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Corallivory varies with water depth to influence the growth of *Acropora hyacinthus*, a reef-forming coral

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Abstract. A long-held paradigm is that water depth has a strong influence on coral performance mainly due to the rapid attenuation of light. Yet, many factors influence coral performance across reefscapes, including corallivory. How coral demographic performance changes with water depth and the intensity of corallivory has not been tested but is intriguing because fish abundance and community composition change substantially with water depth. We tested the independent and interactive effects of water depth and corallivory on the growth rates of a reef-building coral, *Acropora hyacinthus* common throughout the Indo-Pacific. Our study was conducted on the fore reef of Mo'orea, French Polynesia, where shallower coral populations have recovered more quickly than deeper populations after a major disturbance that culminated in 2010. Contrary to predictions of the light-attenuation paradigm, water depth (5 vs. 10 vs. 17 m) did not influence coral growth, regardless from what depth corals were collected. However, the effects of corallivory varied by depth as coral predators significantly reduced the growth rates of *A. hyacinthus* at 5 and 10 m depth, where the abundance of corallivores and rates of corallivory were greatest. There were no effects of predation on coral growth rates at 17 m, where the intensity of corallivory was lowest. Our results imply that corallivory is not a dominant factor establishing the distribution of *A. hyacinthus* corals across water depth. Instead, we found that partial predation may limit the potential for recovery of *A. hyacinthus* in relatively shallow water, where this coral is most abundant. As the frequency and intensity of disturbances impacting coral reef ecosystems increase with climate change and other anthropogenic factors, chronic predation on corals by corallivorous fish may play an increasingly important role in coral community recovery.

Key words: Acropora; *Acropora hyacinthus*; coral reef; corallivory; growth; Mo'orea; predation.

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INTRODUCTION

Coral reefs are dynamic ecosystems that have evolved and persisted through catastrophic disturbances, such as hurricanes (Knowlton et al. 1990, Gardner et al. 2005), predator outbreaks (Cox 1986, De'ath et al. 2012, Kayal et al. 2012), and increasingly frequent coral bleaching events

(Hoegh-Guldberg 1999, Eakin et al. 2010, Sully et al. 2019), all of which can cause the mass mortality of corals. When a coral community is disturbed and corals die, the speed and trajectory of recovery is influenced by a myriad of physical and biological factors (Connell 1978, Kayal et al. 2018, Steneck et al. 2019, Gouezo et al. 2020). Among physical factors, water depth appears to be important (Sheppard and Obura 2005, Adjeroud et al. 2018) because multiple abiotic factors change rapidly with depth (Spencer Davies 1989, Pratchett et al. 2015). For example, light availability, hydrodynamics, temperature, and sedimentation can vary substantially across depths (Dollar 1982, Rogers 1993, Leichter and Miller 1999, Lesser et al. 2009), and all profoundly influence coral performance (e.g., Jokiel and Coles 1977, Fabricius 2005, Lenihan et al. 2011, Nir et al. 2011). Deeper environments are usually less physically disturbed by waves and warm water events than shallower depths, yet can experience cold water intrusions from internal bores and upwelling (Wolanski and Delesalle 1995, Leichter and Miller 1999), slower tidal or wind-driven currents, and lower levels of light (Jackson and Hughes 1985, Madin and Connolly 2006). In turn, lower light levels, temperatures, and current velocities can reduce coral recruitment (Mundy and Babcock 1998, Turner et al. 2018), growth (Baird et al. 2003, Lenihan et al. 2015, Roberts et al. 2019), and survival (Chamberlain and Graus 1975, Lenihan et al. 2008, Hoogenboom and Connolly 2009), thus reducing the capacity of coral communities in deeper water to recover following disturbance (Edmunds 2018).

Biological processes also influence the speed at which coral communities recover from disturbance (Robinson et al. 2019). For example, a robust supply of coral recruits coupled with sufficient recruitment conditions following a disturbance event can hasten the speed at which coral communities recover (Holbrook et al. 2018). Predation by obligate and facultative corallivores can exert significant top-down pressure on coral populations and hinder or impede the reestablishment of corals on some reefs (Knowlton et al. 1990, Rotjan et al. 2006, Cole et al. 2008, Lenihan et al. 2011, Clements and Hay 2018). Indeed, large mortality events that alter coral species abundance, such as bleaching (Hughes et al. 2018), can influence patterns of predation by corallivores (Pratchett et al. 2006, Ikeuchi et al. 2017). Reduced coral cover can also intensify predation on remaining corals (Kayal et al. 2011, Burkepile 2012), possibly fueling a feedback that drives further declines and hinders the reestablishment of coral populations. Despite the potential importance of corallivory in affecting benthic dynamics on disturbed reefs, we know relatively little about how predation varies across depths or interacts with environmental drivers of coral growth to shape patterns in coral community recovery (but see Lenihan et al. 2015).

