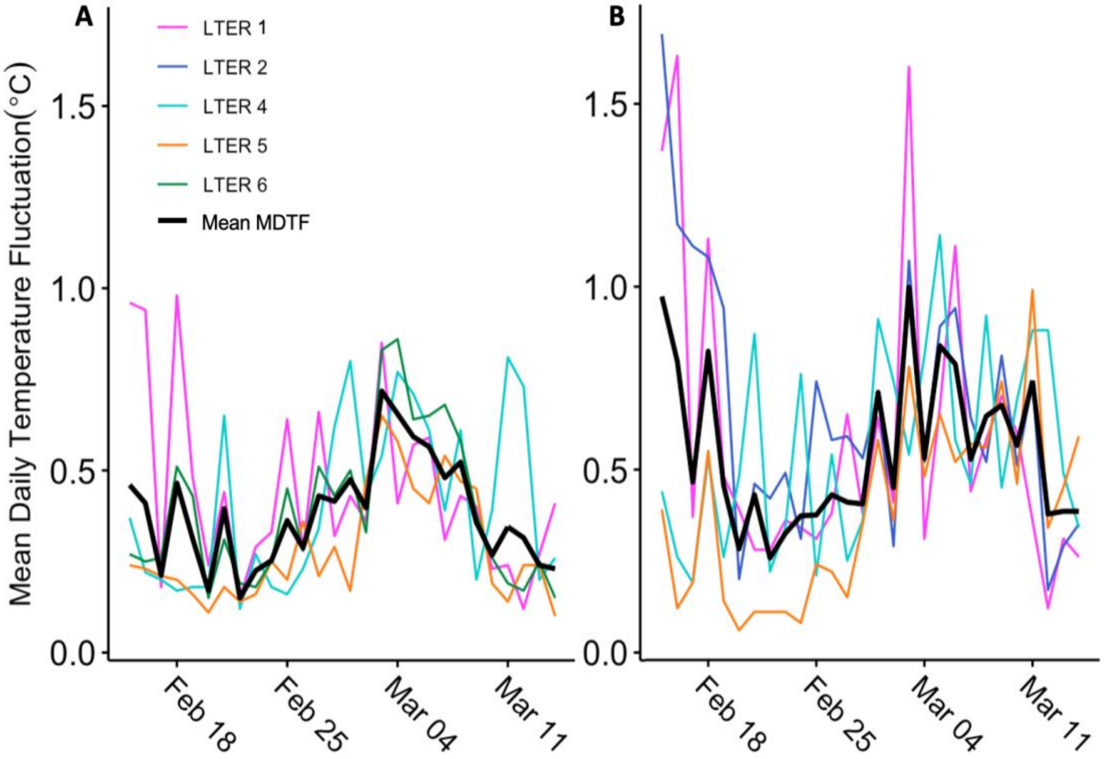


Figure A1. Mean daily temperature fluctuation (MDTF) in the 30 days (February 15 – March 15, 2019) leading up to the first signs of the bleaching event at **A)** 10 m and **B)** 17 m at each site. Solid black line represents the mean daily temperature fluctuation (MDTF) across sites at each depth during this time-period.

