Received: 3 June 2024 | Revised: 30 August 2024 | Accepted: 24 September 2024

DOI: 10.1002/ecy.4510

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Early life stage bottleneck determines rates of coral recovery following severe disturbance

Kelly E. Speare[1,2] | **Lauren N. Enright**[1] | **Allison Aplin**[3] | **Thomas C. Adam**[3] | **Peter J. Edmunds**[4] | **Deron E. Burkepile**[1,3]

[1]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, California, USA

[2]School of Geographical Sciences and Urban Planning, Arizona State University, Tempe, Arizona, USA

[3]Marine Science Institute, University of California, Santa Barbara, Santa Barbara, California, USA

[4]Department of Biology, California State University, Northridge, California, USA

Correspondence
Kelly E. Speare
Email: kellyspeare@gmail.com

Funding information
National Science Foundation, Grant/Award Numbers: NSF-OCE 16-37396, NSF-OCE-1547952; Gordon and Betty Moore Foundation; Schmidt Family Foundation; NSF GRFP

Handling Editor: Daniel S. Gruner

Abstract

Understanding how foundation species recover from disturbances is key for predicting the future of ecosystems in the Anthropocene. Coral reefs are dynamic ecosystems that can undergo rapid declines in coral abundance following disturbances. Understanding why some reefs recover quickly from these disturbances whereas others recover slowly (or not at all) gives insight into the drivers of community resilience. From 2006 to 2010 coral reefs on the fore reef of Moorea, French Polynesia, experienced severe disturbances that reduced coral cover from ~46% in 2005 to <1% in 2010. Following these disturbances, coral cover increased from 2010 to 2018. Although there was a rapid and widespread recovery of corals, reefs at 17 m depth recovered more slowly than reefs at 10 m depth. We investigated the drivers of different rates of coral recovery between depths from 2010 to 2018 using a combination of time-series data on coral recruitment, density, growth, and mortality in addition to field experiments testing for the effects of predation. Propagule abundance did not influence recovery, as the density of coral recruits (spat <6 months old) did not differ between depths. However, mortality of juvenile corals (≤5 cm diameter) was higher at 17 m, leading to densities of juvenile corals 3.5 times higher at 10 m than at 17 m depth. Yet, there were no differences in the growth of corals between depths. These results point to an early life stage bottleneck after settlement, resulting in greater mortality at 17 m than at 10 m as the likely driver of differential coral recovery between depths. We used experiments and time-series data to test mechanisms that could drive different rates of juvenile coral mortality across depths, including differences in predation, competition, and the availability of suitable substratum. The results of these experiments suggested that increased coral mortality at 17 m may have been influenced by higher intensity of fish predation, and higher mortality of corals attached to unfavorable substratum. In contrast, the abundance of macroalgae, a coral competitor, did not explain differences in coral survival. Our work suggests that top-down processes and substratum quality can create bottlenecks in corals that can drive rates of coral recovery after disturbance.

KEYWORDS
coral recruitment, coral reefs, corallivory, demographic processes, herbivory, post-settlement effects, predation, resilience

INTRODUCTION

Foundation species are often disproportionately susceptible to disturbance (Dayton et al., 1992; Ellison et al., 2005), and disturbances that kill foundation species are increasing in frequency and intensity with global climate change (Anderegg et al., 2013; Hughes et al., 2017). Understanding why some communities of foundation species recover quickly, whereas others recover slowly or not at all is key to understanding drivers of resilience (Robinson et al., 2019). Two key components of recovery are the growth of individuals that survive a disturbance and the establishment of new individuals post-disturbance (i.e., recruitment, sensu Keough & Downes, 1982). However, the rates of these demographic processes can be constrained by abiotic (temperature, light, and water) and biotic (predation and competition) forces (Robinson et al., 2019), making it difficult to predict the relative importance of different demographic processes in influencing the rate of recovery of foundation species.

Top-down processes (herbivory and predation, sensu Hairston et al., 1960) govern the dynamics of foundation species in many ecosystems, and top-down processes can act to either accelerate or slow community recovery after disturbance (Adam et al., 2022; Aquilino & Stachowicz, 2012; Watanabe & Harrold, 1991). For example, in rocky intertidal communities, herbivory can increase rates of recovery of algae by controlling the abundance of early successional species that preempt space (Aquilino & Stachowicz, 2012). In contrast, ungulate herbivores can slow forest recovery by browsing on juvenile trees that recruit after disturbances (Andrus et al., 2020). Differences in abiotic factors such as temperature, precipitation, and light across environmental gradients can also strongly shape the recovery of foundation species. For example, tree seedlings are often more successful in low-elevation tree-fall gaps than in high-elevation gaps because warmer temperatures facilitate seedling growth (Benavides et al., 2016). However, it is also common for abiotic conditions and herbivory to interactively shape tree recruitment dynamics (Unkule et al., 2022), resulting in spatially heterogenous patterns of recovery. Environmental gradients or differences in biotic interactions may act on different life stages or processes as foundation organisms recover from disturbance.

In some communities, the supply of new individuals (i.e., seedlings, larvae, and propagules) and their ability to become established after disturbance govern rates of recovery. In kelp forests, for example, high rates of propagule supply, driven by connectivity with other populations, promote the recovery of kelp following disturbance (Castorani et al., 2015). Yet, once individuals recruit to a population, post-recruitment processes can dictate the success of newly established recruits and limit recovery (Edmunds et al., 2024). Population bottlenecks (sensu Caddy, 1986) that limit recolonization after disturbance can slow or prevent population recovery (Castorani et al., 2015; Holbrook et al., 2018; Wijdeven & Kuzee, 2000). For example, intense top-down pressure by grazing sea urchins can slow or prevent kelp forest recovery by consuming newly established kelp recruits (Filbee-Dexter & Scheibling, 2014; Watanabe & Harrold, 1991). Differences in abiotic conditions across environmental gradients (e.g., depth, elevation, and rainfall) or time can also dictate the success of newly established recruits. In aspen forests, for example, intense browsing by elk can interact with harsh climactic conditions to kill entire cohorts of aspen recruits, creating a bottleneck that can inhibit forest recovery for decades (Romme et al., 1995). The population bottlenecks that occur in many taxa at or soon after recruitment can strongly influence population dynamics (Caddy, 1986; Edmunds, 2021; Romme et al., 1995). Understanding the relative importance of the supply of new individuals, the mortality of new individuals, and the growth rates of these individuals, as well as how biotic and abiotic factors shape these processes, is key to understanding how communities recover following a major disturbance.

Here, we examine how biotic and abiotic forces impact the demographic rates and recovery of corals after a major coral-killing disturbance in Moorea, French Polynesia. The fore reef habitat around Moorea experienced an outbreak of the corallivorous crown-of-thorns sea star, *Acanthaster planci* (COTS), from 2006 to 2009 (Kayal et al., 2012), followed by a Category 4 cyclone in 2010. These disturbances resulted in a large decline in the percent cover of live coral from ~46% in 2005 to

<1% in 2010 (mean of 10 and 17 m at the Long-Term Ecological Research [LTER] sites 1 and 2; Adam et al., 2011) (Figure 1). However, from 2010 to 2018, there was widespread recovery of stony coral populations on the fore reef, but with a high degree of heterogeneity in the rate of coral community recovery between sites and depths. We refer to "recovery" as return to a similar abundance (i.e., percentage coverage) of foundation species (stony corals), which may or may not have the same relative abundance of individual taxa as the community prior to disturbance. However, analyses of the coral community on the fore reef revealed that by 2018, community composition was very similar to that of the pre-disturbance (i.e., 2005) communities (Holbrook et al., 2018). The north shore had the fastest rate of recovery, followed by the west and east shores. The variation in the rate of coral recovery among sites around the island was driven by differences in the density of small corals (colonies <3 cm diameter) that recruited after the disturbances (Holbrook et al., 2018).

On the north shore, there were also strong differences in the rate of coral recovery between depths, where shallow reefs recovered faster than deep reefs (reefs at 10 and 17 m water depth, respectively; Figure 1). Here, we investigate the drivers of variation in coral recovery between depths on the fore reef of Moorea from 2010 to 2018 using a combination of time-series data and field experiments. First, to ask whether the supply of coral larvae (i.e., propagules) differed between depths we used time-series data from coral recruitment tiles deployed at 10 and 17 m as a proxy for larval supply. Second, we asked whether the density and mortality of juvenile corals (colonies 0.5–5.0 cm in diameter) differed between depths by using a time series of photoquadrats of the benthos sampled annually at 10 and 17 m depth. Third, we asked whether the growth of juvenile corals differed between depths using the same photoquadrats in which we measured the change in diameter of corals between consecutive years. Fourth, we used time-series photographs to evaluate whether competition with macroalgae influenced differences in coral recovery between depths. Lastly, given that our results showed that the survivorship and density of small corals strongly influenced coral community recovery, we conducted an experiment that manipulated top-down effects (herbivory and predation) on coral recruitment