Like most predators, corallivores are often selective in their choice of prey (Rotjan and Lewis 2005, 2008, Cole et al. 2008, Jayewardene et al. 2009). Preference for particular prey species by predators can exert disproportionally strong top-down control on these prey populations. For example, corallivores on Indo-Pacific reefs often target corals from the genus *Acropora* (Kayal et al. 2011) reducing growth rates and potentially limiting their ability to recover after a disturbance (Lenihan et al. 2015). Corals in the genus *Acropora* comprise approximately 25% of all known coral species and are key provisioners of habitat on tropical coral reefs (Patton 1994, Wilson et al. 2008, 2019) but are declining in abundance globally (Pandolfi and Jackson 2006, Clark et al. 2017). Furthermore, coral predators often target juvenile or small corals preferentially across a reefscape (Penin et al. 2010, Lenihan et al. 2011), thus contributing to a bottleneck in recovery of otherwise highly productive coral habitats (Knowlton et al. 1990, Rotjan et al. 2006, Johnston and Miller 2014, Miller et al. 2014). Partial predation of coral colonies can also reduce colony growth rates, thereby impeding recovery (Edmunds and Lenihan 2010, Lenihan and Edmunds 2010). Consequently, predation by corallivores is probably in some cases an important mechanism mediating the ability for particular coral species to recover and reestablish after a disturbance, which in turn can influence coral community recovery through space and time.

In this study, we examined patterns in the recovery of the branching acroporid coral, *Acropora hyacinthus,* using photoquadrats taken during 2010–2018 across depths on the fore reef of Mo’orea. To investigate whether the distribution of coral predators across a depth gradient explained the abundance and size of *A. hyacinthus,* we conducted surveys to quantify the intensity of predation on *A. hyacinthus* colonies and the abundance of corallivorous fishes at 5, 10, and 17 m water depth. We then tested the hypothesis that corallivory reduces net growth rates of the branching acroporid coral, *Acropora hyacinthus*, and that the effect of corallivory varies with water depth. To test our hypothesis, we conducted a reciprocal transplant experiment using coral nubbins (i.e., fragments) placed in predator exclusion cages distributed across three depths (5, 10, and 17 m) on the fore reef of the north shore of Mo'orea, French Polynesia. The results of our study provide general insights into the patterns of coral recovery following the recent disturbances in Mo'orea and elsewhere in the Indo-Pacific.

METHODS

Study site

Our study was conducted from July to November of 2018 on Mo'orea, which is a high volcanic island in the central south Pacific 20 km west of Tahiti. There are three main coral reef habitats present around the island: (1) an offshore barrier reef (the fore reef) that surrounds the island, (2) a shallow lagoon (the back reef) that is landward of the reef crest, and (3) the fringing reef located at the shoreline next to the island. All surveys and experiments were conducted on the fore reef habitat of the north shore of Mo'orea at water depths of 5, 10, and 17 m.

The coral reefs surrounding the island of Mo'orea, French Polynesia, have undergone significant changes over the past several decades (Done et al. 1991, Adam et al. 2014). In 2006–2009, a massive outbreak of corallivorous crown-of-thorns (COTS) sea stars (*Acanthaster planci*) decimated coral populations around Mo'orea, reducing average coral cover on the fore reef from ~40% to <5% (Adam et al. 2011, Kayal et al. 2012). In February 2010, a large cyclone removed the majority of dead coral material remaining on the north and west shores of Mo'orea, leaving a fore reef with extremely low coral cover and structural complexity (Adam et al. 2014). However, coral cover on the fore reef has rapidly increased over the past decade, particularly on the north shore where some sites have surpassed pre-COTS levels of live coral cover (Holbrook et al. 2018). Despite similar amounts of coral recruitment at 10 and 17 m (Edmunds 2018), recovery on the fore reef of Mo'orea has been markedly stratified by depth, with corals recovering more slowly on deeper reefs than shallow reefs. Here, we tested the effect of corallivory across depths on the growth rate of a common species of coral to better understand the role of depth and coral predation in driving the rate and trajectory of coral community development on the fore reef.

Study species

Our surveys and field experiment focused on the branching scleractinian coral *Acropora hyacinthus*. *Acropora* spp. are the most speciose genera of coral in the Indo-Pacific and are key provisioners of physically complex reef habitat, yet are declining in abundance on tropical reefs worldwide (Done et al. 1991, Pandolfi and Jackson 2006, Clark et al. 2017). We chose *A. hyacinthus* because it is one of the most common acroporid species on the fore reef of Mo'orea and is prey for multiple corallivorous fishes (Cole et al. 2008). All fieldwork described below was conducted by SCUBA divers.

