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Linking coral recruitment to reef recovery in the Anthropocene

Author

Speare, Kelly Elizabeth

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Linking coral recruitment to reef recovery in the Anthropocene

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
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by

Kelly E. Speare

Committee:
Professor Deron E. Burkepile, Chair
Professor Holly V. Moeller
Professor Adrian C. Stier

December 2021

The dissertation of Kelly E. Speare is approved.

Holly V. Moeller

Adrian C. Stier

Deron E. Burkepile, Committee Chair

October 2021

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VITA OF KELLY E. SPEARE

EDUCATION

Bachelor of Science in Biology, University North Carolina at Chapel Hill, May 2013 (Highest Honors)
Doctor of Philosophy in Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, December 2021 (expected)

PROFESSIONAL EMPLOYMENT

2015-2021: Graduate Research Assistant, Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara
2015-2021: Teaching Assistant, Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara

PUBLICATIONS

Speare, K.E., Adam, T.C., Winslow E.M., Lenihan, H.S., Burkepile, D.E. (2021). Size-dependent mortality of corals during marine heatwave erodes recovery capacity of a coral reef *Global Change Biology,* (*In Press*) https://doi.org/10.1111/gcb.16000

Leinbach, S.E., Speare, K.E., Rossin, A.M., Holstein, D.M., Strader, M.S. (2021). Coral bleaching survival strategies differentially impact host energetics and reproductive output *Scientific Reports* (*In Press*)

Donovan, M.K., Adam, T.C., Shantz, A.A., Speare, K.E., (2020). Munsterman, K.S., Rice, M.M., Schmitt, R.J., Holbrook, S.J., Burkepile, D.E. Nutrient Pollution interacts with heat stress to increase coral bleaching across the seascape. *PNAS.* https://doi.org/10.1073/pnas.1915395117

Burkepile, D.E., Shantz, A.A., Adam, T.C., Munsterman, K.S., Speare, K.E., Ladd, M.L., Rice, M.M., McIlroy, S., Brooks, A.J., Schmitt, R.S., Holbrook, S.J. (2020). Nitrogen source drives differential impacts of nutrients on coral bleaching prevalence, duration, and mortality. *Ecosystems.* https://doi.org/10.1007/s10021-019-00433-2

Speare, K.E., Duran, A., Miller, M.W., Burkepile, D.E. (2019). Sediment associated with algal turfs inhibits the settlement of two endangered species of coral. *Marine Pollution Bulletin* https://doi.org/10.1016/j.marpolbul.2019.04.066

Allgeier, J.E., Speare, K.E., Burkepile, D.E. (2018). Estimates of fish and coral larvae as nutrient subsidies to coral reef ecosystems. *Ecosphere.* 9. https://doi.org/10.1002/ecs2.2216

Yang, T., Speare, K.E., McKay, L., MacGregor, B.J., Joye, S.B., Teske, A. (2016). Distinct Bacterial Communities in Surficial Seafloor Sediments Following the 2010 Deepwater Horizon Blowout. *Frontiers in Microbiology.* 7:1384. https://doi.org/10.3389/fmicb.2016.01384

Zhang, S., Speare, K.E., Long, Z.T., McKeever, K.A., Gyoerkoe, M., Ramus, A.P., Mohorn, Z., Atkins, K.L., Hambridge, S.M., Graham, N.A.J., Nash, K.L., Selig, E.R., Bruno, J.F. (2014). Is coral richness related to community resistance to and recovery from disturbance? *PeerJ* https://doi.org/10.7717/peerj.308

AWARDS

Ruth Gates Memorial Young Investigator Travel Award, 2019
Schmidt Foundation Research Fellowship, 2019
Environmental Education Foundation Thomas J. Cashman Post-Graduate Scholarship, 2018
Women Divers Hall of Fame Grant for Marine Conservation, 2018
Environmental Education Foundation Thomas J. Cashman Post-Graduate Scholarship, 2017
Environmental Education Foundation Thomas J. Cashman Post-Graduate Scholarship, 2016
Environmental Education Foundation College Post-Graduate Scholarship, 2015
National Science Foundation, Graduate Research Fellowship, 2014
PADI Foundation Research Grant, 2013
Bermuda Institute of Ocean Sciences Grant-In-Aid of Research, 2013
Coker Award for Outstanding Research in Ecology—University of North Carolina, 2013
National Science Foundation Research Experience for Undergraduates—Bermuda, 2012
NOAA Hollings Scholarship, 2011-2013
Dean's Award—Sea Education Association, 2011
Summer Undergraduate Research Fellowship, 2011
Environmental Education Foundation T. E. Reynolds Endowment Scholarship, 2009-2013

TEACHING AND STUDENTS MENTORED

Instructor – Coral Reef Ecology and Field Methods, Sea Education Association
Taught coral reef ecology and field methods to 20 undergraduate students onboard the *SSV Robert C Seamans* during SEA Semester Class S280. Summer 2018
Teaching Assistant – EEMB 147 Coral Reefs, EEMB 120 Ecology, EEMB 3L Intro to Biology and EEMB 142 Aquatic Community Ecology 2015-Present
Mentor – Mentored Undergraduate Interns Ally Aplin, Andrew Petitt, Lauren Enright, Nelson Beltran, Sriram Ramamurthy, Katherine Le, Andre Nguyen, Alyssa Carney, Channing Mink, Alyssa Chamberlain, Shivam Patel, and Jeremy Marquez, Steffanie Wise, Maya Gorgas, Taylor Traxler during fieldwork in Moorea and in the lab at UCSB (2016-Present)
Mentor – Mentored >60 undergraduate students in the field during SEA Semester Classes C252- C254, 2014