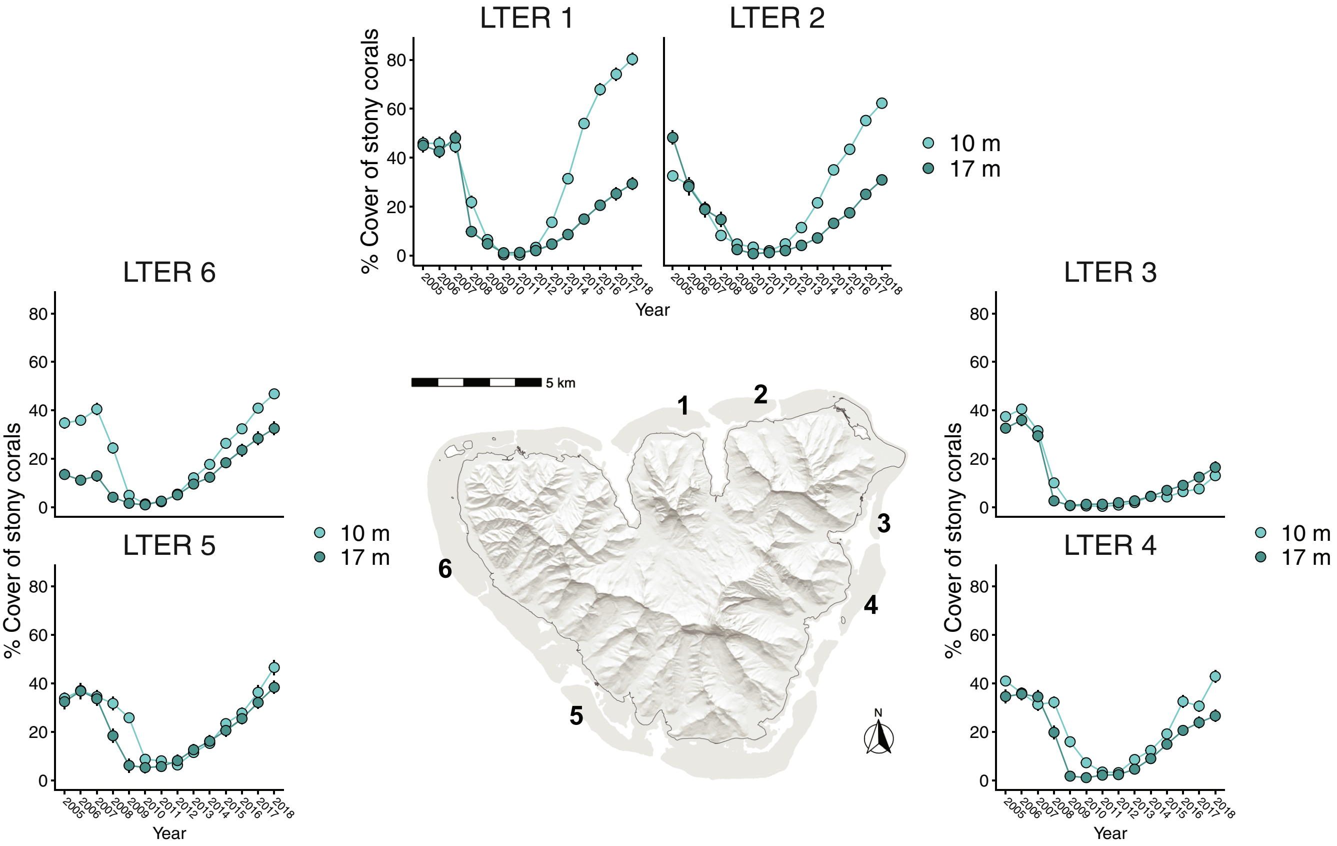

FIGURE 1 Patterns of coral population decline and recovery at the six Moorea Coral Reef (MCR) Long-Term Ecological Research (LTER) sites on the fore reef at 10 and 17 m between 2005 and 2018. Points are the percent cover (mean ± SE) of stony corals for each depth. Island hillshade layer was generated from Gruen et al. (2017).

to test whether consumer-driven mortality was higher at 17 m.

METHODS

Moorea, French Polynesia (17°30′ S, 149°50′ W), is a high volcanic island with a fore reef surrounding a wide shallow lagoon. Reefs around Moorea have been monitored extensively since the 1970s, initially by Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) and then by both CRIOBE and the Moorea Coral Reef Long-Term Ecological Research (MCR LTER) time-series program since 2005. The MCR LTER collects data annually on benthic communities at six sites on the fore reef (Figure 1). Fieldwork was conducted from the University of California Richard B. Gump South Pacific Research Station on Moorea.

Patterns of coral decline and recovery

At each of the MCR LTER sites, one permanently marked 50-m transect was established at 10 and 17 m depth, to collect data on the benthic communities. Each transect is photographed annually at 40 fixed locations using a digital camera in an underwater housing attached to a rigid framer normal to a 50 × 50 cm quadrat, to which a centimeter scale was attached (Moorea Coral Reef LTER & Edmunds, 2020). Photoquadrats are analyzed to quantify the percent cover of benthic organisms using 200 random point IDs using either the CPCe software (through 2014) (Kohler & Gill, 2006) or the CoralNet web-based application (2015–2018) (Beijbom et al., 2015). Stony corals are identified to genus and annotations were done in manual mode. To assess changes in the abundance of stony corals throughout time, we calculated the average percent cover of stony corals (scleractinians and *Millepora*) at each site-depth combination for each year from 2005 to 2018. We also calculated the relative abundance of the three most abundant coral genera, *Pocillopora, Acropora*, and *Porites*, for each year.

Our aim was to evaluate demographic mechanisms (i.e., recruitment, mortality, and growth) driving differences in coral recovery between reefs at 10 and 17 m depth. Of the six MCR LTER sites, the LTER 1 and LTER 2 sites exhibited the greatest difference in coral recovery between the two depths (Figure 1), so we focused our study at these sites. Additionally, throughout the recovery period *Pocillopora* corals were the most abundant genus at both depths and accounted for 76.1% and 66.2% at 10 and 17 m, respectively, of all stony corals by 2018 (Appendix S1: Figure S1B). Thus, we focused only on *Pocillopora* for data on coral recruitment, density, mortality, and growth.

Coral recruitment as a proxy for the supply of coral larvae

Coral larvae, the motile propagules of corals, are challenging to directly quantify in situ because the larvae are microscopic in size. A reliable proxy for the supply of larvae to a reef is the abundance of newly established coral recruits (i.e., coral spat, individuals ≤5 mm diameter) on recruitment tiles, which is as a time-integrated estimate of the availability of larvae. Coral recruitment was quantified on terracotta tiles twice per year at 10 and 17 m at LTER 1 and LTER 2 (Edmunds, 2018; Moorea Coral Reef LTER & Edmunds, 2018). Tiles were deployed during fixed time periods (6 months on average) from late August/early September to late January/early February, and again from late January/early February to late August/early September each year. Dates of deployment and retrieval varied slightly (within 2 weeks) among years but not depths within years. Tiles were collected and replaced during the same dive, and therefore, tiles were deployed continuously throughout the year. The majority of recruits are found on the undersides of these tiles, a cryptic space between the tile and benthos that is inaccessible to fishes. Thus, recruit densities on these tiles reflect the supply of larvae in the absence of top-down processes. At the start of each immersion period, 15 or 16 unglazed terracotta tiles (15 × 15 × 1 cm) were deployed at each site-depth combination. Tiles were secured to the benthos horizontally with the grooved side of the tiles facing down using threaded stainless steel posts and nuts. Tiles were preconditioned in the lagoon for several months prior to each deployment. At the end of each immersion period, tiles were collected and replaced with a new set of preconditioned tiles. Tiles were brought to the laboratory where they were soaked in bleach, dried at 60°C, and scored for coral recruits using microscopy (~40× magnification). Coral recruits were identified to family. Because coral recovery was driven primarily by the increase in the abundance of *Pocillopora* following the disturbances, we only analyzed data on the recruitment of pocilloporids.

For each tile, we summed the mean number of Pocilloporidae recruits per tile recorded during the two sampling periods to calculate the total number of pocilloporid recruits per tile per year. Then, we asked whether the recruitment of pocilloporid corals differed between depths using a generalized linear mixed-effects model (glmm) with a negative binomial error and a log link function. The model included fixed effects of depth, year, and the depth × year interaction, and a random effect of site. We treated "site" as a random effect despite having only two levels, because we were not interested in making inferences about the effect of "site." Although there is disagreement about including random effects with <5 levels, data simulations have shown that the estimates of fixed effects are not biased when there are <5 levels of a random effect, except when sample sizes are small ($N \leq 30$) (Gelman & Hill, 2007; Gomes, 2022), which was not the case for our study. Throughout our analyses, glmm models were fit using glmmTMB (Brooks et al., 2017) and model residual diagnostics were evaluated using the DHARMa package to ensure that there were no or minimal deviations from the expected distribution (Hartig & Hartig, 2022). To test for the effects of fixed effects, we used log-likelihood ratio tests with Type II sums of squares using the car package (Fox & Weisberg, 2019). Predicted means and SEs from the models were calculated using the emmeans package (Lenth, 2023). We used glmms repeatedly throughout our analyses and used the R packages that we describe here in each succeeding section unless noted otherwise. Data analysis was conducted using R version 4.2.1.

Investigating variation in juvenile coral density, mortality, and growth across depths

In contrast to coral recruits (defined above), we defined juvenile corals as corals 0.5–5 cm diameter that are visible on the benthos. The density, mortality, and growth of juvenile corals in the genus *Pocillopora* were quantified by tracking the fate of individual colonies that appeared in the annual time-series photoquadrats. Surveys conducted in situ by divers in April 2010 indicated that the density of juvenile corals was exceptionally low (Edmunds, 2018), but by 2011, many juveniles were visible on the benthos (Holbrook et al., 2018); therefore, we collected data starting in 2011. We quantified the density, mortality, and growth of juvenile corals in photoquadrats at LTER 1 and LTER 2 at 10 and 17 m (see Appendix S1: Table S1 for number of quadrats). We searched each photoquadrat for juvenile colonies and assigned each colony a unique identifying number. In each consecutive year, we searched the photoquadrats to identify corals that were recorded the previous year and also identify new juvenile corals that appeared. Thus, each coral was counted as a new coral once in the time series. We then analyzed the density of juvenile corals (juveniles per square meter per year) using a glmm with a negative binomial error and a log link function and a random effect of quadrat nested within site to account for the repeated measures design.

In each pair of consecutive years (e.g., 2011–2012), we assessed the annual mortality of juvenile corals. The probability of mortality decreases with coral age and size, and corals are most vulnerable to mortality in their early life stages (Hughes & Connell, 1987). We were interested in understanding whether the mortality of corals in the first year after they were detected differed between depths. We asked whether the annual probability of mortality of juvenile corals differed between depths using a glmm with a binomial error structure and a logit link function and a random effect of quadrat nested within site. We analyzed mortality data until 2015 (e.g., juvenile corals arriving by 2014) because the number of new juveniles declined precipitously throughout the time series at both sites and depths and many photoquadrats had no new juvenile corals after 2014.

To quantify the annual growth of juvenile *Pocillopora* corals (colonies ≤5 cm diameter), we measured corals that were visible in photoquadrats in consecutive years using the ImageJ software (Schneider et al., 2012). For each year that a coral was visible, we traced the perimeter of the coral, calculated the planar area, and measured the longest diameter. As corals grew throughout the time series, some corals grew out of the visible frame of the quadrat. We did not measure corals that were partially out of the quadrat; therefore, some corals were omitted from the growth analysis in later years of the time series. Additionally, corals that died were omitted from the growth dataset starting in the first year that they were dead and in all later years.

We estimated the growth of corals between consecutive years by calculating the difference in planar area between consecutive years (in square centimeters per year) for juvenile corals (≤5 cm in the first year). This generated a small number (55 out of 1289) of negative values because corals grow overtop one another and obscure the planar view of other corals. We omitted these negative values because it is not possible to determine the causation of negative values (i.e., shrinkage vs. obscurement by other corals). Growth data were log-transformed to homogenize variances. We analyzed growth data from 2011 to 2016, because by 2017 and 2018, the majority of corals were partially out of the photoquadrats. We asked whether the change in planar area of juvenile corals differed between depths using a glmm with gaussian error structure. Additionally, because colony size has potential to influence growth, we fitted a second version of the model that also included colony size (diameter) as a fixed effect to evaluate whether our results were influenced by coral size.