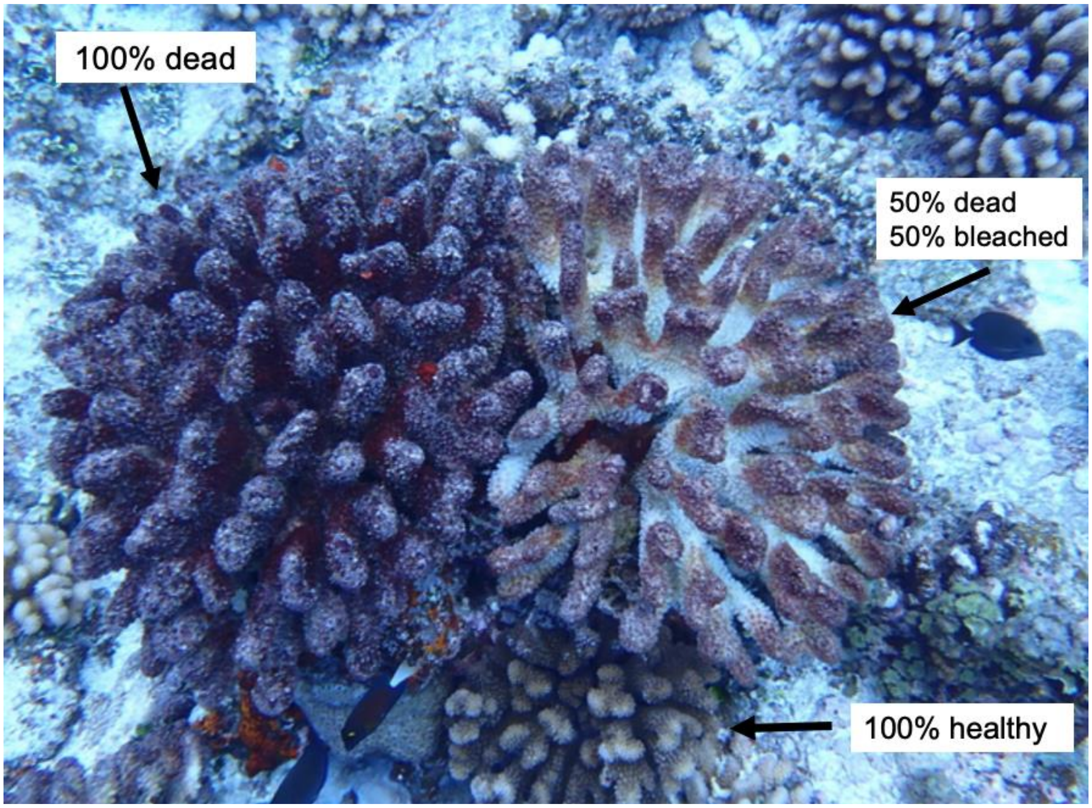


Figure A2: Examples of *Pocillopora* impacted by the bleaching event. The colony on the left was considered 100% dead from recent bleaching and the colony on the right was 50% dead and 50% bleached. Thus, both colonies were considered severely bleached (75% bleached and/or recently dead). The bottom coral was 100% healthy and not considered severely bleached. Image modified from Speare et al. 2022.