ACADEMIC SERVICE, OUTREACH, AND VOLUNTEERING

Session Chair and Organizer – session "*How will the coral populations of today affect the ecology and recovery of reefs in the future?*" at the 2021 and 2022 International Coral Reef Symposium; Bremen, Germany
Journal Reviewer – Ecology, Marine Ecology Progress Series, Coral Reefs, PeerJ
Grant Proposal Reviewer – National Science Foundation, Division of Ocean Sciences (OCE)
Mentor – Women in Science and Engineering (WiSE) at UCSB 2015-2017
Invited Speaker – Schmidt Environmental Solutions open house 2020
UCSB SCUBA Club 2019
Interviewed for NCEAS climate change documentary 2017
Volunteer – Moorea Coral Reef LTER Earth Day Exhibit 2017, 2018, 2019
UNC Office for Undergraduate Research, Peer Advisor and Ambassador 2011-2013

ABSTRACT

Linking coral recruitment to reef recovery in the Anthropocene

by

Kelly E. Speare

Coral reefs are among the most biodiverse and valuable ecosystems on Earth, providing food, coastal protection, and jobs for over a billion people worldwide. Coral reefs are also among the most imperiled by global climate change and local stressors that cause degradation. Disturbances that kill corals are becoming more frequent and intense and it has become increasingly important to understand how disturbances impact the recovery potential of coral reefs and which processes are most important for driving recovery. In my dissertation work I utilized time series data from the Moorea Coral Reef LTER along with observational approaches and field experiments to investigate the impacts of disturbances on coral communities, identify processes that drive recovery after disturbance, and understand the mechanisms shape early demographic processes in corals. I first investigated the impacts of a severe marine heatwave on coral communities in Moorea, French Polynesia, and found that coral bleaching caused disproportionate mortality of the largest, most fecund corals and near complete loss of newly-settled coral recruits. This work suggests that climate change may cryptically erode the recovery capacity of coral reefs by disproportionately impacting the coral life stages most important for recovery. Reefs in Moorea have a history of recovering from disturbance, and prior to the bleaching event reefs were recovering from an outbreak of the coral-eating sea star, *Acanthaster planci,* and a cyclone that killed nearly all corals on the outer reefs. I investigated the drivers of differences in recovery rates between

deep and shallow reefs and found that slower recovery on deeper reefs was driven by lower rates of coral recruitment and post-settlement bottlenecks that limited the establishment of new corals. My work points to the importance of post-settlement processes that dictate rates of coral recruitment and ultimately reef recovery. Next, I investigated how benthic communities shape the settlement choices of coral larvae, and found that larvae made complex settlement choices that were strongly influenced by benthic community composition at the scale of millimeters. This work improves our ability to understand and predict how coral communities will respond to disturbances in the Anthropocene.

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I. Size-dependent mortality of corals during marine heatwave erodes recovery capacity of a coral reef

1. Introduction

Climate change is increasing the intensity and frequency of disturbances across many ecosystems, causing mass mortalities of foundation species (Anderegg, Kane, & Anderegg, 2013; Hughes et al., 2017) that provide essential ecosystem services (Ellison et al., 2005). Many foundation organisms, such as corals and trees, are particularly vulnerable to changing disturbance regimes because they are slow growing and long-lived. In forests, large trees, which typically have low annual mortality (Muller-Landau et al., 2006; Thomas, 1996), often have the highest rates of mortality during disturbances like intense drought (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015; Van Nieuwstadt & Sheil, 2005). These larger trees are more likely than smaller trees to experience failure of vital physiological processes due to deterioration of their internal water-conducting tissues, resulting in their death (Anderegg et al., 2012; Rowland et al., 2015) and the loss of their unique and irreplaceable ecological roles (Lindenmayer, Laurance, & Franklin, 2012). Like trees in forests, corals are the long-lived foundation organisms of tropical reefs, and their annual mortality rates decrease with increasing size (Hughes & Connell, 1987). However, much like drought in forests, marine heatwaves are likely altering the typical patterns of coral mortality on tropical reefs, suggesting commonalities in how climate change is impacting foundation species.

Under climate change, marine heatwaves are driving more frequent, intense coral bleaching events (Hughes et al., 2017; Loya et al., 2001) where the mutualism between corals and their endosymbiotic algae, Symbiodiniaceae, breaks down, often resulting in coral death

(LaJeunesse et al., 2018; Lesser, 2011). Small-scale field studies and experiments suggest that, within a given taxon, larger colonies may be more sensitive to thermal stress than small colonies. For example, larger colonies can exhibit higher bleaching prevalence (proportion of colonies that are bleached) (Pratchett, McCowan, Maynard, & Heron, 2013), higher bleaching severity (proportion of an individual colony that bleached) (Brandt, 2009) and more severe bleaching-induced mortality (Shenkar, Fine, & Loya, 2005) than smaller conspecifics. Further, juvenile corals (typically defined as the smallest colonies visible on the benthos up to 5cm) appear to be resistant to bleaching, even during severe heatwaves that result in high mortality of adult conspecifics (Bena & Van Woesik, 2004; Depczynski et al., 2013; Loya et al., 2001). Although there is increasing evidence that larger corals may be more susceptible to bleaching and mortality, we know little about how this size-dependent mortality will impact coral communities and the likelihood that they recover after marine heatwaves.