Long-term time series data

To quantify patterns in the abundance of *A. hyacinthus* across depths during recovery (2010–2018) after the COTS outbreak and Cyclone Oli, we analyzed permanent photoquadrats from the Mo'orea Coral Reef Long Term Ecological Research site (MCR-LTER). As part of their annual surveys, the MCR-LTER takes photographs of permanent quadrats (50 × 50 cm) along a single ~50 m permanent transect at 10 and 17 m on the fore reef at six study sites around the island (Edmunds 2019). At each MCR-LTER site, there is one transect at 10 and 17 m. Each transect contains ~40 permanent quadrats located along five sequential pieces of the transect. The number of photoquadrats per transect ranged from 37 to 40 photographs/yr because some years all quadrats were not photographed. The MCR-LTER photographic surveys are not conducted at 5 m depth. We analyzed images from the first year of recovery (2010) through 2018 at two MCR-LTER sites (i.e., LTER 1 and LTER 2), which are located nearest to our focal study site, specifically 2 km and 1 km away, respectively. To quantify coral density from the MCR-LTER photoquadrats, we analyzed each photograph and recorded the presence of all *A. hyacinthus* colonies.

Coral and fish surveys

In October 2018, we conducted surveys to estimate the abundance and size structure of *A. hyacinthus* at our study site (LTER Rapid) located near to sites LTER 1 and LTER 2 (Appendix S1: Fig. S1). Coral counts and size measurements were made on five replicate 25 × 0.5 m phototransects placed at 5, 10, and 17 m depth, all situated within a ~1 km-wide section of the fore reef. Phototransects were comprised of still images taken consecutively every 50 cm along the transect. Images from each phototransect were cropped to generate 50 × 50 cm non-overlapping images for photograph analysis (*n* = 48–52 images per transect). From these photographs, we quantified the density of *A. hyacinthus* colonies, which are easily distinguishable from congenerics and thus can be reliably identified photographically. A total of *n* = 5 photographic transects were sampled each of the three depths for our *A. hyacinthus* coral density analysis. We also analyzed the photographs in ImageJ to quantify the size of each *A. hyacinthus* colony (estimated as two-dimensional area in cm^2) and used these values to calculate mean colony size at each depth. Only corals that were completely within the photograph images were measured to provide accurate estimates of coral colony size.

Many corallivorous fishes leave distinctive scars on their coral prey (Rotjan and Lewis 2008, Bonaldo et al. 2011). To quantify the prevalence of coral predation on *A. hyacinthus* colonies, we conducted in situ surveys at LTER Rapid in October 2018 also at 5, 10, and 17 m, using non-overlapping 25 × 1 m transects. For in situ surveys, we included only those *A. hyacinthus* colonies for which ≥50% of their surface area fell within our transect. For each *A. hyacinthus* colony, we recorded the number of bite scars, counting only those that could unequivocally be attributed to a corallivore. Our estimates are conservative and probably underestimate the prevalence of corallivory in our model system.

In September 2018, we quantified the abundance of fish species that are known obligate and facultative corallivores (sensu Cole et al. 2008, Rotjan and Lewis 2008, Lenihan et al. 2015) on six 5 × 25 m belt transects (complete list of species included provided in Appendix S1: Table S1) at 5, 10, and 17 m depth at our study site LTER Rapid. To quantify corallivore communities along each transect, a diver slowly swam the length of the transect recorded the number of known obligate and facultative corallivorous fish within the 125 m^2 swath. Similar to those for coral counts, the transects were oriented parallel to the reef crest along the same depth contour.

Field experiment

In August to November 2018, we conducted a reciprocal transplant experiment to test whether corallivory and depth interact to influence coral growth on the fore reef of Mo'orea. The experiment was initiated on 8 August at 5, 10, and 17 m, at the LTER Rapid site on the fore reef of Mo'orea (Appendix S1: Fig. S1). In August 2018, we tagged eight colonies of *A. hyacinthus* at each depth (*n* = 8 colonies per depth; 24 colonies total). Fourteen branches, each approximately 10 cm in length, were collected from each colony, placed into a labeled bag, and transported in a cooler filled with fresh seawater to onshore water tables. Onshore, each coral nubbin was epoxied into the base of a 50-mL Falcon tube that was severed 2 cm below the threads using ZSPAR. Each nubbin was individually labeled, photographed, and buoyant weighed following Spencer Davies (1989). Experimental nubbins were returned to the reef within 24 h and secured to large acclimation tables anchored to the reef at 10 m depth. Corals remained on acclimation tables for 14 d, where they were protected from coral predators via cages, and were visually assessed every 2–3 d to observe signs of stress (e.g., paling or bleaching).

After 14 d of acclimation, corals were randomly assigned to one of three predator exclusion cage treatments: (1) without predation (full predator exclusion; controls), (2) with predation (no exclusion; exposed), or (3) with predation controlling for exclusion effects (partial exclusion). Full exclusions were constructed of PVC-coated mesh cage (hole size 2.54 × 2.54 cm) 15 × 7.5 × 15 cm (length × width × height). Partial exclusions were of the same design but were missing two sides, thus exposing corals to corallivores but creating the anticipated cage artifacts, including some shading and baffling of flow. Exposed corals had no protection from corallivory. One coral nubbin per treatment was placed on a single, stainless steel mesh table, 15 × 15 cm in size.