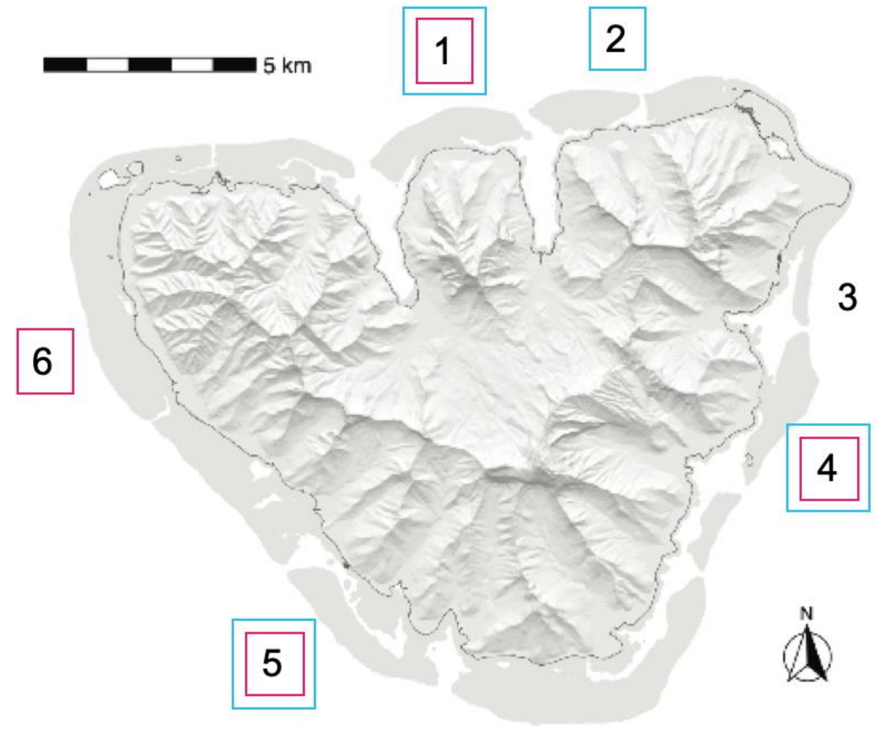


Figure A3: Locations of the six permanent LTER sites around Moorea. Divers completed bleaching surveys at 10 and 17 m depths at all six sites, but we only utilized sites with continuous temperature data from 1 August 2018 to 31 July 2019. Sites with continuous temperature data at 10 m are indicated with a pink box, and sites with continuous temperature data at 17 m are indicated with a blue box. Thermistors at both 10 m and 17m failed at LTER 3 resulting in no temperature data from this site.

Table A1: Severe bleaching linear mixed model (LMM) results for *Acropora* corals. **A)** random effects, **B)** Wald Chi-square test of LMM, **C)** Pairwise differences in predicted severe bleaching means for *Acropora* corals of different colony sizes, and **D)** pairwise differences of predicted severe bleaching means in *Acropora* corals for different depths. Pairwise comparisons were calculated using a Tukey HSD (honest significant difference) test. SE: standard error; DF: degrees of freedom; SD: standard deviation.

A. Linear Mixed Effects model random effects

	Variance	SD
Site (intercept)	95.66	9.78

B. Wald Chi-square test

	Chi square	DF	p value
AHS	0.42	1	0.558
Size (diameter in cm)	6.32	2	**0.011**
Depth (m)	11.24	1	**0.014**
AHS*Size	0.65	2	0.535

C**.** Pairwise differences of predicted severe bleaching means in *Acropora* corals for different colony sizes across depth and the mean AHS value, 5.0147.

Pairwise differences of Size (cm)	Estimate	SE	DF	p value
(5-9) - (10-29)	-12.63	4.39	13.7	**0.031**
(5-9) - (≥ 30)	-14.29	4.39	13.7	**0.015**
(10-29) - (≥ 30)	-1.66	4.39	13.7	0.925

D. Pairwise differences of predicted severe bleaching means in *Acropora* corals for different depths across size classes and the mean AHS value, 5.0147.

Pairwise differences of Depth	Estimate	SE	DF	p value
10 m depth – 17 m depth	27.2	8.12	6.5	**0.014**

Table A2: Severe bleaching linear mixed model (LMM) results for *Pocillopora* corals. **A)** random effects**, B)** Wald Chi-square test of LMM, and **C)** Pairwise differences in predicted severe bleaching means for *Pocillopora* corals of different colony sizes interacting with accumulated heat stress (AHS). Pairwise comparisons were calculated using a Tukey HSD (honest significant difference) test. SE: standard error; DF: degrees of freedom; SD: standard deviation.

A. Linear Mixed Effects model random effects

	Variance	SD
Site (intercept)	8.33	2.89

B. Wald Chi-square test

	Chi square	DF	p value
AHS	9.60	1	0.099
Size (diameter in cm)	7.88	2	**0.005**
Depth (m)	1.61	1	0.238
AHS*Size	8.60	2	**0.004**

C. Pairwise differences of predicted severe bleaching means in *Pocillopora* corals for different colony sizes and mean maximum AHS (5.0147) across depth.

Pairwise differences of Size (cm)	Estimate	SE	DF	p value
(5-9; AHS:5.0147) - (10-29; AHS:5.0147)	0.47	5.58	14.2	0.996
(5-9; AHS:5.0147) - (≥ 30; AHS:5.0147)	-18.95	5.58	14.2	**0.011**
(10-29; AHS:5.0147)- (≥ 30; AHS:5.0147)	-19.42	5.58	14.2	**0.010**

CHAPTER 3 APPENDIX

Table A1. List of known excavating corallivores in Moorea, French Polynesia considered in our study. All species except for *Arothron meleagris* are facultative corallivores, in that their dietary composition is < 80% coral (Cole, 2011). Table was modified from Ladd et al. 2021 and accompanying references(Moorea Coral Reef LTER and Brooks, 2022; Rotjan and Lewis, 2008).