Although juvenile corals (~1-5 cm diameter) may have higher resistance to bleaching than adult corals, they are not the smallest corals on the reef. Coral recruits (coral spat; ~500 µm-1cm) are the newly-established members of a coral community and are typically undetectable to the naked eye for the first weeks to months of their lives. Limited data from laboratory experiments suggest that coral recruits may be highly sensitive to thermal stress (Fourney & Figueiredo, 2017; Nozawa & Harrison, 2007). However, because of their microscopic size, coral recruits are difficult to observe *in situ,* and, to the best of our knowledge, no published data exists on the survivorship of coral recruits *in situ* during a marine heatwave. Therefore, we have very limited understanding of how coral recruits fare during bleaching events. Coral recruits are extremely sensitive to external stressors, and have high rates of post-recruitment mortality early in life (Penin et al., 2010). Understanding how these events may drive size- and stage-specific mortality of foundational coral taxa is central to our understanding of how reef ecosystems will fare in a changing climate.

In the Austral summer of 2019, Moorea, French Polynesia, experienced a prolonged marine heatwave with *in situ* ocean temperatures consistently above the long-term mean from December 2018 until July 2019. In response to this heatwave, we examined how bleaching-induced mortality of the two dominant genera of corals varied with coral size. The aim of our study was to describe the impacts of bleaching and mortality around the island of Moorea, and to evaluate the hypothesis that larger corals of the two dominant genera experienced higher rates of mortality than smaller corals. We then evaluated the potential for size-dependent bleaching and mortality to have cascading impacts on coral fecundity and recruitment, two factors closely tied to the resilience of reef communities.

We first conducted island-wide surveys on >2,200 individual corals and binned them into three coarse size classes to examine overall patterns of coral mortality and size at the island scale. Then, we chose one representative site on the north shore to examine finer-scale relationships between coral size and mortality where we collected data on >2,700 corals measured to the nearest centimeter. Next, we used long-term demographic data to ask whether coral mortality from this bleaching event resulted in different patterns of size-dependent mortality than are typical in years without bleaching events. We then estimated how size-dependent patterns of coral mortality following the heatwave influenced coral fecundity. We used published relationships between colony size, surface area, and gamete production to estimate how the loss of corals following this event changed the quantity of gametes produced by the dominant coral taxa. Finally, we examined how this marine heatwave influenced survival of the most recently settled corals by repeatedly surveying coral recruits *in situ* before and after the heatwave. Our goal was to not only examine the effects of marine heatwaves on corals across the size spectrum but to understand how severe bleaching events may impact the future dynamics of coral communities, specifically by disproportionately affecting the life stages most important for reproduction and recruitment of new individuals.

2. Materials and Methods

2.1. Ocean Temperature Data

Ocean temperature data (Fig. 1a) were collected continuously from 2005-2019 at six sites on the outer reef of Moorea as part of the Moorea Coral Reef LTER time series (LTER 1-6, See Fig. S1 for site locations)(Leichter, Seydel, & Gotschalk, 2019). At each site a bottom-mounted thermistor (Seabird SBE 39) recorded temperature at 20 min intervals at 10 m water depth, which we then used to calculate the average temperature at each site for each day of the 14-year time series. We used data through 31 July 2018 to analyze long-term mean temperature trends in Moorea. We first calculated the mean ocean temperature at each site on each day of the time series. We then used these daily means for each site to calculate the mean ocean temperature across all sites ± one standard deviation for each day in a 365-day year. To analyze temperature trends for August 2018-19, we considered data from 1 August 2018- 31 July 2019. A subset of four of the six LTER sites (at least one from each of the 3 sides of the island) had continuous data throughout this time series, and therefore we considered only those 4 sites in our analysis of temperature trends for this year. Using the same approach as the long-term trends, we first calculated the mean temperature for each day at each site, and then averaged the daily data at the four sites to calculate the mean daily temperature for this year (Fig. 1a).

Thermal stress that corals experience is a function of the magnitude and duration of warm water events. We used the site × day mean temperature from August 2018-August 2019 to calculate accumulated heat stress throughout this bleaching event. In Moorea, 29.0°C is the maximum monthly mean (MMM) temperature, a known threshold at which corals accumulate thermal stress in Moorea (Pratchett et al., 2013). We quantified accumulated heat stress as a 12-week running sum of mean weekly temperatures for which the mean water temperature exceeded 29.0°C. This is calculated similarly to NOAA Degree Heating Weeks (or °C-weeks) (Liu, Strong, & Skirving, 2003; Pratchett et al., 2013) which accumulate when the weekly mean water temperature is ≥MMM +1°C, except our metric accumulated heat stress any week when the water temperatures were +0.1°C >MMM (29.0°C). We calculated accumulated heat stress for 2018-2019 (Fig. 1b) and throughout our 14-year time series (Fig. S2). In 2018-2019, accumulated heat stress at 10 m on the outer reef peaked at 5.6 °C weeks which far exceeded the magnitude of other thermal stress events on the outer reef in Moorea in the last 14 years (Fig. S2). All statistical analyses and data visualization were performed in R (Version 3.5.2) and figures were made using the ggplot2 package (Wickham, 2010).