We deployed 24 experimental tables at each depth thus establishing eight replicates of each individual origin depth (5, 10, and 17 m) by caging (control, exposed, partial exclusion) treatment, for a total of 216 *A. hyacinthus* nubbins in the experiment. Nubbins were sampled from the experiment on 4 November from 10 m water depth and on 5 November from 5 and 17 m depth. All coral nubbins were transported to shore where they were re-weighed for a final buoyant weight. We calculated the growth rate (mg/d) for each coral by subtracting the initial coral weight from the final coral weight, and then dividing by the number of days elapsed under experimental treatment. To remove any potentially confounding effects of initial coral size on growth rates, we also calculated the percent change in mass over the course of the experiment via the formula: $\Delta w_i = ((w_{i(\text{final})} - w_{i(\text{initial})})/w_{i(\text{initial})}) \times 100\%$, where $w_{i(\text{initial})}$ is the weight of coral i at the beginning of the experiment and $A_{i(\text{final})}$ is the weight of coral I at the end of the experiment.

Statistical analyses: field surveys

We tested for differences in the density of *A. hyacinthus* between depths (10 vs. 17 m) from the MCR-LTER photoquadrats with a Mann-Whitney U-test. For these tests, we considered each quadrat a replicate and pooled replicates from surveys at LTER 1 and LTER 2 at each depth for each year. We conducted an individual Mann-Whitney U-test for each year from 2010 to 2018 to compare the density of *A. hyacinthus* colonies at 10 vs. 17 m.

We assessed differences in the size of *Acropora hyacinthus* colonies and coral density (number of colonies m^{-2}) across water depths (5, 10, and 17 m) from our phototransects at LTER Rapid using mixed-model ANOVAs with depth as a fixed effect and transect as a random effect. For colony size ANOVAs, we calculated the mean colony size per transect and used transect as a replicate (n = 5 per depth). To test for differences in bite density (bites cm^{-2}), we used a linear mixed-effects model that considered depth a fixed effect and transect a random effect. When significant interactions or effects were detected in the main model, we tested for differences among the three depths using post hoc tests with Tukey's corrections using the emmeans package (Lenth 2018). Coral colony size data were square-root transformed, and bite density data were log-transformed to meet ANOVA assumptions. To test for a relationship between colony size and the density of bites for colonies with at least one bite, we used multiple linear regression with depth and log-transformed estimate of the coral colony surface area as fixed interacting factors.

To test for differences in the abundance of corallivorous fishes among depths at LTER Rapid, we used a one-factor ANOVA with depth as a fixed effect. Corallivorous fish densities were log-transformed to meet ANOVA assumptions.

Statistical analyses: field experiment

We tested for differences in the growth rates (mg/d) and percent change in mass in our experiment with a mixed-effects ANOVA model that considered origin depth, experimental depth, and treatment as interacting, fixed effects. These models included parent colony as a random effect to account for inherent differences in colony growth rates. When significant interactions or effects were detected in the main model, we tested for differences among the treatment-depth combinations using post hoc tests with Tukey's corrections using the *multcomp* package (Hothorn et al. 2008).

All data were checked for normality and homogeneity of variance via visual inspection of residuals, and all analyses were conducted in R version 4.0.0 (R Core Team 2020). Mixed-effects ANOVAs were conducted using the nlme package (Pinheiro et al. 2015), and p values from each model were calculated using Wald F-tests via the Kenward-Roger coefficient covariance matrix and Satterthwaite approximate degrees of freedom using the car package (Fox and Weisberg 2011).

RESULTS

Coral abundance 2010–2018

We recorded no *A. hyacinthus* colonies in photoquadrats from 10 and 17 m in 2010. The density of *A. hyacinthus* at the two MCR-LTER sites (LTER 1 and LTER 2) on the north shore of Mo'orea did not differ between depths from the start of recovery (i.e., 2010) through 2013. However, in the years 2014 and 2015 the density of *A. hyacinthus* colonies was higher at 10 m than 17 m depth (Mann-Whitney U-test; $P < 0.05$), suggesting density increased more slowly at 17 m than 10 m (Fig. 1). In 2014, *A. hyacinthus* density at 10 m was 7.3 ± 2.3 (mean ± 1 SE) colonies per 10 m^{-2}, more than three times higher than at 17 m (2.1 ± 0.7). However, by 2018 the density of *A. hyacinthus* colonies was similar between depths (10 m, 10.6 ± 2.4; 17 m, 8.5 ± 2.3).

Coral colony distribution and size surveys

Results from coral abundance surveys found that *A. hyacinthus* density decreased with depth (depth effect: $\chi^2(2) = 13.51$, $P = 0.001$; Fig. 2). Colonies of *A. hyacinthus* were 2.6 times more abundant at 5 m, and 1.5 times more abundant at 10 m, than at 17 m. We also found a significant effect of depth ($\chi^2(2) = 45.79$, $P < 0.001$; Fig. 2) on the size of coral colonies (two-dimensional surface area; cm^2). The mean size of *A. hyacinthus* varied more than threefold across depths (Tukey test, $P < 0.05$ for all depth contrasts). On average, *A. hyacinthus* colonies were largest in size at 5 m depth (318 ± 37 cm^2; mean ± SE) and smallest at 17 m (80 ± 35 cm^2).