Functional Group	**Species**
Herbivore/facultative corallivore	*Chlorurus frontalis*
Herbivore/facultative corallivore	*Chlorurus spilurus*
Herbivore/facultative corallivore	*Leptoscarus vaigiensis*
Herbivore/facultative corallivore	*Scarus altipinnis*
Herbivore/facultative corallivore	*Scarus forsteni*
Herbivore/facultative corallivore	*Scarus frenatus*
Herbivore/facultative corallivore	*Scarus ghobban*
Herbivore/facultative corallivore	*Scarus globiceps*
Herbivore/facultative corallivore	*Scarus niger*
Herbivore/facultative corallivore	*Scarus oviceps*
Herbivore/facultative corallivore	*Scarus psittacus*
Herbivore/facultative corallivore	*Scarus rubroviolaceus*
Herbivore/facultative corallivore	*Scarus schlegeli*
Omnivore	*Balistapus undulatus*
Omnivore	*Balistoides viridescens*
Invertivore	*Cantherhines dumerilii*
Corallivore	*Cantherhines sandwichiensis*
Invertivore	*Canthigaster solandri*
Corallivore	*Arothron meleagris*

Figure A1. A tagged *A. hyacinthus* colony at 10 m on July 16, 2020.

Table A2: Dates that each sampling was conducted at each depth. Resampling was dependent on weather, swell for the shallow 5m site, and boat availability.

Sampling dates	Depth	Sampling event no.
Initial tags: July 11-16, 2019	5 m	1
Initial tags: July 11-16, 2019	10 m	1
Initial tags: July 14-16, 2019	17 m	1
August 12, 2019	5 m	2
August 13, 2019	10 m	2
August 13, 2019	17 m	2
October 23, 2019	5 m	3
October 23, 2019	10 m	3
October 23, 2019	17 m	3
October 25, 2020	5 m	4
October 30, 2020	10 m	4

November 8, 2020	17 m	4

Table A3. ANOVA results for the abundance of excavating corallivores across depth before and after bleaching.

	Sum of Squares	DF	F value	P value
year	0.04	1	0.01	0.92
depth	21.93	2	2.80	0.06
Year x depth	21.91	2	2.80	0.07

Table A4A. Random effects for the abundance of excavating corallivore species at 10 m on the north shore before and after bleaching using the MCR LTER data (Moorea Coral Reef LTER and Brooks, 2022).

	Variance	SD
Site x transect (intercept)	1.37	1.17
Residual	62.70	7.92

Table A4B. ANOVA results for whether the abundance of excavating corallivore species varied at 10 m on the north shore before and after bleaching using the MCR LTER data.

	Chi-square	DF	P value
year	2.19	2	0.33

Table A5A. Random effects for the biomass of corallivore species (g/250m^2) at 10 m on the north shore from 2018-2020 using the MCR LTER data (Moorea Coral Reef LTER and Brooks, 2022).

	Variance	SD
Site x transect (intercept)	<0.001	0.003
Residual	812256	901.3

Table A5B. ANOVA results for whether the biomass (g/250m^2) of excavating corallivore species at 10 m on the north shore varied before and after bleaching (2018-2020).

	Chi-square	DF	P value
year	3.13	2	0.21

Table A6A. Random effects for the linear mixed model of bite density (bites per 100cm^2 of live *A. hyacinthus* tissue) across depth before bleaching.

	Variance	SD
Transect (intercept)	5.15	2.27
Residual	53.62	7.32

Table A6B. ANOVA results for the bite density (bites per 100cm^2 of live *A. hyacinthus* tissue) before bleaching across depth.

	Chi-square	DF	P value
Depth	1.40	2	0.50

Table A7A. ANOVA results for the bite density (bites per 100cm^2 of live *A. hyacinthus* tissue) after bleaching across depth.