2.2. Island-wide patterns in coral bleaching and mortality

All benthic surveys were conducted along the 10 m isobath on the outer reef of Moorea. On 9-15 July 2019, approximately two months after the peak of accumulated heat stress, two divers on SCUBA conducted coral bleaching and mortality surveys (Fig. 2) at six sites on the outer reef, with two sites on each side of the island (Fig. S1) (Speare, Adam, Winslow, Lenihan, & Burkepile, 2021). *Pocillopora* were substantially more abundant than *Acropora* so we employed slightly different survey methods for the two genera. At each site, divers surveyed *Pocillopora* and *Acropora* along two 50 m transects, in which divers quantified bleaching and mortality for every *Pocillopora* that intercepted the transect. *Pocillopora* corals exhibit high phenotypic plasticity and cannot be reliably identified in the field based on morphology (Marti-Puig et al., 2014; Pinzón et al., 2013), therefore we identified pocilloporid corals to genus.

Acropora were much less abundant than *Pocillopora* so divers collected data for every *Acropora* within 1 m wide swath along the transect. There are at least 12 species of *Acropora* in Moorea (Carroll, Harrison, & Adjeroud, 2006), at least eight of which are common on the outer reef (*Acropora retusa, Acropora cerealis, Acropora hyacinthus, Acropora globiceps, Acropora lutkeni, Acropora nasuta, Acropora elseyi, and Acropora horrida*). *A. elseyi* and *A. horrida* are two species that have delicate branching morphologies and reproduce frequently by asexual fragmentation and reattachment. These species were uncommon in our dataset, but we omitted all individuals of these two species from our analyses for two reasons. First, both species fragment easily and therefore change size, and second, clusters of reattached fragments likely originated from one individual and therefore do not represent independent samples. Several of the common species (*A. retusa, A. cerealis, A. lutkeni, A. globiceps, A. nasuta*) share similar morphological characteristics and are difficult to identify *in situ*, particularly when colonies are bleached or dead and overgrown by algae. We pooled all *Acropora* in our dataset and considered patterns of *Acropora* mortality at the genus level because of the challenges of identifying dead individuals to species. While we recognize that pooling these taxa by genus may obscure possible differences in bleaching and mortality among species, pooling data by genus is common for ecological studies of corals at the landscape- and regional-scale, including studies that investigate size-specific impacts of disturbances on corals (Dietzel, Bode, Connolly, & Hughes, 2020; Gilmour, Smith, Heyward, Baird, & Pratchett, 2013).

Divers quantified bleaching and mortality for each individual coral colony ≥5 cm in diameter, which totaled 2,209 corals (1,446 *Pocillopora* and 763 *Acropora*). Each colony was binned into one of three size bins (5-9 cm, 10-29 cm, 30+ cm), and the percent that was bleached and recently dead was then estimated for each colony. Portions of colonies were considered 'recently dead' if they were visibly colonized by turf algae but not yet colonized by macroalgae (see Fig. S3). We categorized each coral in our surveys into one of four categories: Bleached (if any portion of the coral was bleached but there was no mortality), 1-49% mortality, 50-100% mortality, or Healthy (if no bleaching or mortality was present) and then calculated the mean proportion of corals in each category for each site and size class. Because the means of each category are not independent, we only tested for the effects of coral size on the proportion of colonies that were impacted by the heatwave (combining Bleached and Dead categories) for each genus. For each genus, we used linear mixed effects models to ask whether colony size (as an ordinal variable where 5-9 cm < 10-29 cm < 30+ cm) had a significant effect on the proportion of corals that were impacted (i.e., Bleached or Dead) using the *lmer()* function in the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). Differences in thermal stress at different sites could cause variation in the prevalence of bleaching and mortality, therefore we included site as a random effect in each of our models.

2.3. Fine-scale patterns in size-dependent coral mortality

To better understand how bleaching and mortality varied with coral colony size, we conducted more size-explicit coral bleaching and mortality surveys of 2,704 corals (2,395 *Pocillopora* and 309 Acropora) using finer scale resolution of colony size (Fig. 3) from 30 July – 7 August 2019 (Speare et al., 2021). Due to the time-intensive nature of these surveys, we conducted them only at 10 m depth at one site (the LTER Experimental Site, see Fig. S1) on the outer reef of the north shore of Moorea. Two SCUBA divers conducted ten 15 x 1 m-belt transects in which they visually estimated bleaching and mortality for every colony >5 cm diameter for 2,147 corals using the same methods as described earlier. For these surveys, we measured the longest diameter of each colony to the nearest centimeter using a meter stick with centimeter markings. We then surveyed the same transects a second time and expanded the width to 2 m (15 × 2 m belt transects) to quantify bleaching and mortality of juvenile corals 1-5 cm diameter (557 corals). We measured the diameter of each coral to the nearest centimeter using a ruler, and visually estimated the percent of the colony that was bleached and recently dead. To visualize the population size structure prior to bleaching-induced mortality, we generated size frequency distributions (binned in 5 cm increments) for all colonies that were healthy, bleached, or recently dead at the time of the surveys. We normalized counts of corals to the area surveyed to calculate size frequency distributions for *Pocillopora* and *Acropora* (Fig. S4c,d). To assess the relationship between colony size and the probability of mortality we calculated the proportion of individuals that had at least 50% partial mortality for each 5 cm size class (Fig. 3a,b). For *Pocillopora* and *Acropora,* we evaluated the relationship between colony size and the probability of having at least 50% partial mortality using a logistic regression (Fig. 3a,b).