In situ corallivory and corallivore surveys

Bite marks on *A. hyacinthus* colonies indicate injuries caused by corallivores generally declined with water depth. The density of bite marks was significantly lower at 17 m depth than at 5 and 10 m ($\chi^2(2) = 20.66$, $P < 0.001$; Fig. 3). More specifically, the scars were 7.5 times more abundant at 10 m than 17 m, and ~4 times more abundant at 5 m than 17 m. Although bite marks on *A. hyacinthus* colonies were twice as common at 10 m than 5 m, this difference was not statistically significant due to high variation among replicate transects ($P = 0.1$). Similarly, the abundance of corallivorous fishes was nearly two times higher at 10 m depth compared with 5 and 17 m (depth effect: ($\chi^2(2) = 35.13$, $P < 0.001$; Fig. 3)). There were 7.7 ± 0.4 corallivores per 100 m^{-2} at 5 m depth, 13.1 ± 0.7 corallivores per 100 m^{-2} at 10 m depth, and 7.9 ± 0.3 corallivores per 100 m^{-2} at 17 m depth.

We detected a negative relationship between the density of bites on a colony and colony surface area that varied with depth (depth × surface area effect: $F_{(2,68)} = 4.38$; $P = 0.016$; Fig. 4). Post hoc tests revealed that the slope of the line was

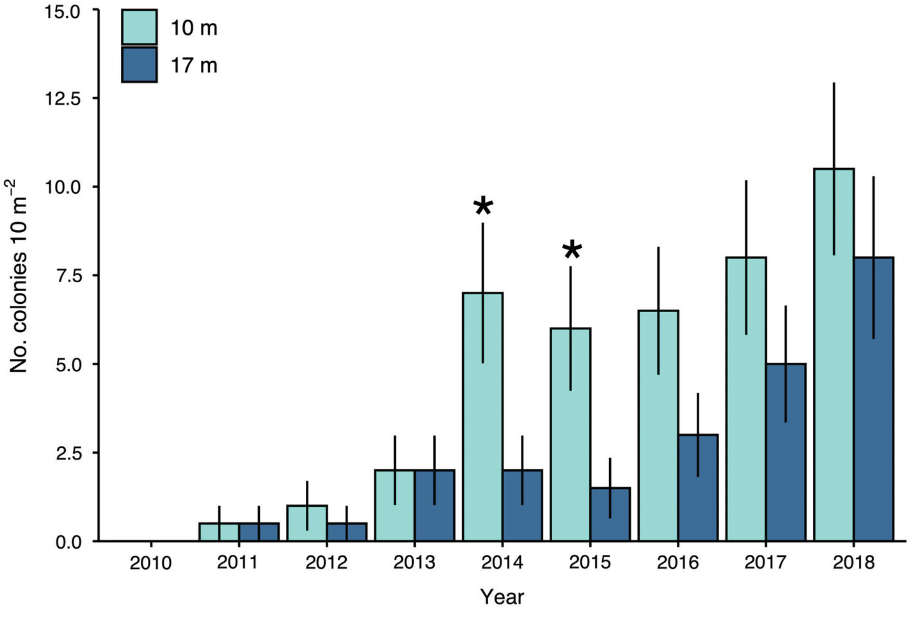

Fig. 1. Density of *Acropora hyacinthus* colonies from 2010 to 2018 from MCR-LTER permanent photoquadrats at 10 and 17 m depth. Data are means ± standard errors (SE). Asterisk indicates that *A. hyacinthus* colony density significantly differed between depths for that year per Mann-Whitney U-test.