Evaluating the relationship between juvenile coral density and the rate of coral recovery

There were significant differences in the density and mortality of juvenile corals, but not coral recruitment or growth, between depths (see *Results*). The density of juvenile corals was higher at 10 m than at 17 m, which matched patterns of higher coral recovery at 10 m than at 17 m. In addition to these broad scale patterns, we also tested whether the density of coral recruits was related to the rate of coral recovery at smaller spatial scales (individual quadrats). Pocilloporid corals accounted for 71.1% of coral cover on the fore reef by 2018 (76.1% and 66.2% at 10 and 17 m, respectively); therefore, we considered the rate at which *Pocillopora* cover increased. First, we calculated the recovery rate (% cover of *Pocillopora* per year) for each quadrat. Some quadrats reached minimum coral cover in 2010, and some reached minimum coral cover in 2011; therefore, quadrats were in a recovery phase for 7 or 8 years depending on the year in which they reached minimum coral cover. We standardized the recovery rate by the number of years in the recovery phase (i.e., % increase per year). For each photoquadrat, we first identified the year of minimum coral cover, which was 2010 or 2011 for virtually all (99%) photoquadrats. Some photoquadrats had two years of minimum coral cover (e.g., 0% cover in both 2010 and 2011), and in these cases, we used the first year for our data analysis. We then subtracted the minimum coral cover from the percent coral cover in 2018 and divided this change in coral cover by the number of years in the recovery phase (i.e., the number of years between the year of minimum coral cover and 2018) (Holbrook et al., 2018). We then used this recovery rate to evaluate the relationship between the rate of recovery of pocilloporid corals, the density of juvenile corals, and depth. We analyzed our data on the recovery rate of pocilloporid corals at the quadrat level using a glmm with gaussian error structure. The model included the cumulative number of unique juvenile corals in the first three years of the recovery phase (2011–2013) and depth as fixed effects, and site as a random effect.

Investigating substratum type as a driver of juvenile coral mortality

Next, we tested whether differences in the availability of substratum types between depths resulted in different rates of juvenile coral mortality. Cyclone Oli in 2010 broke and removed the majority of the coral skeletons from the reef, resulting in patchy substratum types with a mix of coral rubble, attached remnants of dead branching coral skeletons, and hard consolidated substratum. We hypothesized that the density and mortality of juvenile corals would differ among substratum types. First, we quantified the availability of different substratum types for each quadrat in our analysis using the time-series photoquadrats from 2011. Twenty random points were annotated for each photoquadrat using CoralNet, in which the substratum type underneath each point was classified as (1) hard substratum, (2) dead coral skeletons still attached to the substratum ("dead skeletons"), or (3) remnants of dead coral skeletons that appeared to be unattached ("rubble"). For each juvenile coral, the same three categories were used to classify the substratum type to which each coral was attached. We recognize the limitations of discriminating substratum types in photographs, and therefore, the substratum was only scored as rubble if they appeared to not be part of an antecedent framework. We hypothesized that juvenile coral mortality may be higher on rubble than on other substratum types because unattached rubble moves with ocean swell and may be a poor habitat for corals (Kenyon et al., 2023). First, we used a glmm with gaussian error to ask whether the abundance of rubble differed by depth. The model included fixed effects of substratum, depth, and substratum × depth interaction, and a random effect of site. Second, we asked whether the probability of juvenile corals being on each substratum type differed by depth. We fit three separate models, one for each substratum type. Models were glmms with binomial error structure and a logit link function, and each model included a fixed effect of depth and random effect of photoquadrat nested within site. The response had binary observations where "1" represented a coral attached to that substratum type, and "0" represented a coral that was not attached to that substratum type. Third, we used a glmm with binomial error structure and a logit link function to ask whether the mortality of juvenile corals differed by substratum type and depth. The response variable had binary observations where "1" represented a coral that died, and "0" represented a coral that survived. The model included fixed effects of substratum, depth, and substratum × depth interaction, and a random effect of photoquadrat nested within site.

We found the proportion of juvenile corals on the different substratum types and the rates of morality on some substrata varied across depths (see *Results*). Juvenile corals were found on rubble more often at 17 m where they experienced the highest levels of mortality. In addition, juvenile corals on dead coral skeletons experienced higher levels of mortality at 17 m than at 10 m. To determine the relative contributions of differences in the availability of substratum types and differences in mortality rates on dead coral skeletons to overall mortality patterns, we calculated a weighted average mortality rate for each depth, where mortality at each depth was the product of the number of juveniles on each substratum type times the mortality rate for that substratum type. We then calculated a projected mortality rate for 17 m using the same distribution of juvenile densities on each substratum type as we observed at 10 m. In other words, calculating what the mortality rate would have been at 17 m if reefs had the same proportion of juveniles on each substratum type as reefs at 10 m. We then used the projected mortality to calculate the percentage of the difference in mortality between depths that was due to differences in substratum availability (i.e., more rubble at 17 m) versus differential mortality rates on a particular substratum (i.e., higher mortality on dead coral skeletons at 17 m).

Investigating relationships between macroalgae abundance and juvenile coral density

Macroalgae, which often compete with adult corals for space, can also negatively impact the recruitment and survivorship of juvenile corals through several mechanisms such as deterring coral larval settlement, preemption of space, and competition (Adam et al., 2022; Johns et al., 2018; Kuffner et al., 2006). If the abundance of macroalgae differed across depths, interactions with macroalgae could influence densities of juvenile corals. We used time-series data from MCR LTER benthic transects (Moorea Coral Reef LTER & Edmunds, 2020) to ask whether the abundance (% cover) of fleshy macroalgae differed between depths. First, we used a glmm with gaussian error structure to contrast the abundance of fleshy macroalgae between depths. Then, we asked whether there was a relationship between the mean abundance of macroalgae in a quadrat in the first three years of the recovery phase (2011–2013) and the cumulative number of unique juvenile corals in that photoquadrat from 2011 to 2013 and depth using a glmm with gaussian error structure. The abundance of macroalgae was log-transformed to improve model residuals.

Testing the effects of top-down processes on coral recruitment and recruit mortality

Our data indicated that the abundance of coral recruits on tiles (a proxy for the supply of coral larvae) did not differ between depths, but that the density of juvenile corals on the benthos was higher at 10 m than at 17 m. Together, these results suggested there is a demographic bottleneck between the time that corals recruit and the time that they grow large enough to be visible on the benthos as juveniles (0.5–5 cm). This motivated an experiment testing mechanisms that could drive differences in the mortality of coral recruits between 10 and 17 m.

Our past work has shown that top-down processes including predation by herbivorous and corallivorous fishes (e.g., parrotfishes and butterflyfishes) have a strong influence on the dynamics of small corals (Adam et al., 2022; K. E. Speare, unpublished data). We hypothesized that differences in top-down pressure by fishes may create the bottleneck between the time when corals recruit and when they grow big enough to visible as juvenile corals on the benthos (i.e., 0.5–5 cm). We conducted a fish exclusion experiment with coral recruits on tiles to test this hypothesis. At one site on the fore reef (S17° 28.386′, W149° 49.059′) between LTER 1 and LTER 2, we deployed 26 settlement tiles made of coral limestone at 10 and 17 m for one year to accumulate naturally settled coral recruits. Tiles were secured to the benthos using a stainless steel post drilled into the reef substratum and secured with a washer and nuts. We excluded fishes from half of the tiles at each depth using $15 \times 15 \times 15$ cm cages constructed of plastic-coated wire mesh with 2.5-cm diameter mesh size that prevented fishes larger than this size from accessing the tiles. Thirteen tiles were deployed in each depth × herbivore exclusion treatment ($n = 52$ tiles total). Tiles were deployed in July 2017 and retrieved in July 2018 to count coral recruits. Tiles were brought to the laboratory while keeping them submerged in seawater during transport and held at the laboratory in a flow-through seawater table for ~24 h while being examined for coral recruits. Tiles were searched under a microscope for coral recruits at 20–40× magnification. For each coral recruit, we mapped its location onto a high-resolution digital photograph of the tile. Coral recruits are notoriously difficult to identify while alive because their skeletal structures are not visible. Therefore, we did not identify coral recruits to family and instead collected data on all coral recruits. In our analysis, we only considered recruits located on the tops and sides of these tiles, as these habitats were exposed to fishes. Therefore, densities of recruits reflected the influence of top-down processes. We analyzed data on the number of coral recruits per tile using a generalized linear model with negative binomial error structure and a log link function. The model included fixed effects of depth, caging, and depth × caging interaction.

After one year, tiles in the herbivore exclusion treatment had more coral recruits than uncaged tiles (see *Results*). To test the hypothesis that differences in the strength of top-down processes between 10 and 17 m drove different rates of coral recruit mortality, we used these tiles in a second experiment to test the effect of depth on recruit survivorship. In this experiment, we only used tiles that had at least one coral recruit and recruit densities ranged from 1 to 23 recruits tile^{-1} (mean 6.2, median 5.5 recruits tile^{-1}). We assigned each tile to one of the four groups such that the number of coral recruits and tiles per group was as similar as possible. Tiles were either transplanted back to its original depth, or transplanted to the opposite depth, which created four treatments: (1) 10–10 m, (2) 10–17 m, (3) 17–17 m, and (4) 17–10 m. *t* tests confirmed that the initial densities of recruits on tiles did not differ by depth to which they were transplanted (df = 18.368, $p = 0.486$, Welch two sample *t* test), or the original depth from which they originated (df = 27.920, $p = 0.592$, Welch two sample *t* test). We transplanted the coral recruitment tiles back to the reef and left tiles uncaged such that fishes had access to the tiles. Initially, we planned to replicate the cage treatment in this stage of the experiment in order to directly test the effects of top-down processes on coral recruit mortality. However, we were concerned that the densities of coral recruits would not be high enough replication across four treatments (crossed depth and caging) so all tiles were deployed uncaged at the two depths.

After 21 days, we collected the tiles and brought them back to the laboratory, keeping the tiles submerged in seawater. We searched the tiles for coral recruits using microscopy and used the digital maps of recruit locations to look for the previously mapped recruits. We scored each coral recruit as either dead or alive and assigned each recruit into a category based on the condition of its skeleton, or lack thereof. Coral recruits whose skeletons appeared intact and had no physical damage were scored as "intact," recruits with some physical damage, such as damage to the skeletal structure, were scored as "damaged," and recruits that were no longer present and had no remnants of skeleton left on the tile were scored as "removed." We used a glmm with binomial error structure and a logit link function to ask whether there was an effect of depth on the probability of recruit mortality. The model included a fixed effect of depth, and random effects of tile and original depth. Then, of the recruits that died, we used a glmm with binomial error structure and a logit link function to ask whether there was an effect of depth on the probability of a recruit being either "damaged" or "removed" (categories that were impacted by predation from fishes). The response variable had binary observations of individual coral recruits where "1" represented a recruit that was either damaged or removed, and "0" represented a recruit that was not damaged or removed ("intact"). The model included a fixed effect of depth and random effects of tile and original depth.