For corals that exhibited partial colony mortality, most of the mortality was concentrated on the ends of the branches, and generally the only remaining live tissue was deep within the branches and around the base where there is limited access to light (see Fig. S3). Additionally, much of the remaining live tissue on colonies with partial mortality was still bleached at the time of our surveys (See Fig. S3). Coral colonies often exhibit delayed bleaching-induced mortality months after thermal stress subsides (Brown & Phongsuwan, 2012; Oxenford, Roach, & Brathwaite, 2008), therefore it is likely that colonies with severe partial mortality continued to lose live tissue after our surveys. Thus, we assumed that colonies with ≥50% partial mortality in our August surveys would be unlikely to survive long-term. We conducted follow-up surveys on 15-16 October 2019 to confirm this assumption. Here, we used the same methods as described above to survey >500 individual colonies of *Pocillopora* and >200 individuals of *Acropora* on the north shore (See Table S1 for the number of corals surveyed in each sampling period). We calculated the proportion of corals with 100% mortality for each 5 cm size class and evaluated the relationship between colony size and the probability of 100% mortality using a logistic regression (Fig. 3c,d).

2.4. Annual patterns of size-dependent mortality

Demographic surveys of coral were conducted at 10 m depth at four of the six LTER sites (LTER 1, 2, 4, and 5, see Fig. S1) from 2013 to 2019. At each site, four permanent 5 m^2 quadrats were established and all *Acropora* corals were mapped and measured (Lenihan, Ake, & Winslow, 2019). Nested within each 5 m^2 quadrat was a 1 m^2 quadrat where all *Pocillopora* corals were mapped and measured. Each coral was mapped on an x, y, z coordinate system, which served as a unique identifier for each coral and enabled tracking of individuals annually (Kayal et al., 2018). We measured the longest diameter of each colony to the nearest centimeter each year. These surveys resulted in 3,001 observations of annual survivorship from 2013-2019, of which 2,179 were for *Pocillopora*, and 822 were for *Acropora*. These annual surveys were used to calculate the probability of annual mortality of *Pocillopora* and *Acropora* across the size spectrum. In our data analysis, we used the size of the coral in the previous year (its last known size) to predict the probability of mortality in that year. Corals that died were removed from the dataset for all subsequent years. Corals were not surveyed in 2017 so data from 2016-2018 represents mortality over a two-year period.

We analyzed the relationship between colony size and the probability of mortality between years using generalized linear mixed models (Fig. 4a,b). We were interested in evaluating how this relationship between coral size and mortality may differ between high thermal stress years and low thermal stress years. To do this, we assigned each year a categorical variable of “year type” with categories of either “low thermal stress” (2013-2014, 2014-2015, 2015-2016, 2016-2018) or “high thermal stress” (2018-2019). We then used generalized linear mixed models (GLMMs, R package ‘lme4’) with a binomial distribution and fit models by maximum likelihood using the Laplace approximations (Bolker et al., 2009; Raudenbush, Yang, & Yosef, 2000). We modeled the probability of coral mortality using fixed effects of coral size, year type, and their interaction, and included random effects of site and year. We then used χ^2 likelihood ratio tests to evaluate the significance of fixed effects (Bolker et al., 2009). As a more conservative approach we also evaluated the significance of fixed effects using the parametric bootstrapping method (R package ‘pbkrtest’) (Halekoh & Højsgaard, 2014), but the significance patterns were quantitatively the same as results from the χ^2 tests in all cases, so we only report the χ^2 results here. Separate analyses were computed for *Pocillopora* and *Acropora*.

Throughout our demographic data collection, the outer reefs of Moorea were recovering from catastrophic disturbances from 2008-2010 (corallivorous crown-of-thorns seastar outbreak and a cyclone) that reduced coral cover to <1%. Therefore, all of the corals in our initial surveys in 2013 were newly-recruited juveniles, and population size structure shifted strongly from juvenile to adult size classes throughout the duration of our surveys (Fig. S5). We restricted analysis of our demographic data to individuals ≤30 cm diameter because there were no corals >30 cm in our initial surveys, and small numbers in our surveys up until 2018. Therefore, there were not enough individuals >30 cm in the first several years of our surveys to evaluate differences in survival of the largest individuals between high thermal stress (2018-2019) and low thermal stress years (2013-2018).

2.5. Estimating Coral Fecundity

We used our size-explicit coral bleaching and mortality survey data (August 2019) from the LTER Experimental Site to estimate coral fecundity before and after this mortality event for *Pocillopora* and *Acropora*. There are thought to be 6 common species of *Pocillopora* in Moorea (Edmunds, Leichter, Johnston, Tong, & Toonen, 2016), but corals in the genus *Pocillopora* exhibit significant phenotypic plasticity and cannot be identified reliably to species in the field based on morphology (Marti-Puig et al., 2014; Pinzón et al., 2013). For purposes of our fecundity estimates, we considered the fecundity of *Pocillopora* at the genus level, recognizing that there are likely differences among the cryptic species in this genus. In contrast, there are at least 12 species of *Acropora* in Moorea (Carroll et al., 2006). We acknowledge that these are distinct species, however, relationships between colony size and live tissue surface area have not been established at the species level. Reliable estimates of live surface area of corals can be made based on coral morphology (i.e. branching, massive, encrusting) (House et al., 2018), and estimates of gamete output are only available for certain species. Therefore, we estimated *Acropora* fecundity at the genus level using established relationships between colony size and surface area (House et al., 2018) and estimates of gamete output per unit coral surface area averaged at the genus level (Table S2).