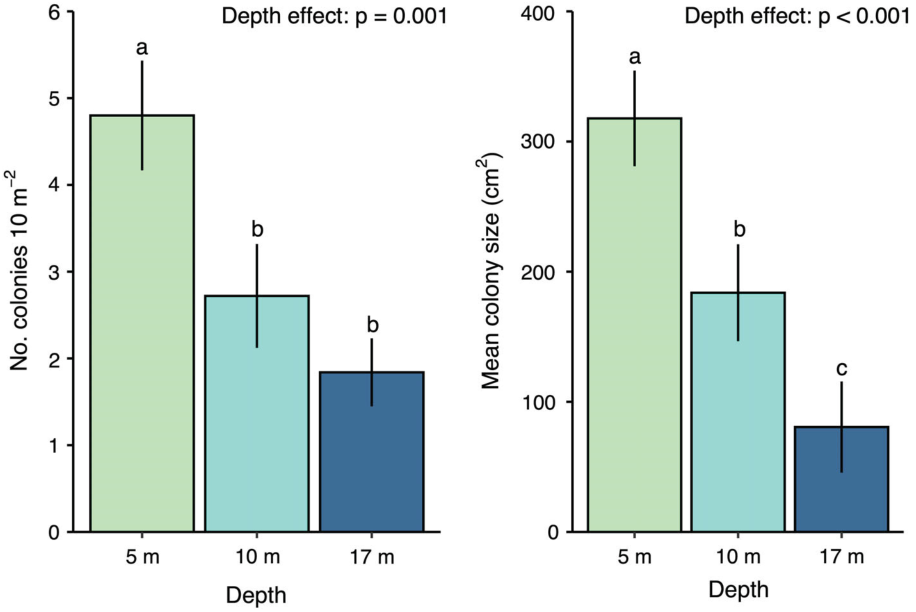

Fig. 2. Density (left) and size (right) of *A. hyacinthus* colonies at 5, 10, and 17 m water depth from surveys conducted in October 2018. Data are means ± SE. Statistics are from linear mixed-effects model. Different letters above bars denote statistically significant differences ($P < 0.05$) in colony density or size per post hoc tests.

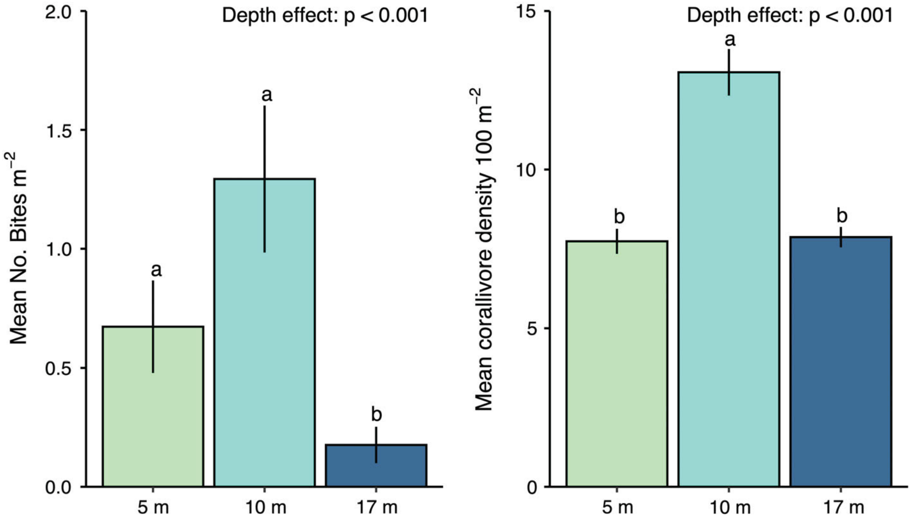

Fig. 3. (Left) Mean number of bites m^{-2} from corallivorous fishes on *A. hyacinthus* colonies at each depth. (Right) Mean density of all corallivorous fishes at each depth. Data are means ± SE. Statistics are from linear mixed-effects model. Different letters above bars denote statistically significantly differences ($P < 0.05$) in number of bites or corallivore density per post hoc tests.

less negative at 10 m than 5 m, indicating that the density of bite scars remained higher for larger colonies at 10 m than 5 m (Tukey test, $P < 0.05$), but not 17 m (Tukey test, $P > 0.05$).

Field experiment

Growth rates of individual *A. hyacinthus* nubbins ranged from −61 to 73 mg/d and on average grew at a rate of 17.0 ± 1 mg/d (mean ± SE)

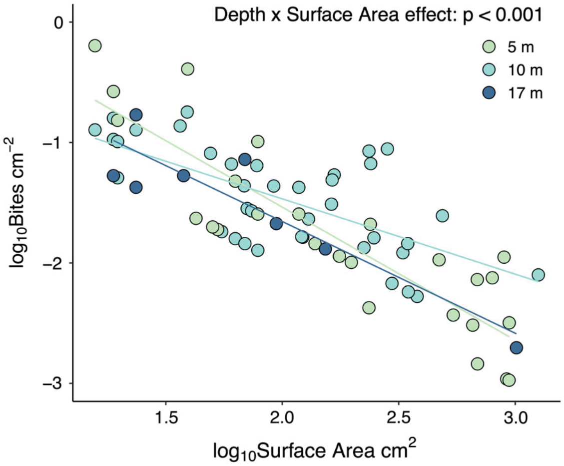

Fig. 4. Log_{10} corallivore bite density (bites/cm^2 of planar coral surface area) regressed against the $\log_{10}$ surface area of each coral colony for *A. hyacinthus* colonies at 5, 10, and 17 m depth. Figure and analyses only included colonies with at least one corallivory scar. Statistics from multiple linear regression.

across experimental depths and treatments. We detected a significant treatment × experimental depth effect ($\chi^2(4) = 9.67$, $P = 0.046$) but no effect of origin depth ($\chi^2(2) = 1.42$, $P = 0.49$) on *A. hyacinthus* growth rates. Corals exposed to predators grew slower than corals protected from predation at 5 and 10 m depth, but there was no effect of predation on coral growth at 17 m. For corals deployed to 5 m depth, exposed corals grew significantly less than 5 m control corals but did not differ from partial exclusion corals at 5 m depth (Tukey test, $P < 0.05$). Similarly, at 10 m exposed corals grew significantly slower than controls at both 5 and 10 m (Tukey test, $P < 0.05$; Appendix 1: Fig. S2). At 17 m depth, there were no differences between any of the three treatments (Tukey test, $P > 0.05$). In addition to growth rates (mg/d), we also calculated growth as percent change in mass during the course of the experiment to account for the initial size of each coral (Fig. 5). Patterns in percent change in mass were similar to growth rates, indicating