RESULTS

Patterns of coral decline and recovery

Prior to the COTS outbreak and Cyclone Oli, the percent cover of stony corals at sites LTER 1 and 2 peaked in 2005, at 39.1 ± 3.9% and 46.7 ± 3.9% (mean ± SE) at 10 and 17 m, respectively (Figure 1; Appendix S1: Figure S1A). At the peak of coral cover in 2005, the relative abundance of *Acropora, Porites*, and *Pocillopora* was 29.5 ± 1.2%, 22.6 ± 2.2%, and 39.9 ± 2.8% at 10 m and 25.2 ± 8.3%, 28.3 ± 2.7%, and 29.3 ± 8.8% at 17 m, respectively (mean ± SE, Appendix S1: Figure S1B). Reefs at 17 m depth reached a minimum coral cover of 0.9 ± 3.9% in 2010 and reefs at 10 m depth reached a minimum of 1.2 ± 3.8% (mean ± SE) coral cover in 2011. The rate of increase in coral cover was higher for reefs at 10 m than for reefs at 17 m, and the mean annual rate of increase in coral cover was 7.5 ± 0.4% year^{-1} and 2.9 ± 0.2% year^{-1} at 10 and 17 m, respectively (mean ± SE). Reefs at 10 m depth surpassed pre-disturbance coral cover (which was 39.1 ± 3.9%, mean ± SE) by 2015, whereas reefs at 17 m had not returned to pre-disturbance coral cover by 2018. Reefs at 10 and 17 m reached peak coral cover of 71.1 ± 3.9% and 30.1 ± 3.9%, respectively, by 2018 (mean ± SE, Appendix S1: Figure S1A).

Coral recruitment as a proxy for the supply of coral larvae

In our analysis of pocilloporid recruitment, there was a marginally nonsignificant interaction between depth and year ($\chi^2 = 10.662$, df = 5, $p = 0.059$), a significant effect of depth ($\chi^2 = 4.537$, df = 1, $p = 0.033$, Figure 2A), and a significant effect of year ($\chi^2 = 160.669$, df = 5, $p < 0.0001$). Post hoc Tukey tests did not show significant differences between depths for any year ($p > 0.05$, see Appendix S1: Table S2 results of post hoc pairwise Tukey test). Pocilloporid recruitment peaked in 2011 for both depths, with an average of 6.4 ± 1.4 and 8.1 ± 1.7 recruits tile^{-1} at 10 and 17 m, respectively (model predicted mean ± SE, averaged between sites). This peak in coral recruitment occurred at approximately the same time as minimum coral cover for reefs at both depths. Recruitment declined between 2011 and 2015, and on average, there was <1 pocilloporid recruit per tile in 2014 and 2015.

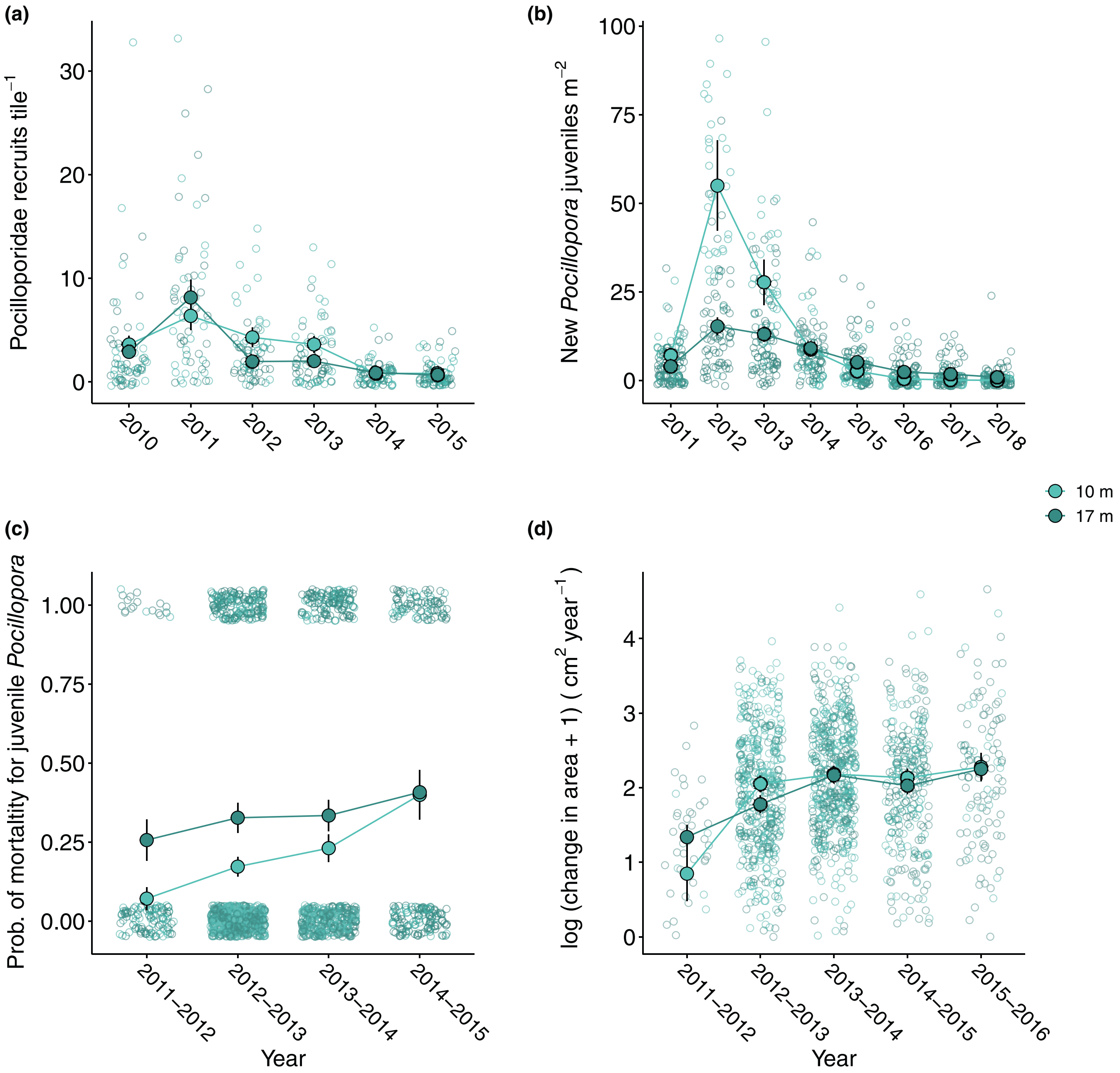

FIGURE 2 (a) Density of pocilloporid recruits on tiles per year at 10 and 17 m. (b) Density of new juvenile *Pocillopora* corals per square meter per year at 10 and 17 m. (c) Annual probability of juvenile *Pocillopora* mortality at 10 and 17 m. (d) Log change in planar area of corals between pairs of consecutive years in each quadrat at 10 and 17 m. In all panels, open points represent (a) individual recruitment tiles or (b–d) corals and closed points are model predicted means or probabilities (±SE) for each depth and year.

Investigating variation in juvenile coral density, mortality, and growth across depths

This analysis yielded a total of 1605 juvenile *Pocillopora* corals. In our analysis of juvenile coral density, there was a significant depth × year interaction ($\chi^2 = 76.519$, df = 7, $p < 0.0001$), and significant main effect of year ($\chi^2 = 334.156$, df = 7, $p < 0.0001$), but not depth ($\chi^2 = 0.542$, df = 1, $p = 0.462$, Figure 2B). The density of new juvenile *Pocillopora* peaked in 2012, one year after the peak in recruitment of pocilloporid corals, with densities more than three times greater at 10 m than at 17 m, likely driving the depth × year interaction. On average, there were 55.0 ± 1.3 and 15.3 ± 2.5 new juvenile *Pocillopora* m^{-2} on reefs at 10 and 17 m, respectively, in 2012. The density of new juveniles declined from 2012 to 2018 as the percent cover of corals increased at both depths.

When we analyzed data on juvenile coral mortality, there were significant effects of depth and year on the percent that died ($\chi^2 = 11.892$, df = 1, $p < 0.001$ and $\chi^2 = 17.240$, df = 3, $p < 0.001$for depth and year, respectively, Figure 2C), but no interaction between depth and year ($\chi^2 = 6.400$, df = 3, $p = 0.094$). At both depths, the probability of annual juvenile coral mortality was lowest from 2011 to 2012 and increased moderately until 2014–2015, the last pair of years for which we analyzed mortality data. The probability of annual juvenile coral mortality was higher at 17 m than at 10 m. From 2011 to 2012, the probability of annual juvenile mortality was 0.071 ± 0.036 (predicted mean ± SE) at 10 m depth, compared with 0.256 ± 0.065 at 17 m depth. By 2014–2015, the probability of annual juvenile mortality was 0.399 ± 0.078 and 0.408 ± 0.058 at 10 and 17 m, respectively (predicted mean ± SE, Figure 2C).

In our analysis of annual coral growth (measured as the change in planar area between consecutive years), there was a significant effect of year ($\chi^2 = 60.707$, df = 4, $p < 0.0001$, Figure 2D), but the effect of depth and the depth by year interaction was not significant ($\chi^2 = 3.384$, df = 1, $p = 0.066$, and $\chi^2 = 8.252$, df = 4, $p = 0.083$, respectively, Figure 2D). Mean coral growth was lowest from 2011 to 2012 and increased throughout the time series. Results from a second model that included coral size as a fixed effect showed that coral size had a positive effect on coral growth ($\chi^2 = 444.231$, df = 1, $p < 0.0001$, Appendix S1: Figure S2). There was also a significant effect of year and depth × year interaction ($\chi^2 = 63.548$, df = 4, $p < 0.0001$, and $\chi^2 = 15.385$, df = 4, $p = 0.004$) but no effect of depth ($\chi^2 = 0.009$, df = 1, $p = 0.924$, Appendix S1: Figure S2). Both of these models show depth had little influence on coral growth.