For each genus, we estimated fecundity before and after the bleaching event. Using the coral bleaching and mortality surveys from August 2019, we made two estimates of coral fecundity for each genus. In the Pre-Bleaching estimate we assumed that all individuals that were healthy, bleached, or recently dead ($\geq$50% colony mortality) at the time of our surveys were alive and reproductive prior to the bleaching event. For the Post-Bleaching estimate we assumed that all individuals that had $\geq$50% colony mortality at the time of our surveys ultimately died and were no longer reproductive. This assumption is reasonable given that the majority of the colonies that had 50% mortality in August had 100% mortality by October (Fig. 3). For each estimate, we only included individuals that were likely to be reproductive based on previously published size thresholds. For *Pocillopora* we assumed that the size of the onset of sexual maturity is 14 cm diameter, given existing data for *Pocillopora meandrina* (Stimson, 1978). For *Acropora* most colonies at least 14 cm in diameter are reproductive (Hall & Hughes, 1996). Therefore, for both genera, we included only colonies $\geq$14 cm diameter for each fecundity estimate.

For each individual in our surveys, we used a calibration curve to estimate coral planar surface area from coral diameter (Table S2, described below) and then used published relationships between colony diameter and live surface (House et al., 2018) area to estimate fecundity of each colony in our dataset. Corals are colonial animals and individual polyps reproduce by releasing sexually-produced gametes (Richmond & Hunter, 1990). Therefore, the reproductive potential of a given colony can be estimated as a function of the number of individual polyps of the colony (*sensu* Tsounis & Edmunds, 2016). The number of polyps per colony scales linearly with the surface area of tissue of the colony, therefore, we can estimate the fecundity of each colony by calculating colony surface area and multiplying it by the number of eggs released per unit surface area.

We first created calibration curves to convert colony diameter to planar (2D) surface area using top-down photos of individual colonies (Table S2). For each colony, we measured colony diameter and traced the perimeter to calculate planar area in ImageJ. We then created calibration curves of diameter to planar surface area for colonies of *Pocillopora* and *Acropora* separately. We then estimated live tissue area of each colony from the planar surface area of each colony using published relationships (House et al., 2018). Next, we used our estimates of live tissue area for each colony to estimate fecundity of each colony (expressed as eggs cm^{-2} yr^{-1} for *Pocillopora,* and oocytes cm^{-2} yr^{-1} for *Acropora*) based on published estimates of fecundity per unit coral surface area (Kotb, Hanafy, & Monir, 2018; Tsounis & Edmunds, 2016). See Table S3 for parameter estimates.

Using these relationships between colony diameter, surface area, and gamete output, we estimated the fecundity of each coral in our dataset and propagated error using a Monte Carlo simulation framework. For each run of the simulation we used a random draw of each parameter estimate (assuming normal distribution of standard errors, which were estimated in original studies given in Table S2) and applied those parameters to all individuals in the genus to estimate individual colony fecundity. Fecundity of individual colonies was summed and divided by the total area surveyed in the fine resolution surveys to estimate annual area normalized genus-level fecundity (eggs or oocytes m^{-2} yr^{-1}) for each run of the simulation. We then calculated the relative change in fecundity as the difference between Pre-Bleaching and Post-Bleaching fecundity divided by the Pre-Bleaching fecundity. We repeated this process 1000 times. The mean was then calculated as the average fecundity of 1,000 runs of the simulation with 95% confidence intervals (Fig. 5a,c). We also summed fecundity for each coral size class for each run of the simulation. We then calculated the relative contribution that each size class made to total fecundity at the genus level before and after the bleaching event (Fig. 5b,d).

2.6. Survivorship of coral recruits

We assessed survivorship of coral recruits *in situ* during the bleaching event using 64 coral limestone settlement tiles deployed at 10 m on the outer reef at the LTER Experimental Site (see Fig. S1)(Speare et al., 2021). Coral settlement tiles were deployed in August 2018 and accumulated naturally-settled recruits throughout the timeframe of our study. Coral recruits are notoriously difficult to identify while alive so it was not possible to identify the recruits on our tiles to genus. However, prior data shows that typically most recruits on the north shore of Moorea are Pocilloporidae and some Acroporidae (Edmunds, 2018). The overwhelming majority of *Pocillopora* coral species and all *Acropora* species on the outer reef of Moorea are broadcast spawning species, therefore it is unlikely that different modes of reproduction influenced the patterns of recruitment on our tiles.

During 23-31 March 2019, coral settlement tiles were collected from the reef daily in groups of eight and transported to the wet lab at the Richard B. Gump research station in a cooler of seawater. The surfaces of each tile were digitally photographed (Olympus Stylus Tough TG-4 camera). We searched each tile for coral recruits using a dissecting microscope, and the location of each individual recruit was marked and numbered on the digital photos of each tile. Tiles were kept submerged in seawater throughout this process and returned to the reef within 24 hours of collection. This method has been used to successfully track the fate of individual coral recruits in the field without significant handling effects (Price, 2010).