	Sum of Squares	DF	F value	P value
depth	0.021	2	3.61	0.03
Residuals	0.285	99		

T**able A7B.** Pairwise differences of predicted means of the number of bites per 100 cm2 of *Acropora hyacinthus* corals between depths.

Pairwise differences of Depth	Estimate	lower	upper	p value
5m – 10m	0.017	-0.018	0.052	0.49
5m – 17m	0.037	0.002	0.072	0.03
17m – 10m	-0.020	-0.049	0.008	0.20

Table A8A. Bite density (number of bites on 100 cm^2 of live tissue) linear mixed effects model random effects.

	Variance	SD
Coral ID (intercept)	<0.001	0.003
Residual	<0.001	0.024

Table A8B. Wald Chi-square test of Linear Mixed Model Results assessing how depth and survey number (time elapsed post bleaching) influenced the mean bite density (number of bites on 100 cm^2 of live tissue) on *A. hyacinthus.*

	Chi square	DF	p value
Survey number	182.80	3	<0.001
Depth	15.85	2	<0.001
Survey number x depth	133.86	2	<0.001

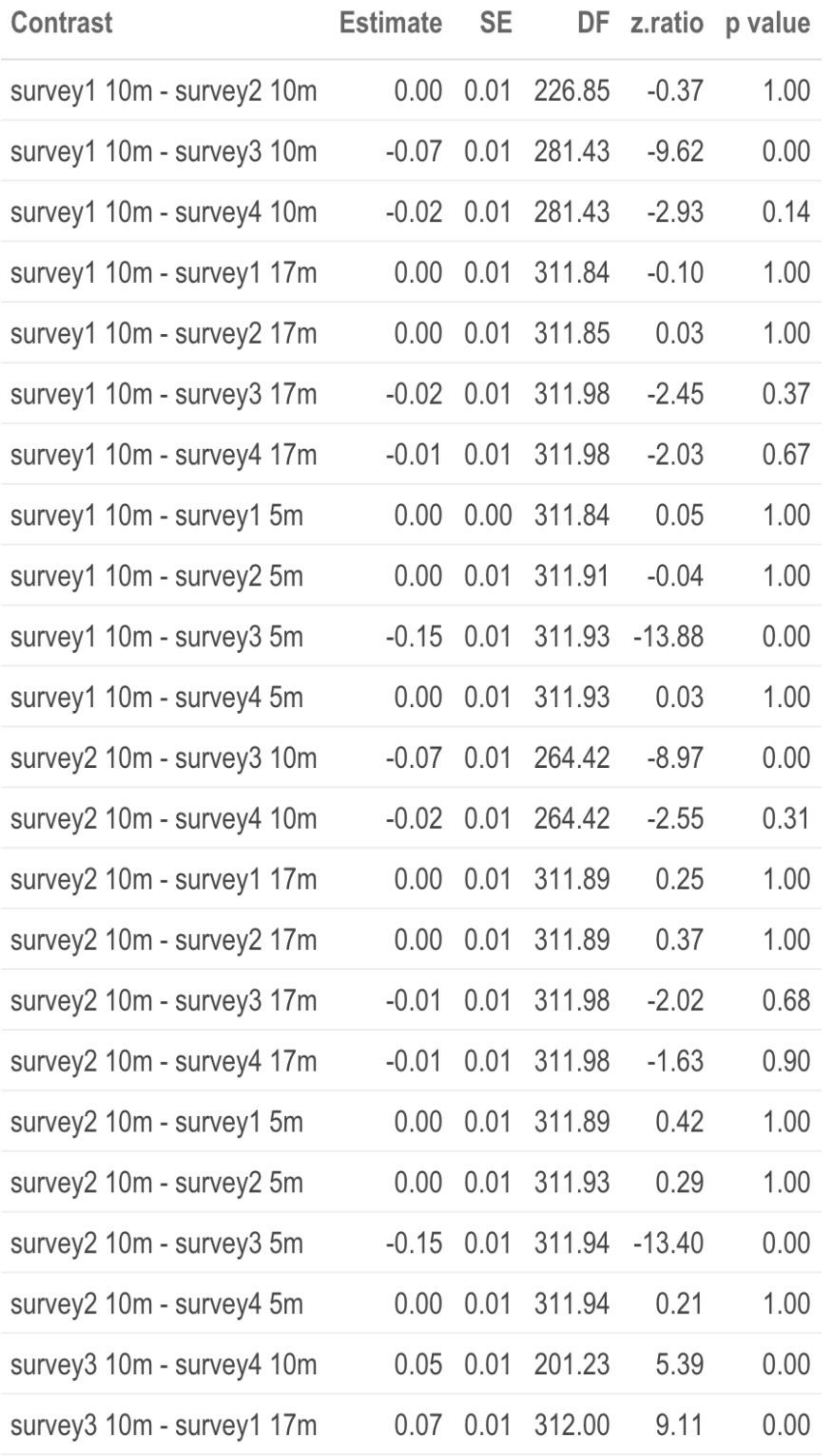
Table A8C. Pairwise comparison of predicted bite density (number of bites per 100 cm^2) means on *Acropora hyacinthus* corals for each survey date.