Evaluating the relationship between juvenile coral density and the rate of coral recovery

The density of juvenile *Pocillopora* corals differed significantly between 10 and 17 m depth, particularly in the first three years after reefs reached minimum coral cover (2011–2013). The density of juvenile *Pocillopora* corals in each photoquadrat was a strong predictor of the recovery rate in each photoquadrat ($\chi^2 = 24.780$, df = 1, $p < 0.0001$, Figure 3) with faster rates of recovery positively associated with higher densities of juvenile *Pocillopora*. Depth also had a significant effect on the rate of recovery ($\chi^2 = 20.329$, df = 1, $p < 0.0001$, Figure 3), where recovery rates were higher at 10 m than at 17 m, likely because of the higher mortality rates of juvenile corals at 17 m than at 10 m. Importantly, there was no interaction between the density of juvenile corals and depth ($\chi^2 = 0.054$, df = 1, $p = 0.816$, Figure 3).

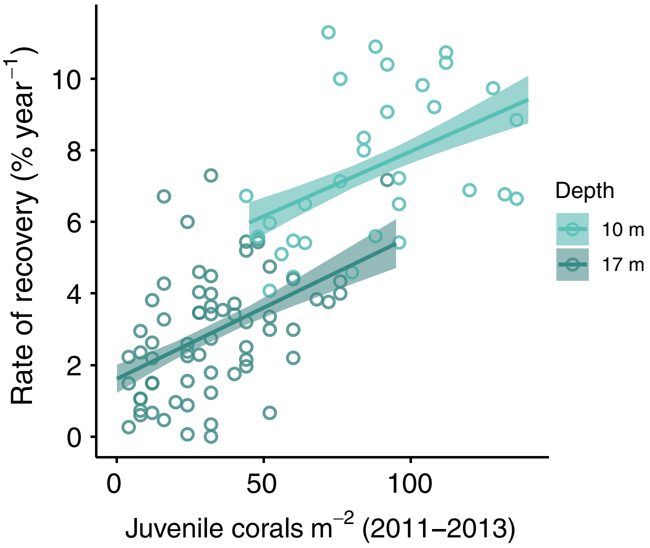

FIGURE 3 Relationship between the rate of coral recovery (in percentage per year) and the density of juvenile *Pocillopora* from 2011 to 2013 (juveniles per square meter), showing a positive relationship that is consistent across depths. Data points represent individual photoquadrats from permanent transects at LTER 1 and LTER 2 at 10 and 17 m. Lines are relationships between the density of juvenile corals and rate of recovery at 10 and 17 m, and shaded areas are SEs predicted from the glmm. Note that the effect of depth is consistent with the higher mortality rates of juvenile corals at 17 m than at 10 m.

Investigating substratum type as a driver of juvenile coral mortality

There was a significant interaction between depth and substratum type on substratum abundance ($\chi^2 = 36.705$, df = 2, $p < 0.0001$, Figure 4A). Hard substratum was the most abundant substrata at both depths, and rubble was more abundant at 17 m than at 10 m ($p < 0.05$, Tukey honestly significant difference [HSD], Figure 4A). There was a significant effect of depth on the probability that a juvenile coral was attached to rubble, where more juvenile corals were attached to rubble at 17 m than at 10 m ($\chi^2 = 22.282$, df = 1, $p < 0.0001$, Figure 4B). There was a significant effect of depth on the probability that a juvenile coral was on a dead skeleton, where more juvenile corals were more likely to be attached to dead skeletons at 10 m than at 17 m ($\chi^2 = 17.520$, df = 1, $p < 0.0001$, Figure 4B). There was no effect of depth on the probability that juvenile corals were on hard substratum (χ^2

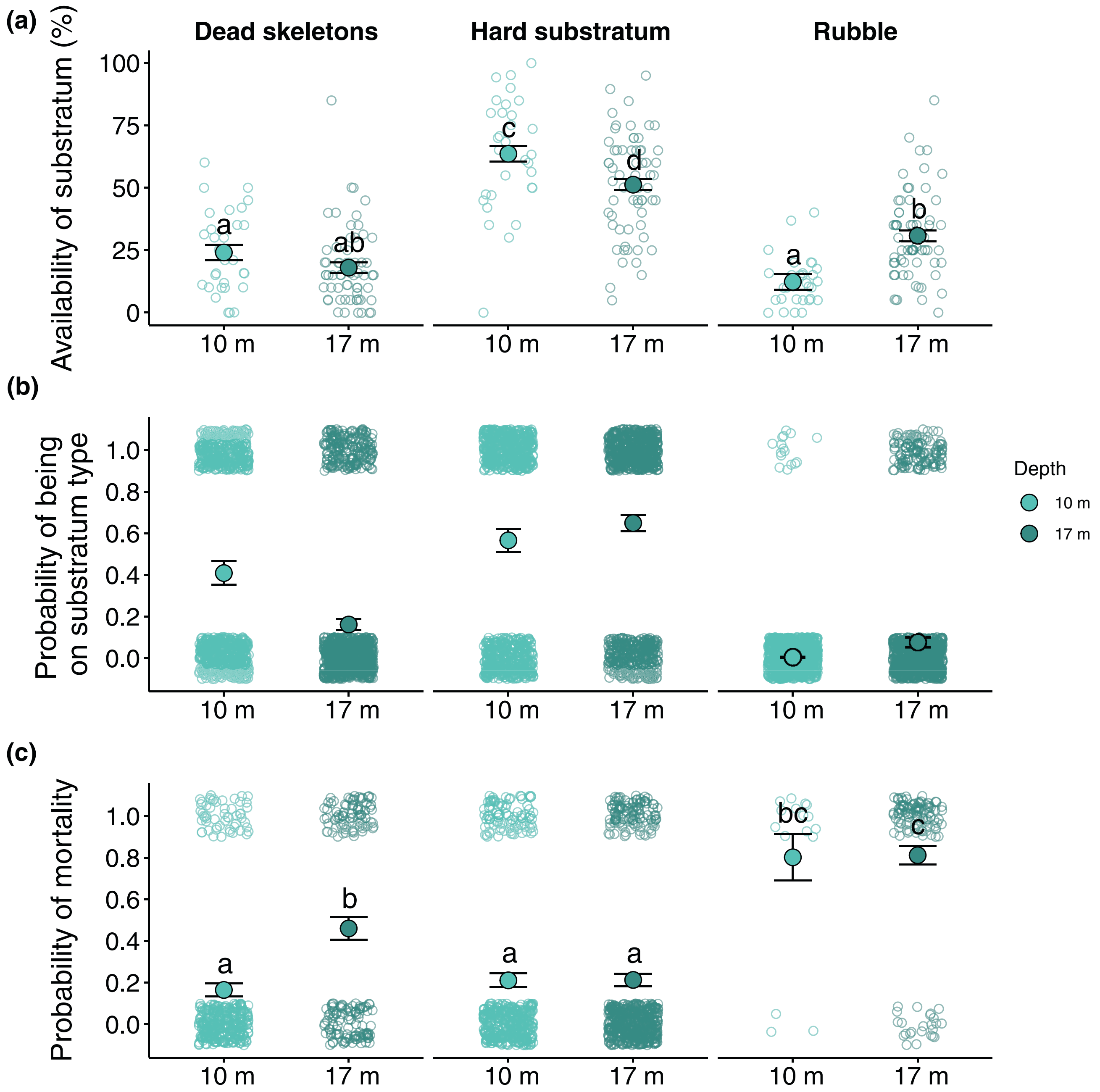

FIGURE 4 (a) The relative abundance of each substratum type across depths. (b) Probability of a juvenile coral being on a substratum type at each depth. (c) Probability of mortality of juvenile corals on each substratum type. Points with common letters are not significantly different ($p < 0.05$) determined from post hoc Tukey tests. In all panels, open points are data from individual (a) photoquadrats or (b, c) corals and closed points are model predicted means or probabilities ± SE.

= 1.520, df = 1, $p = 0.218$, Figure 4B). There was a significant substratum × depth effect (χ^2 = 23.901, df = 2, $p < 0.0001$, Figure 4C) and significant effects of substratum and depth (χ^2 = 96.803, df = 2, $p < 0.0001$, χ^2 = 7.571, df = 1, $p < 0.0001$, respectively, Figure 4C) on the probability of mortality of juvenile corals. At both depths, the probability of mortality of juvenile corals on rubble was significantly higher than either hard substratum or dead skeletons ($p < 0.05$, Tukey's HSD, Figure 4C), and the probability of mortality of corals on dead skeletons was higher at 17 m than at 10 m ($p < 0.05$, Tukey's HSD, Figure 4C). The substratum-weighted average mortality estimate showed that overall juvenile mortality was 20.4% at 10 m and 36.3% at 17 m. If reefs at 17 m had the same proportion of juveniles on each substratum type as 10 m, the projected mortality rate at 17 m would have been 33.3%. Overall, 19.0% of the difference in mortality between 10 and 17 m was attributed to differences in the availability of substratum types, where reefs at 17 m had more rubble, on which the mortality of juvenile corals was elevated. The remaining 81% of the difference in mortality rates was attributed to higher mortality of juveniles on dead coral skeletons at 17 m than at 10 m.

Investigating relationships between macroalgae abundance and juvenile coral density

The year after the disturbances that culminated in the lowest coral cover (2010) the abundance of macroalgae was higher at 10 m than at 17 m (11.5 ± 0.8% vs. 0.0 ± 0.8% cover, mean ± SE, Appendix S1: Figure S3), but by 2018, the abundance of macroalgae was similarly low at 10 and 17 m (1.8 ± 0.8% and 3.8 ± 0.8% cover, mean ± SE, Appendix S1: Figure S3). Overall, there was a significant interaction between depth and year on the abundance of macroalgae ($\chi^2 = 146.170$, df = 8, $p < 0.0001$, Appendix S1: Figure S3), suggesting higher abundance of macroalgae at 10 m early in the time series but no differences later on. At the quadrat level, the relationship between the abundance of macroalgae and the density of juvenile corals was not significant ($\chi^2 = 1.134$, df = 1, $p = 0.286$). There was a significant effect of depth ($\chi^2 = 26.396$, df = 1, $p < 0.0001$), but the interaction between depth and macroalgae was not significant ($\chi^2 = 1.966$, df = 1, $p = 0.161$).

Testing the effects of top-down processes on coral recruitment and recruit mortality

After one year of deployment, tiles in cages that excluded fishes had ~2.5 times as many coral recruits as tiles exposed to fishes (5.9 vs. 2.4 coral recruits tile^{-1}, respectively). There was a significant effect of caging ($\chi^2 = 20.650$, df = 1, $p < 0.0001$; Figure 5A) but no effect of depth and no interaction between depth and caging ($\chi^2 = 0.483$, df = 1, $p = 0.487$; $\chi^2 = 0.033$, df = 1, $p = 0.856$, respectively, Figure 5A). At the end of the transplant experiment in which all coral recruits were exposed to fishes, there was a significant effect of depth on the probability that a recruit died ($\chi^2 = 9.268$, df = 1, $p < 0.01$, Figure 5B) where recruits were more likely to die at 17 m (0.87 ± 0.05, probability ± SE) than at 10 m (0.56 ± 0.10, probability ± SE). Of the coral recruits that died, recruits were more likely to be either damaged or removed at 10 m (0.83 ± 0.05) than at 17 m and 0.94 ± 0.02; $\chi^2 = 4.227$, df = 1, $p < 0.05$, Figure 5C.