Tiles were returned to the reef for 4 months and collected again from 14-30 July 2019, after the thermal stress event was over. Of the 64 tiles originally deployed, 34 tiles had 1-9 coral recruits per tile in March 2019. We searched these tiles again for coral recruits, looking specifically in locations where recruits were previously mapped. Recruits that were mapped in March were then scored as either Alive or Dead in July. For the tiles that had coral recruits we computed mean survival for each tile (n=34). In 2017, we tracked coral recruit survival during the same timeframe (March – July) using the same methods (n=12 tiles). We therefore can compare the recruit survival data in 2019, a year with high prolonged thermal stress, to recruit survival in 2017, a year with low thermal stress (Fig. 6). We first compared survivorship at the tile level in 2017 vs. 2019 using a t-test. Next, we asked whether there was a relationship between tiles having at least one surviving recruit and the year (2017 or 2019) using a contingency test as a more conservative approach.

The settlement tiles that were scored in 2019 were part of a factorial *in situ* experiment that artificially manipulated herbivore abundance (via herbivore exclusion) and nutrient enrichment (via nutrient diffusers filled with Osmocote slow-release fertilizer), and adult coral community disturbance (adult corals removed or adult coral community intact). We used a linear mixed effects model to test the null hypothesis that the experimental treatments (herbivore exclusion, nutrient enrichment, and coral disturbance) had no effect on coral recruit survival. This was a blocked factorial experiment, therefore, we included the experimental blocked as a random effect. There was no effect of herbivore exclusion, nutrient enrichment, or coral disturbance on coral recruit survival during this thermal stress event (Table S3). We therefore conclude that the effects of thermal stress overwhelmed any effects of the experimental treatments.

3. Results

3.1. Magnitude of thermal stress

Moorea experienced a prolonged marine heatwave in the Austral summer of 2019. From December 2018 until July 2019, the ocean temperature at 10 m water depth (measured *in situ*) was consistently above the long-term mean ocean temperature by at least one standard deviation (Fig. 1a). From 14 December 2018 until 1 May 2019, ocean temperatures were above 29.0°C, which is the threshold often used for predicting the accumulation of thermal stress in corals in Moorea (Pratchett et al., 2013), for 115 of 139 days, including 63 consecutive days from 28 February until 1 May 2019. These sea surface temperatures resulted in a maximum of 5.6 degree weeks of accumulated thermal stress (defined as accumulated degrees above 29.0°C during a 12-week period, Fig. 1b) (Liu et al., 2003; Pratchett et al., 2013) in late April. This level of thermal stress is one of the highest seen on these reefs over the past 30 years (Fig. S2) (Leichter et al., 2019; Pratchett et al., 2013).

3.2. Island-wide patterns of coral bleaching and mortality

Prior to the thermal stress event, coral cover on the forereefs of Moorea ranged from 13-80% (mean 47%) at 10 m water depth across six sites around the island that are part of the Moorea Coral Reef Long Term Ecological Research (MCR LTER) time series (see Fig. S1 for site locations). *Pocillopora* spp. and *Acropora* spp. were the two most abundant genera, representing 52-81% (mean 63%) and 4-20% (mean 10%) of the coral community, respectively (Edmunds, 2020). In early July 2019, we conducted bleaching and mortality surveys using coarse colony size bins (5-9 cm, 10-29 cm, 30+ cm diameter) at 10 m depth at each of these six sites. By this time, the marine heatwave had passed as ocean temperatures were 26.7°C, well below the 29.0°C threshold for accumulating thermal stress (Fig. 1a,b).

In our survey of >2,200 individual corals, we found that the marine heatwave drove strong size-dependent patterns in bleaching and mortality for the two dominant genera of corals (Fig. 2). Although ocean temperatures had cooled considerably since their peak in late April, 47% of remaining live *Acropora* (but only 6% of *Pocillopora*) were still bleached in early July. There was also extensive recent mortality for both genera, indicating that bleaching had been widespread and intense. On average, 46% of *Pocillopora* and 89% of *Acropora* colonies (≥5 cm diameter) showed some bleaching or partial mortality in early July, and 25% of *Pocillopora* and 54% of *Acropora* colonies had at least 50% partial mortality (Fig. 2). At the island-wide scale, the proportion of colonies impacted with either bleaching or mortality was significantly skewed towards the largest size classes for *Pocillopora* and *Acropora* (mixed effects model $P<0.0001$ and $P=0.0190$, respectively), although the strength of this effect varied somewhat across sites (Fig. 2).

3.3. Fine-scale patterns of size-dependent coral mortality

To more thoroughly examine the impact of bleaching-induced mortality across the size spectrum of corals, we conducted additional size-explicit surveys of >2,700 corals on the north shore of Moorea in August 2019, including individuals from 1 cm diameter juveniles to the largest adults (>50 cm diameter) (Fig. 3a,b, see Table S1 for the number of corals surveyed in each size class). At the time of these surveys there was high prevalence of severe partial mortality (≥50% of the colony dead). Similar to our island-wide surveys using coarse size bins, our size-explicit surveys of coral mortality in August 2019 showed that for both *Pocillopora* and *Acropora* larger corals were significantly more likely to have at least 50% partial mortality than smaller corals (Fig. 3a,b and logistic regression; $P<0.0001$ for both *Pocillopora* and *Acropora*). For *Pocillopora,* 76% of individuals ≥30 cm diameter had at least 50% partial mortality, compared with 17% of individuals <30 cm diameter. *Pocillopora* ≥30 cm covered >40% of the benthos (Fig. S3a,b), therefore the loss of the largest individuals resulted in a substantial loss of live coral cover. For *Acropora,* the size dependent pattern was less stark, though still significant, with 65% of individuals ≥30 cm diameter having at least 50% partial mortality, compared to 50% of individuals <30 cm diameter. Notably, severe mortality (>50% partial mortality) of juvenile corals (<5 cm diameter) was minimal with <2% of individuals for both *Acropora* and *Pocillopora* experiencing severe partial mortality (Fig. 3a,b).