Pairwise differences of Depth	Estimate	SE	DF	T ratio	p value
Survey 1 – Survey 2	-0.001	0.003	221	-0.18	0.99
Survey 1- Survey 3	-0.078	0.005	287	-16.07	<0.001
Survey 1 – Survey 4	-0.011	0.005	287	-2.34	0.09
Survey 2 – Survey 3	-0.077	0.005	276	-15.52	<0.001
Survey 2 – Survey 4	-0.011	0.005	276	-2.16	0.14
Survey 3 – Survey 4	-0.067	0.006	201	10.89	<0.001

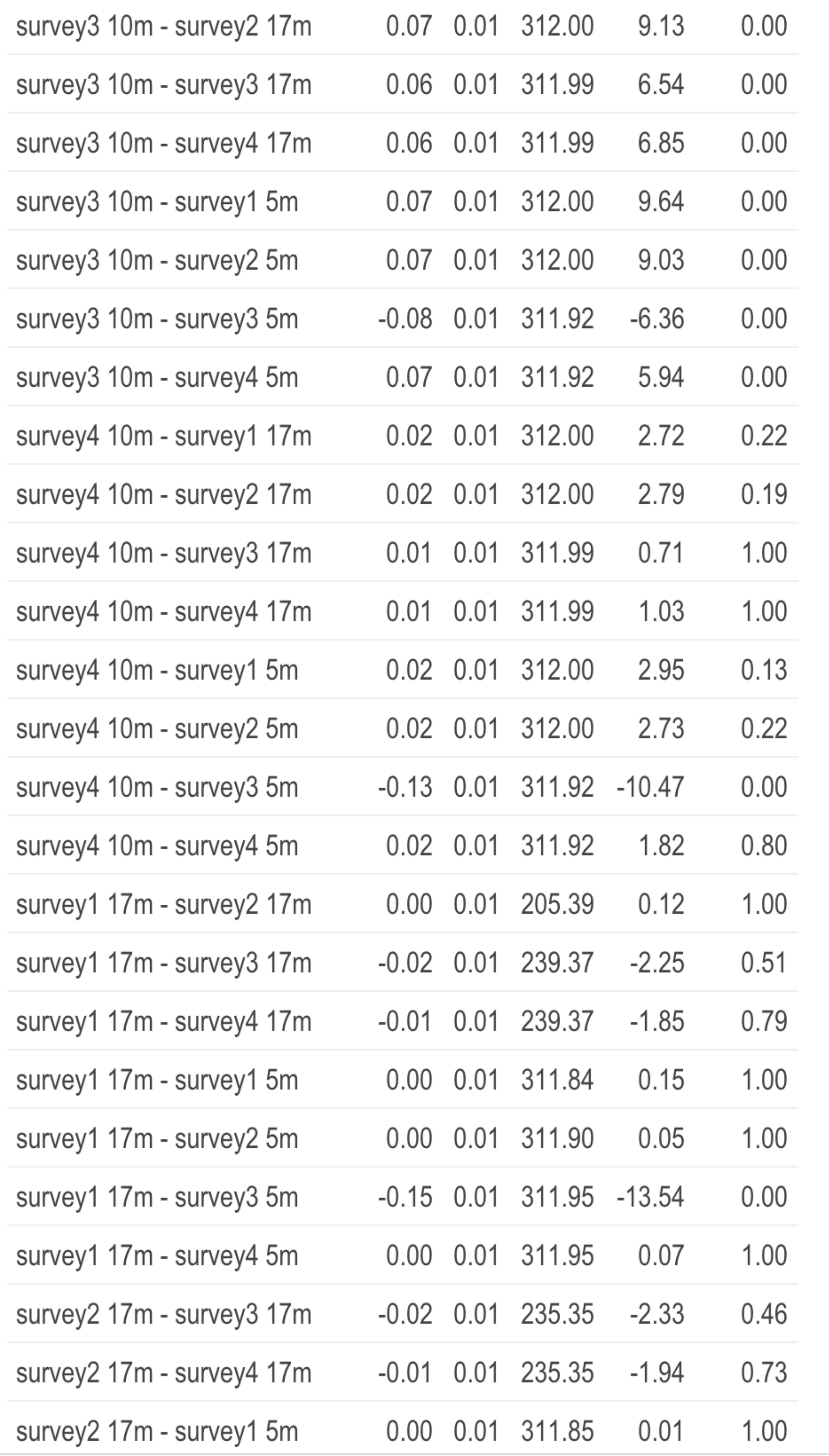
Table A8D. Pairwise comparison of predicted bite density (number of bites per 100 cm^2) means on *Acropora hyacinthus* corals for each depth.