DISCUSSION

Similar to work on foundation species in other ecosystems, our work suggests that top-down forcing and the differential survival of the newly established individuals interact to drive demographic rates of corals and ultimately the rate of recovery of coral communities after disturbance. Following a COTS outbreak and cyclone that together killed nearly all corals on the fore reef of Moorea, coral reefs at 10 m depth recovered more quickly than reefs at 17 m depth. Following these disturbances, there was high recruitment of pocilloporid corals, but there was little evidence that recruitment differed between depths for any year, suggesting that differences in the supply of coral larvae did not drive differences in coral recovery. Although rates of recruitment were similar on deep and shallow reefs, the density of juvenile *Pocillopora* corals was ~3.5 times higher at 10 m than at 17 m, pointing to a demographic bottleneck between

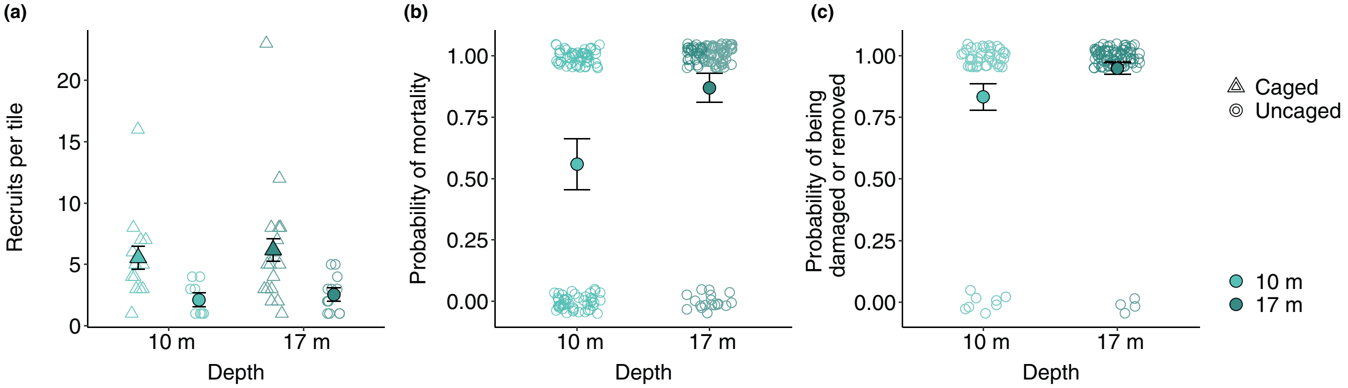

FIGURE 5 (a) The number of coral recruits per tile on tiles where fishes were excluded (caged = triangles) and where fishes were not excluded (uncaged = circles) at 10 and 17 m. Open points are counts from individual tiles, and closed points are model predicted means ± SE. (b) Probability of mortality of coral recruits on tiles at 10 and 17 m. (c) Of the coral recruits that were dead, the probability of coral recruits being either "damaged" or "removed". In (b) and (c), open points represent individual recruits and closed points are model predicted probabilities ± SE.

recruitment and when corals grew big enough to be visible on the benthos as juveniles. Ultimately, the density of juvenile corals in a photoquadrat strongly predicted the rate of *Pocillopora* coral recovery, indicating that processes that determine the density of small corals influence rates of coral recovery. When we tested for potential mechanisms driving differential mortality, our results suggest that predation by fishes in addition to differential mortality on different substrata both contributed to differences in coral density, and subsequently, recovery rates of corals. Taken together, our results suggest that top-down processes by consumers and the availability of different substratum types dictated the density of juvenile corals on reefs at 10 and 17 m and that these differences in density drove rates of coral recovery on the fore reef of Moorea.

One of our major findings is that differences in the density of juvenile corals drove rates of coral recovery following disturbance. Supply-side ecology (e.g., the supply of seedlings, larvae, and propagules) often determines the abundance of juvenile organisms, influences population dynamics, and governs the recovery of foundation organisms following disturbances across disparate ecosystems (Caddy, 1986; Castorani et al., 2018; Holbrook et al., 2018; Hughes et al., 2000; Romme et al., 1995). However, in our study, the supply of new corals appeared to have little influence on coral recovery across depths given that the density of coral recruits on settlement tiles, a proxy for the supply of coral larvae, did not differ between depths. Yet, we did find that the density of juvenile corals, the first coral life stage that is visible on the natural benthos, differed by depth in the early years of the recovery phase. Thus, a survivorship bottleneck between recruitment and when recruits grow large enough to be visible on the benthos as juveniles likely drove differences in the density of juvenile corals.

Surprisingly, differences in coral growth rates did not drive differences in rates of coral recovery between depths. Light attenuates with water depth, and coral calcification is dependent on light (Buddemeier et al., 1974; Marubini et al., 2001); therefore, it is reasonable to hypothesize that corals may grow slower at 17 m than at 10 m, although we did not observe differences in *Pocillopora* growth rates with depth. Recent work has shown that different cryptic species of *Pocillopora* corals differ in their relative abundance across depths on the fore reef of Moorea (Johnston et al., 2022). It is possible that the cryptic species that are common on deeper reefs are well adapted for lower light habitats and have comparable growth rates to those on neighboring shallower reefs. Regardless of the reason for similar growth rates of corals at both depths, we found no evidence that differences in growth rates contributed to differences in the rate of coral recovery. This finding is in contrast to other studies showing the growth rates are strong determinants of recovery dynamics. For example, in a tropical forest in Nicaragua, a catastrophic hurricane toppled or snapped the trunks of 80% of trees (Vandermeer et al., 1995). Forest recovery was driven by regrowth of damaged trees, but almost no new recruitment, because trees with surviving roots regrew from severely damaged trunks (Vandermeer et al., 1995). In contrast, in our study corals were nearly completely removed by wave action of the cyclone, leaving virtually no surviving individuals to regrow. Recruitment of new individuals was necessary to initiate recovery, and any influence of growth was overwhelmed by the strong effect of density of new individuals. As foundation organisms respond to disturbances, the relative importance of recruitment of new individuals versus growth likely depends on how a disturbance impacts foundation organisms and their survival following a perturbation.

Our experiment with coral recruits on settlement tiles suggests that top-down forcing from coral predation created a survival bottleneck after corals recruit, driving lower densities of juvenile corals on deeper reefs. Notably, we did not see differences in the densities of recruits that accumulated on settlement tiles in our experiment (Figure 5A) or in the time series of recruitment on tiles (Figure 2A), suggesting that predation from fishes had little effect on the accumulation of coral settlers between depths. However, we did see differences between depths in mortality from predation after recruits were established (Figure 5B,C). This suggests that consumers have negative effects on coral recruits after settlement, which has been shown by other studies that quantify recruit mortality with and without fishes (Evensen et al., 2021). Our work joins other literature showing that consumers can negatively affected the recovery of foundation species through top-down processes. On coral reefs both corallivorous fishes, such as pufferfishes, butterflyfishes, and filefishes, as well as herbivorous fishes, including parrotfishes, commonly bite corals, often leaving visible predation scars from the physical damage caused by bites (Burkepile, 2012). This physical damage from predation can cause reduced growth and increased mortality of small newly settled coral recruits (Doropoulos et al., 2016; Penin et al., 2010; Rotjan & Lewis, 2008). Analogous to fishes slowing recovery of corals by predation, ungulate herbivores can negatively affect tree communities through herbivory and by causing nonconsumptive physical damage to trees (Gill, 1992). In the context of coral reefs recovering from disturbance, the negative effects of consumers on corals may be particularly intense when coral abundance is low because top-down pressure by consumers becomes concentrated on a smaller number of individuals (Burkepile, 2012). Knowlton et al. (1990) showed that the recovery of *Acropora* corals after a hurricane was slowed by coral predators. The negative effects of consumers can affect the trajectory of communities, such as in forests where ungulate browsing on juvenile trees can suppress tree recruitment and slow forest recovery after disturbances (Andrus et al., 2020; Kuijper et al., 2010). In contrast, consumers can also expedite recovery of foundation organisms by controlling the abundance of their competitors (Aquilino & Stachowicz, 2012). Thus, the net effects of consumers may be context dependent on the intensity of top-down pressure or preferences of consumers.

Our experiment with coral recruits suggested that bites from fishes likely caused more coral recruits to be damaged or removed on deeper reefs than on shallower reefs. Another possible mechanism that could cause physical damage to coral recruits is debris (i.e., sand or rubble) that can become mobilized during swell events. It is unlikely, however, that damage from mobile debris contributed to mortality in our experiment because we conducted our experiment during the Austral winter, when wave energy on the north shore of Moorea is very low relative to other seasons (Edmunds et al., 2010). Further, wave energy declines with depth, making it unlikely that mobile debris would cause higher rates of damage and mortality to recruits on deep reefs than on shallow reefs. Damage from fish bites is a more probable explanation for higher recruit mortality on deeper reefs given that wave energy was low during our experiment and that wave energy declines with depth.

Competition can also affect the recovery dynamics of foundation species, and in some cases, top-down processes by consumers determine the outcome of competition. In savannahs, for example, grasses and tree seedlings compete for space after fires, but herbivory can alter the outcome of these competitive interactions, resulting in landscapes dominated by either trees or grasses (Donaldson et al., 2022). On coral reefs, macroalgae are often the main competitors with corals by deterring coral larvae and by preempting space (Adam et al., 2022; Kuffner et al., 2006), but we did not find evidence that competition with macroalgae influenced recovery dynamics of reefs in Moorea. This is likely because herbivorous fishes consumed macroalgae and kept the abundance of macroalgae low throughout the recovery phase (Appendix S1: Figure S3), giving corals an opportunity to colonize the benthos after disturbance. Our mechanistic experiments showed that top-down processes by fishes likely drove lower densities of juvenile corals on deeper reefs, but some of the same fishes that feed on corals also consume macroalgae (e.g., parrotfishes). In other words, fishes slowed the rate of coral recovery through predation on corals, but they also likely facilitated coral recovery by limiting the abundance of macroalgae. These results are corroborated by work in other coral reef systems showing that the indirect positive effect of consumers (via herbivory) outweigh the direct negative effects of predation on corals (Evensen et al., 2021).