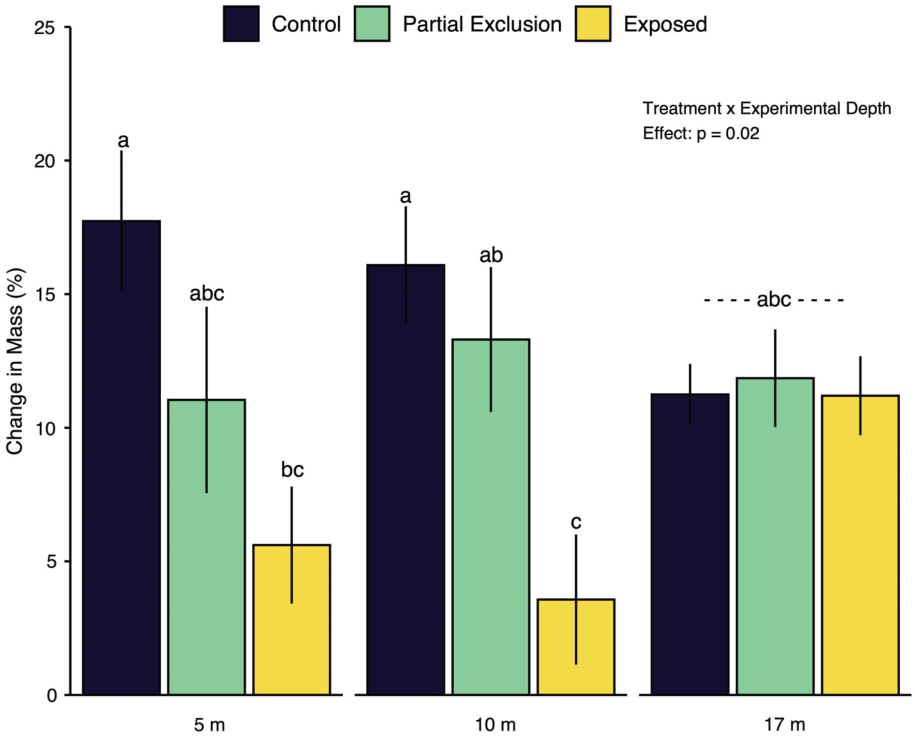

Fig. 5. Mean percent change in mass of experimental *A. hyacinthus* corals after twelve weeks at each experimental depth and treatments. Data are means ± SE. Statistics are from linear mixed-effects model. Different letters above bars denote statistically significantly differences ($P < 0.05$) between growth rates or percent change in mass per post hoc tests.

that predation reduced growth at 5 and 10 m, but had no effect at 17 m. Using percent change in mass as a measure of growth, we also found a significant treatment × experimental depth effect ($\chi^2(6) = 11.52$, $P = 0.02$). At both 5 and 10 m depth, exposed corals increased in mass at a slower rate than control corals deployed to those depths (Tukey test, $P < 0.05$).

DISCUSSION

Partial predation of coral colonies by corallivorous fish substantially reduced the net growth rate of *A. hyacinthus* nubbins in the experiment at 5 and 10 m depths, but had no significant effect on growth at 17 m. In fact, there was no physical evidence of predation for any nubbin situated at 17 m depth. Observations from our predation-injury surveys indicated that the incidence of corallivory by fish on natural populations of *A. hyacinthus* colonies was ~4 and 7.5 times higher at 5 and 10 m, respectively, than 17 m. These patterns were supported by our fish surveys in which we found twice as many corallivorous fishes on the fore reef at 10 m than at 5 and 17 m. In addition, we found no quantitative or qualitative evidence suggesting that butterflyfish or other tissue-eating corallivores were causing cryptic injuries to exposed corals at depth. Similar results were reported by both Harmelin-Vivien and Bouchon-Navaro (1983) and Berumen and Pratchett (2006), who found that the density of butterflyfish (Family Chaetodontidae) was highest at 10 m on the forereef of Mo’orea compared with all other depths. Together, our results imply that predation by corallivorous fishes did not limit the recovery of *A. hyacinthus* in deeper water on the forereef of Mo’orea following recent major natural disturbances.

We cannot dismiss outright the possibility that corallivores helped to drive the patterns of recovery observed in Mo’orea. Corallivory may have dampened the relatively high rate of recovery of species like *A. hyacinthus* at shallow depths, such that recovery would have been faster overall for this species of coral had not corallivores reduced growth rates (Fig. 5 and Appendix S1: Fig. S2). Chronic, low levels of corallivory, especially predation targeting new recruits and small colonies, can help establish general patterns of acroporid abundance and distribution (Lenihan et al. 2011, 2015) and influence their recovery after disturbance (Knowlton et al. 1990, Rotjan et al. 2006). Here, we provide further evidence that partial predation by fish may influence patterns of recovery from disturbance by decreasing growth rates of the most productive coral populations.