Pairwise differences of Depth	Estimate	SE	DF	T ratio	p value
10m – 17m	0.016	0.004	89.8	4.48	<0.001
10m – 5m	-0.01	0.004	133.2	-2.77	0.018
17m – 5m	-0.03	0.006	120.7	-6.45	<0.001

Table A8E. Pairwise comparison of the interaction of survey number and depth predicted means on the bite density (number of bites per 100 cm^2) on *Acropora hyacinthus* corals.



Contrast	Estimate	SE	DF	z.ratio	p value
survey1 10m - survey2 10m	0.00	0.01	226.85	-0.37	1.00
survey1 10m - survey3 10m	-0.07	0.01	281.43	-9.62	0.00
survey1 10m - survey4 10m	-0.02	0.01	281.43	-2.93	0.14
survey1 10m - survey1 17m	0.00	0.01	311.84	-0.10	1.00
survey1 10m - survey2 17m	0.00	0.01	311.85	0.03	1.00
survey1 10m - survey3 17m	-0.02	0.01	311.98	-2.45	0.37
survey1 10m - survey4 17m	-0.01	0.01	311.98	-2.03	0.67
survey1 10m - survey1 5m	0.00	0.00	311.84	0.05	1.00
survey1 10m - survey2 5m	0.00	0.01	311.91	-0.04	1.00
survey1 10m - survey3 5m	-0.15	0.01	311.93	-13.88	0.00
survey1 10m - survey4 5m	0.00	0.01	311.93	0.03	1.00
survey2 10m - survey3 10m	-0.07	0.01	264.42	-8.97	0.00
survey2 10m - survey4 10m	-0.02	0.01	264.42	-2.55	0.31
survey2 10m - survey1 17m	0.00	0.01	311.89	0.25	1.00
survey2 10m - survey2 17m	0.00	0.01	311.89	0.37	1.00
survey2 10m - survey3 17m	-0.01	0.01	311.98	-2.02	0.68
survey2 10m - survey4 17m	-0.01	0.01	311.98	-1.63	0.90
survey2 10m - survey1 5m	0.00	0.01	311.89	0.42	1.00
survey2 10m - survey2 5m	0.00	0.01	311.93	0.29	1.00
survey2 10m - survey3 5m	-0.15	0.01	311.94	-13.40	0.00
survey2 10m - survey4 5m	0.00	0.01	311.94	0.21	1.00
survey3 10m - survey4 10m	0.05	0.01	201.23	5.39	0.00
survey3 10m - survey1 17m	0.07	0.01	312.00	9.11	0.00