Differences in the availability of substratum types, and rates of coral mortality on different substratum types, were another mechanism that contributed to higher mortality of small corals and slower recovery on deeper reefs. Differences in the proportion of rubble, on which juvenile corals died at elevated rates at both depths, accounted for only 19% of the difference in mortality between deep and shallow reefs. The availability of hard substrata, dead skeletons, and rubble differed between deep and shallow reefs, and our data showed that the mortality of juvenile corals (colonies $\leq$5 cm) was higher for corals attached to rubble than to the other two substrata. This mechanism is analogous to mortality of plant recruits in cobble beach plant communities, where physical instability of cobble prevents the establishment of foundation grasses (Bruno, 2000). Similarly, rubble is an unfavorable habitat for small corals because it is unstable and can move with ocean currents and swell, causing abrasion, damage, and mortality of small corals (reviewed in Kenyon et al., 2023).

In contrast to rubble, which caused high rates of juvenile mortality at both depths, mortality on dead coral skeletons was higher at 17 m than at 10 m, and this accounted for 81% of the difference in juvenile mortality between depths. Although coral recruits and juvenile corals are commonly observed on skeletons of dead branching corals (Yadav et al., 2016), this substratum type can be a sink (Pulliam, 1988) habitat for small corals because skeletons are prone to erosion and breakage (Swanson, 2016). Other work on tropical reefs has shown that coral skeletons can erode completely within five years of a coral dying, leading to mortality of attached coral recruits and juveniles (Swanson, 2016). Erosion of skeletons is caused by both internal bioerosion by invertebrates and external bioerosion by consumers. Urchins and fishes are two groups of consumers that cause bioerosion of the reef framework; however, given that the abundance of urchins was very low at both 10 and 17 m throughout the study (0.23 ± 0.08 and 0.18 ± 0.05 at 10 and 17 m, respectively, mean ± SE of *Diadema, Echinometra, and Echinothrix* urchins m^{-2}) (Moorea Coral Reef LTER & Carpenter, 2023), fishes are the more likely driver of erosion of dead coral skeletons and mortality of attached juvenile corals. Dead skeletons erode much more quickly than hard substratum (Swanson, 2016; Yadav et al., 2016), and therefore, differences in mortality between depths for juvenile corals on dead skeletons, but not hard substratum, is not surprising. Higher rates of juvenile coral mortality on dead skeletons at 17 m is consistent with the hypothesis that consumer pressure drives higher rates of mortality of small corals on deeper reefs. More broadly, differences in the success of early life-history stages (e.g., recruits and seedlings) as a result of differences in substratum or microhabitat quality is a common driver of early life-history dynamics of foundation species and community dynamics across marine and terrestrial ecosystems (Donaldson et al., 2022; Macek et al., 2017; Price, 2010).

Early life-history dynamics can have profound effects on the population dynamics and recovery of foundation species. We show that for corals in Moorea, top-down processes by consumers and differences in substratum quality created a demographic bottleneck that dictated rates of recovery after disturbance. These cryptic life stages are challenging to study because of their small size and high rates of recruitment and mortality, but investigating the processes that govern these rates can lead to significant insights about their population dynamics. Our study adds to a growing body of work showing that multiple biotic and abiotic mechanisms may act synchronously to create a bottleneck and determine the dynamics of foundation species. In our study, corals rebounded remarkably quickly and returned to a coral-dominated state after disturbance because of high rates of coral recruitment and survival; however, there are many examples from other coral reef systems where corals do not recover or remain persistently low in abundance after disturbance (Gardner et al., 2003; Hughes & Tanner, 2000). Understanding how anthropogenic influence, such as modifying herbivore communities or habitat quality, may be influencing mechanisms of recovery of foundation species remains a challenge in ecology.

ACKNOWLEDGMENTS

This research was funded by the U.S. National Science Foundation Grants NSF-OCE 1547952 and NSF-OCE 16-37396 (and earlier awards to the MCR LTER) as well as a generous gift from the Gordon and Betty Moore Foundation. This work was supported by a grant from the Schmidt Family Foundation and an NSF GRFP awarded to Kelly E. Speare. We thank H. Clover, M. Gorgas, A. Pettit, and S. Ramamurthy for field and lab assistance. Research was completed under permits issued by the Territorial Government of French Polynesia (Délégation à la Recherche) and the Haut-Commissariat de la République en Polynésie Francaise (DTRT) (Protocole d'Accueil 2013–2019), and we thank the Délégation à la Recherche and DTRT for their continued support.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Time-series data on benthic community dynamics (Moorea Coral Reef LTER & Edmunds, 2020) are available in the Environmental Data Initiative at https://doi.org/10.6073/pasta/10ee808a046cb63c0b8e3bc3c9799806. Time-series data on coral recruitment (Moorea Coral Reef LTER & Edmunds, 2018) are available in the Environmental Data Initiative at https://doi.org/10.6073/pasta/57b3d0d926dd643b471d261a5984f078. Data on the density, mortality, and growth of small corals collected from the time-series photographs (Moorea Coral Reef LTER et al., 2024) are available in the Environmental Data Initiative at https://doi.org/10.6073/pasta/f006b56623d3dd61d689237b048b53d8. Code (Speare, 2024) is available in Zenodo at https://doi.org/10.5281/zenodo.13994351.

ORCID

Kelly E. Speare https://orcid.org/0000-0002-0016-3606
Lauren N. Enright https://orcid.org/0009-0007-2442-2805
Allison Aplin https://orcid.org/0009-0004-8077-247X
Thomas C. Adam https://orcid.org/0000-0001-6146-0260
Peter J. Edmunds https://orcid.org/0000-0002-9039-9347
Deron E. Burkepile https://orcid.org/0000-0002-0427-0484

REFERENCES

Adam, T. C., S. J. Holbrook, D. E. Burkepile, K. E. Speare, A. J. Brooks, M. C. Ladd, A. A. Shantz, R. Vega Thurber, and R. J. Schmitt. 2022. "Priority Effects in Coral-Macroalgae Interactions Can Drive Alternate Community Paths in the Absence of Top-Down Control." *Ecology* 103: e3831.

Adam, T. C., R. J. Schmitt, S. J. Holbrook, A. J. Brooks, P. J. Edmunds, R. C. Carpenter, and G. Bernardi. 2011. "Herbivory, Connectivity, and Ecosystem Resilience: Response of a Coral Reef to a Large-Scale Perturbation." *PLoS One* 6: e23717.

Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg. 2013. "Consequences of Widespread Tree Mortality Triggered by Drought and Temperature Stress." *Nature Climate Change* 3: 30–36.

Andrus, R. A., S. J. Hart, and T. T. Veblen. 2020. "Forest Recovery Following Synchronous Outbreaks of Spruce and Western Balsam Bark Beetle Is Slowed by Ungulate Browsing." *Ecology* 101: e02998.

Aquilino, K. M., and J. J. Stachowicz. 2012. "Seaweed Richness and Herbivory Increase Rate of Community Recovery from Disturbance." *Ecology* 93: 879–890.

Beijbom, O., P. J. Edmunds, C. Roelfsema, J. Smith, D. I. Kline, B. P. Neal, M. J. Dunlap, et al. 2015. "Towards Automated

Annotation of Benthic Survey Images: Variability of Human Experts and Operational Modes of Automation." *PLoS One* 10: e0130312.

Benavides, R., A. Escudero, L. Coll, P. Ferrandis, R. Ogaya, F. Gouriveau, J. Peñuelas, and F. Valladares. 2016. "Recruitment Patterns of Four Tree Species along Elevation Gradients in Mediterranean Mountains: Not Only Climate Matters." *Forest Ecology and Management* 360: 287–296.

Brooks, M., K. Kristensen, K. van Benthem, A. Magnusson, C. Berg, A. Nielsen, H. Skaug, M. Mächler, and B. Bolker. 2017. "GlmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *The R journal* 9: 378.

Bruno, J. F. 2000. "Facilitation of Cobble Beach Plant Communities through Habitat Modification by *Spartina alterniflora*." *Ecology* 81: 1179–92.

Buddemeier, R. W., J. E. Maragos, and D. W. Knutson. 1974. "Radiographic Studies of Reef Coral Exoskeletons: Rates and Patterns of Coral Growth." *Journal of Experimental Marine Biology and Ecology* 14: 179–199.

Burkepile, D. E. 2012. "Context-Dependent Corallivory by Parrotfishes in a Caribbean Reef Ecosystem." *Coral Reefs* 31: 111–120.

Caddy, J. F. 1986. "Modelling Stock–Recruitment Processes in Crustacea: Some Practical and Theoretical Perspectives." *Canadian Journal of Fisheries and Aquatic Sciences* 43: 2330–44.

Castorani, M. C. N., D. C. Reed, F. Alberto, T. W. Bell, R. D. Simons, K. C. Cavanaugh, D. A. Siegel, and P. T. Raimondi. 2015. "Connectivity Structures Local Population Dynamics: A Long-Term Empirical Test in a Large Metapopulation System." *Ecology* 96: 3141–52.

Castorani, M. C. N., D. C. Reed, and R. J. Miller. 2018. "Loss of Foundation Species: Disturbance Frequency Outweighs Severity in Structuring Kelp Forest Communities." *Ecology* 99: 2442–54.

Dayton, P., M. J. Tegner, P. E. Parnell, and P. B. Edwards. 1992. "Temporal and Spatial Patterns of Disturbance and Recovery in a Kelp Forest Community." *Ecological Monographs* 62: 421–445.

Donaldson, J. E., R. Holdo, J. Sarakikya, and T. M. Anderson. 2022. "Fire, Grazers, and Browsers Interact with Grass Competition to Determine Tree Establishment in an African Savanna." *Ecology* 103: e3715.

Doropoulos, C., G. Roff, Y. Bozec, M. Zupan, J. Werminghausen, and P. J. Mumby. 2016. "Characterizing the Ecological Trade-Offs throughout the Early Ontogeny of Coral Recruitment." *Ecological Monographs* 86: 20–44.

Edmunds, P. J. 2018. "Implications of High Rates of Sexual Recruitment in Driving Rapid Reef Recovery in Mo'orea, French Polynesia." *Scientific Reports* 8: 1–11.

Edmunds, P. J. 2021. "Spatiotemporal Variation in Coral Recruitment and its Association with Seawater Temperature." *Limnology and Oceanography* 66: 1394–1408.

Edmunds, P. J., J. J. Leichter, and M. Adjeroud. 2010. "Landscape-Scale Variation in Coral Recruitment in Moorea, French Polynesia." *Marine Ecology Progress Series* 414: 75–89.