The most important predators in our study system other than corallivorous fish were COTS (*Acanthaster planci*), the cushion star *Culcita novaeguineae*, and two muricid snails, *Coralliophila violacea* and *Drupella cornus* (Kayal et al. 2011, 2012, Hamman 2018). We observed very few corallivorous sea stars on the forereef at any depth during our study, and both species of snail prefer to prey upon other coral taxa (poritids and pocilloporids), are usually found in relatively very low numbers on the fore reef in Mo’orea (Hamman 2018), and were never observed preying on *A. hyacinthus*. In summary, we found little evidence that corallivory limits coral recovery at 17 m, and surmise that abiotic factors, such as light availability, are generally more important in limiting coral growth than biotic factors in relatively deep water (>10 m depth).

Rotjan et al. (2006) revealed that injuries caused by corallivores can reduce the density of zooxanthellae symbionts, thus decreasing coral growth rates and a coral’s capacity to recover (see also Ezzat et al. 2020). Others have hypothesized that the energy used to heal wounds from partial predation reduces the energy needed to maintain high growth rates (Edmunds and Lenihan 2010, Lenihan and Edmunds 2010). This body of evidence suggests that without chronic corallivory the recovery *A. hyacinthus* at 5 and 10 m water depths would have been more rapid and we would now see a greater abundance of this important habitat-providing coral on the fore reef. Branching coral species such as *Acropora* are important provisioners of habitat on Indo-Pacific reefs (Patton 1994, Wilson et al. 2008, 2019), yet are declining across the Pacific including in the lagoon and fore reef habitats of Mo’orea (Done et al. 1991, Clark et al. 2017). Along with bleaching events and disease outbreaks, corallivory may play an important role in the decline of acroporid populations on Mo’orea and elsewhere in the Indo-Pacific, especially if corallivore populations increase with declines in large predatory fish due to intensive fishing (Clements and Hay 2018).

We suggest that the most important mechanism by which chronic partial predation dampened recovery in shallow depths was reducing net growth rates of otherwise relatively fast-growing *A. hyacinthus*. Corals grew at substantially lower rates when preyed on by fish at 5 and 10 m in our experiment. Furthermore, our findings support the hypothesis that intensified predation on smaller corals may be the most important mechanism mediating the per capita growth and thus population recovery of *Acropora* corals (Bonaldo et al. 2011). Several lines of evidence support this hypothesis. First, the coral nubbins in the experiment, which were intensively attacked, mimicked small colonies of corals that could be reasonably considered juvenile corals that were about 1.5–2.5 yr old (e.g., Holbrook et al. 2018). Second, the mean number of predation scars on *A. hyacinthus* colonies recorded in our surveys varied with depth and qualitatively mirrored patterns in the abundance of corallivores (10 > 5 > 17 m). Penin et al. (2010) also found that mortality of recruits attributed to corallivory occurred at higher rates at 12 m depth than at 6 and 18 m depths. However, when we standardized the number of predation scars for the total surface area available to corallivores, there was no difference among depths. Yet, bites were not evenly distributed: Smaller corals had a higher bite density across depths compared with larger corals. Similar to this study, Lenihan et al. (2011) and Jayewardene et al. (2009) found that smaller corals were more likely to be preyed on than larger colonies on reefs in Mo’orea and Hawaii, respectively. Work in the Caribbean has shown the opposite pattern, whereby larger colonies were more likely to be impacted by corallivory (Meesters et al. 1997, Curaçao; Burkepile 2012, Florida Keys, USA). Prior work in Mo’orea indicates that corallivory has an important influence on patterns of early post-recruitment mortality, especially on corals <3 months old (Lenihan et al. 2011). However, data from MCR-LTER annual recruitment surveys indicate that recruitment did not vary as a function of depth during the period 2008–2017 (Edmunds 2018).

Perhaps new recruits at 17 m are especially vulnerable to even low levels of chronic corallivory. While we did not observe any instances of predation on our experimental corals at 17 m, those uninjured corals grew 30–36% slower than uninjured corals at 5 and 10 m. Although these differences were not statistically significant, even modest differences in growth among depths might be compounded by predation and provide an important mechanism hindering the ability of corals at depth to increase colony size compared with recruits at shallower depths, especially if they are also light limited. Without intensive predation at 5 m, and especially 10 m, the recovery of *A. hyacinthus* and other branching acroporids probably would have been much more rapid. In addition, faster growth rates at shallower depths may compensate for losses caused by chronic corallivory, contributing to the mismatch between higher coral predation and *A. hyacinthus* density and colony size that we observed in this study. As the frequency and intensity of disturbances impacting coral reef ecosystems continues to increase, chronic predation on corals by corallivorous fish may play an increasingly important role in coral community recovery.

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