survey3 10m - survey2 17m	0.07	0.01	312.00	9.13	0.00
survey3 10m - survey3 17m	0.06	0.01	311.99	6.54	0.00
survey3 10m - survey4 17m	0.06	0.01	311.99	6.85	0.00
survey3 10m - survey1 5m	0.07	0.01	312.00	9.64	0.00
survey3 10m - survey2 5m	0.07	0.01	312.00	9.03	0.00
survey3 10m - survey3 5m	-0.08	0.01	311.92	-6.36	0.00
survey3 10m - survey4 5m	0.07	0.01	311.92	5.94	0.00
survey4 10m - survey1 17m	0.02	0.01	312.00	2.72	0.22
survey4 10m - survey2 17m	0.02	0.01	312.00	2.79	0.19
survey4 10m - survey3 17m	0.01	0.01	311.99	0.71	1.00
survey4 10m - survey4 17m	0.01	0.01	311.99	1.03	1.00
survey4 10m - survey1 5m	0.02	0.01	312.00	2.95	0.13
survey4 10m - survey2 5m	0.02	0.01	312.00	2.73	0.22
survey4 10m - survey3 5m	-0.13	0.01	311.92	-10.47	0.00
survey4 10m - survey4 5m	0.02	0.01	311.92	1.82	0.80
survey1 17m - survey2 17m	0.00	0.01	205.39	0.12	1.00
survey1 17m - survey3 17m	-0.02	0.01	239.37	-2.25	0.51
survey1 17m - survey4 17m	-0.01	0.01	239.37	-1.85	0.79
survey1 17m - survey1 5m	0.00	0.01	311.84	0.15	1.00
survey1 17m - survey2 5m	0.00	0.01	311.90	0.05	1.00
survey1 17m - survey3 5m	-0.15	0.01	311.95	-13.54	0.00
survey1 17m - survey4 5m	0.00	0.01	311.95	0.07	1.00
survey2 17m - survey3 17m	-0.02	0.01	235.35	-2.33	0.46
survey2 17m - survey4 17m	-0.01	0.01	235.35	-1.94	0.73
survey2 17m - survey1 5m	0.00	0.01	311.85	0.01	1.00

Table A9A. Wald Chi-square test of Generalized Linear Model Results assessing the drivers of mortality for bleached *A. hyacinthus*.

	Chi square	DF	p value
Max bite density	5.97	1	0.01
Depth	21.98	2	<0.001
Surface area (cm^2)	0.11	1	0.74
Max bite density x depth	2.25	2	0.32
Max bite density x surface area	0.11	1	0.73
Depth x surface area	1.63	2	0.44

Table A9B. Pairwise comparison of predicted means for the mortality of *Acropora hyacinthus* between depths.

Pairwise differences of Depth	Estimate	SE	DF	Z ratio	p value
10m - 17m	2.54	0.93	Inf	2.74	0.02
10m - 5m	-3.32	2.35	Inf	-1.42	0.33
17m - 5m	-5.86	2.41	Inf	-2.43	0.04

Table A10A. Anova table for the effect of corallivory on the growth (g/day) of *A. hyacinthus* prior to bleaching.

	Sum of Squares	DF	F value	P value
depth	0.18	2	5.46	0.008
residuals	0.71	44		

Table A10B. Pairwise comparison of the effect of corallivory on the growth (g/day) of A. hyacinthus between depth.

Contrast	estimate	SE	DF	T. ratio	P value
10m - 17m	-0.02	0.05	44	-0.47	0.88
10m - 5m	0.12	0.05	44	2.37	0.05
17m - 5m	0.14	0.05	44	3.20	0.01

Table A11. ANOVA table for the effect of corallivory on the growth (g/day) of *A. hyacinthus* after the bleaching event.

	Sum of Squares	DF	F value	P value
depth	0.04	2	1.61	0.22
residuals	0.28	24		