Edmunds, P. J., S. Maritorena, and S. C. Burgess. 2024. "Early Post-Settlement Events, Rather than Settlement, Drive Recruitment and Coral Recovery at Moorea, French Polynesia." *Oecologia* 204: 625–640.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, et al. 2005. "Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems." *Frontiers in Ecology and the Environment* 3: 479–486.

Evensen, N. R., I. Vanwonterghem, C. Doropoulos, M. Gouezo, E. S. Botté, N. S. Webster, and P. J. Mumby. 2021. "Benthic Micro- and Macro-Community Succession and Coral Recruitment under Overfishing and Nutrient Enrichment." *Ecology* 102: e03536.

Filbee-Dexter, K., and R. E. Scheibling. 2014. "Sea Urchin Barrens as Alternative Stable States of Collapsed Kelp Ecosystems." *Marine Ecology Progress Series* 495: 1–25.

Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*. Thousand Oaks CA: Sage.

Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. "Long-Term Region-Wide Declines in Caribbean Corals." *Science* 301: 958–960.

Gelman, A., and J. Hill. 2007. *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge: Cambridge University Press.

Gill, R. M. A. 1992. "A Review of Damage by Mammals in North Temperate Forests: 1. Deer." *Forestry* 65: 145–169.

Gomes, D. G. E. 2022. "Should I Use Fixed Effects or Random Effects When I Have Fewer than Five Levels of a Grouping Factor in a Mixed-Effects Model?" *PeerJ* 10: e12794.

Gruen, A., S. Kocaman, T. Guo, S. Ural, and M. Troyer. 2017. "DSM/DTM – Related Investigations of the Moorea Avatar Project."

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. "Community Structure, Population Control, and Competition." *The American Naturalist* 94: 421–25.

Hartig, F., and M. F. Hartig. 2022. "Package 'DHARMa.' R Package." https://CRAN.R-project.org/package=DHARMa.

Holbrook, S. J., T. C. Adam, P. J. Edmunds, R. J. Schmitt, R. C. Carpenter, A. J. Brooks, H. S. Lenihan, and C. J. Briggs. 2018. "Recruitment Drives Spatial Variation in Recovery Rates of Resilient Coral Reefs." *Scientific Reports* 8: 7338.

Hughes, T., A. Baird, E. Dinsdale, N. Moltschaniwskyj, M. Pratchett, J. Tanner, and B. Willis. 2000. "Supply-Side Ecology Works Both Ways: The Link between Benthic Adults, Fecundity, and Larval Recruits." *Ecology* 81: 2241–49.

Hughes, T. P., and J. H. Connell. 1987. "Multiple Stressors on Coral Reefs: A Long-Term Perspective." *The American Naturalist* 129: 818–829.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, et al. 2017. "Global Warming and Recurrent Mass Bleaching of Corals." *Nature* 543: 373–77.

Hughes, T. P., and J. E. Tanner. 2000. "Recruitment Failure, Life Histories, and Long-Term Decline of Caribbean Corals." *Ecology* 81: 2250–63.

Johns, K. A., M. J. Emslie, A. S. Hoey, K. Osborne, M. J. Jonker, and A. J. Cheal. 2018. "Macroalgal Feedbacks and Substrate Properties Maintain a Coral Reef Regime Shift." *Ecosphere* 9: e02349.

Johnston, E. C., A. S. J. Wyatt, J. J. Leichter, and S. C. Burgess. 2022. "Niche Differences in Co-Occurring Cryptic Coral Species (*Pocillopora* spp.)." *Coral Reefs* 41: 767–778.

Kayal, M., J. Vercelloni, T. Lison de Loma, P. Bosserelle, Y. Chancerelle, S. Geoffroy, C. Stievenart, et al. 2012. "Predator Crown-of-Thorns Starfish (*Acanthaster planci*)

Outbreak, Mass Mortality of Corals, and Cascading Effects on Reef Fish and Benthic Communities.” *PLoS One* 7: e47363.

Kenyon, T. M., C. Doropoulos, K. Wolfe, G. E. Webb, S. Dove, D. Harris, and P. J. Mumby. 2023. “Coral Rubble Dynamics in the Anthropocene and Implications for Reef Recovery.” *Limnology and Oceanography* 68: 110–147.

Keough, M. J., and B. J. Downes. 1982. “Recruitment of Marine Invertebrates: The Role of Active Larval Choices and Early Mortality.” *Oecologia* 54: 348–352.

Knowlton, N., J. C. Lang, B. D. Keller, and D. C. Washington. 1990. “Case Study of Natural Population Collapse: Post-Hurricane Predation on Jamaican Staghorn Corals.” *Smithsonian Contributions to the Marine Sciences* 31: 1–25.

Kohler, K. E., and S. M. Gill. 2006. “Coral Point Count with Excel Extensions (CPCe): A Visual Basic Program for the Determination of Coral and Substrate Coverage Using Random Point Count Methodology.” *Computers & Geosciences* 32: 1259–69.

Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. S. Beach. 2006. “Inhibition of Coral Recruitment by Macroalgae and Cyanobacteria.” *Marine Ecology Progress Series* 323: 107–117.

Kuijper, D. P. J., B. Jedrzejewska, B. Brzeziecki, M. Churski, W. Jedrzejewski, and H. Zybura. 2010. “Fluctuating Ungulate Density Shapes Tree Recruitment in Natural Stands of the Białowieża Primeval Forest, Poland.” *Journal of Vegetation Science* 21: 1082–98.

Lenth, R. 2023. “emmeans: Estimated Marginal Means, Aka Least-Squares Means.” R Package Version 1.8.7.

Macek, M., J. Wild, M. Kopecký, J. Červenka, M. Svoboda, J. Zenáhlíková, J. Brůna, R. Mosandl, and A. Fischer. 2017. “Life and Death of *Picea abies* after Bark-Beetle Outbreak: Ecological Processes Driving Seedling Recruitment.” *Ecological Applications* 27: 156–167.

Marubini, F., H. Barnett, C. Langdon, and M. J. Atkinson. 2001. “Dependence of Calcification on Light and Carbonate Ion Concentration for the Hermatypic Coral Porites Compressa.” *Marine Ecology Progress Series* 220: 153–162.

Moorea Coral Reef LTER, and R. Carpenter. 2023. “MCR LTER: Coral Reef: Long-Term Population and Community Dynamics: Other Benthic Invertebrates, Ongoing Since 2005.” ver 28. https://doi.org/10.6073/pasta/8e7b3a0c7a8bf315739921861cc79d10.

Moorea Coral Reef LTER, and P. J. Edmunds. 2018. “MCR LTER: Coral Reef: Coral Community Dynamics: Coral Recruitment ver 13.” https://doi.org/10.6073/pasta/57b3d0d926dd643b471d261a5984f078.

Moorea Coral Reef LTER, and P. J. Edmunds. 2020. “MCR LTER: Coral Reef: Long-Term Population and Community Dynamics: Corals, Ongoing since 2005 ver 38.” https://doi.org/10.6073/pasta/10ee808a046cb63c0b8e3bc3c9799806.

Moorea Coral Reef LTER, K. E. Speare, L. N. Enright, A. Aplin, P. Edmunds, D. E. Burkepile, and T. Adam. 2024. “MCR LTER: Coral Reef: Early Life Stage Bottleneck Determines Rates of Coral Recovery Following Severe Disturbance; Data for Speare et al., 2024, Ecology ver 1.” Environmental Data Initiative. https://doi.org/10.6073/pasta/f006b56623d3dd61d689237b048b53d8.

Penin, L., F. Michonneau, A. Baird, S. Connolly, M. Pratchett, M. Kayal, and M. Adjeroud. 2010. “Early Post-Settlement Mortality and the Structure of Coral Assemblages.” *Marine Ecology Progress Series* 408: 55–64.

Price, N. 2010. “Habitat Selection, Facilitation, and Biotic Settlement Cues Affect Distribution and Performance of Coral Recruits in French Polynesia.” *Oecologia* 163: 747–758.

Pulliam, H. R. 1988. “Sources, Sinks, and Population Regulation.” *The American Naturalist* 132: 652–661.

Robinson, J. P. W., S. K. Wilson, and N. A. J. Graham. 2019. “Abiotic and Biotic Controls on Coral Recovery 16 Years after Mass Bleaching.” *Coral Reefs* 38: 1255–65.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. “Aspen, Elk, and Fire in Northern Yellowstone National Park.” *Ecology* 76: 2097–2106.

Rotjan, R. D., and S. M. Lewis. 2008. “Impact of Coral Predators on Tropical Reefs.” *Marine Ecology Progress Series* 367: 73–91.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. “NIH Image to ImageJ: 25 Years of Image Analysis.” *Nature Methods* 9: 671–75.

Speare, K. 2024. “kellyspeare/Moorea_coral_recovery_depth: v1.1 (v1.1). Zenodo.” https://doi.org/10.5281/zenodo.13994351.

Swanson, S. 2016. “Echinoid Herbivores and Coral Reef Resilience.” Doctoral diss., University of California, Santa Barbara.

Unkule, M., C. Piedallu, P. Balandier, and B. Courbaud. 2022. “Climate and Ungulate Browsing Impair Regeneration Dynamics in Spruce-Fir-Beech Forests in the French Alps.” *Annals of Forest Science* 79: 11.

Vandermeer, J., M. A. Mallona, D. Boucher, K. Yih, and I. Perfecto. 1995. “Three Years of Ingrowth Following Catastrophic Hurricane Damage on the Caribbean Coast of Nicaragua: Evidence in Support of the Direct Regeneration Hypothesis.” *Journal of Tropical Ecology* 11: 465–471.

Watanabe, J. M., and C. Harrold. 1991. “Destructive Grazing by Sea Urchins *Strongylocentrotus* spp. in a Central California Kelp Forest: Potential Roles of Recruitment, Depth, and Predation.” *Marine Ecology Progress Series* 71: 125–141.

Wijdeven, S. M. J., and M. E. Kuzee. 2000. “Seed Availability as a Limiting Factor in Forest Recovery Processes in Costa Rica.” *Restoration Ecology* 8: 414–424.

Yadav, S., P. Rathod, T. Alcoverro, and R. Arthur. 2016. ““Choice” and Destiny: The Substrate Composition and Mechanical Stability of Settlement Structures Can Mediate Coral Recruit Fate in Post-Bleached Reefs.” *Coral Reefs* 35: 211–222.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Speare, Kelly E., Lauren N. Enright, Allison Aplin, Thomas C. Adam, Peter J. Edmunds, and Deron E. Burkepile. 2025. “Early Life Stage Bottleneck Determines Rates of Coral Recovery Following Severe Disturbance.” *Ecology* 106(1): e4510. https://doi.org/10.1002/ecy.4510