We conducted follow-up surveys in October with a smaller number of corals (Table S1). These data showed that for both *Pocillopora* and *Acropora,* the size-specific patterns in total colony mortality (100% mortality of coral tissue on a colony) closely matched the size-specific patterns of colonies with at least 50% mortality in August (Fig. 3 a-d). These data suggest that most colonies with severe partial mortality (>50% mortality) in our August surveys had died completely by October.

3.4. Bleaching reverses past patterns of size-dependent mortality

The pattern of increasing mortality with increasing colony size during the recent marine heatwave reversed the patterns of typical size-structured mortality. Annual surveys tracking the fate of individual *Pocillopora* in permanently marked plots at 10 m depth at four of the six LTER sites (LTER 1, 2, 4, and 5) showed that, in years with no or low thermal stress, juvenile corals (<5 cm) had more than twice the annual mortality rate (41%) of corals over 20 cm diameter (18%, Fig. 4a). Similarly, for *Acropora,* juvenile corals (<5 cm) had approximately three times the annual mortality rate (32%) of corals over 20 cm (11%, Fig. 4b) in years with minimal thermal stress. These patterns of high annual mortality for small corals and low annual mortality for large corals differ dramatically from patterns following the 2019 heatwave where intense thermal stress increased mortality of larger colonies substantially. Thus, in 2018-19, the relationship between colony size and annual mortality for both genera was significantly different as compared to all other years (GLMM; Size x Year Type interaction P=0.0001 and P=0.0083 for *Pocillopora* and *Acropora*, respectively; Fig. 4a,b). Therefore, the 2019 thermal stress event eliminated the typical pattern of higher annual survivorship of larger individuals.

3.5. Estimating effects on coral fecundity

Using our data on the size structure of coral populations from our August 2019 surveys, we estimated fecundity (as the number of eggs produced m^{-2} yr^{-1}) for *Pocillopora* and

Acropora before and after the thermal stress event. To estimate fecundity, we used published relationships between coral size, surface area, and gamete output using a Monte Carlo simulation framework. We found that mortality from the thermal stress event significantly reduced fecundity by 58% and 64% of pre-bleaching levels for *Pocillopora* and *Acropora*, respectively (Fig. 5a,c).

Although this event likely decreased fecundity by approximately the same magnitude in the two genera it did so by affecting fecundity differently across size classes. For *Pocillopora*, the bleaching event caused a major shift in the size of individuals responsible for the majority of reproduction due to the loss of the largest individuals (Fig. 5b). Prior to the bleaching event, we estimated that individuals ≥30 cm in diameter produced >58% of the total eggs released from *Pocillopora.* However, we estimated that following the bleaching event individuals <30 cm will now be responsible for the majority of reproduction, producing at least 70% of the eggs released by *Pocillopora*. For *Acropora,* the impact on total fecundity was similar to *Pocillopora* but was much less size-specific. In other words, higher overall rates of *Acropora* mortality of individuals large enough to reproduce substantially reduced the total number of eggs released by *Acropora*, but did not result in major changes in the size classes of corals responsible for the majority of reproduction relative to pre-bleaching levels (Fig. 5d).

3.6. Survivorship of coral recruits

In addition to large reductions in fecundity, we also found that survivorship of recently-settled recruits was extremely low during the 2018-2019 marine heatwave. We quantified recruit survivorship using used repeated surveys of removable settlement tiles before and after the thermal stress event. At the first census each tile had 1-9 recently-settled 1-3 mm coral recruits that were <1 yr old (likely mostly Pocilloporidae with some Acroporidae (Edmunds, 2018), although recruits are notoriously difficult to identify while alive). Mortality of recently-settled coral recruits was extremely high, with 98% of recruits dying between March and July 2019 during the marine heatwave (n=34 tiles, Fig. 6a). By comparison, for the same time period in 2017, a year with low thermal stress, only 67% of coral recruits died (n=12 tiles). Thus, survivorship of coral recruits declined by over an order of magnitude, from 33% in 2017, a year with low thermal stress, to 2% in 2019, a year with extreme thermal stress (two tailed t-test, t=2.9549, df=11.38, P=0.0126, Fig. 6a) Applying a more conservative analysis, we asked whether tiles were equally likely to have at least one surviving coral recruit in 2017 and 2019. Our results showed that the likelihood of a tile having at least one surviving coral recruit was an order of magnitude lower in 2019 than in 2017 (6% of tiles vs. 67% of tiles having a surviving coral recruit respectively; contingency test, χ^2=15.855, df=1, P<0.0001, Fig. 6b).

4. Discussion

Coral bleaching events will likely increase in frequency and intensity as climate change progresses, causing mass-mortalities of corals, the foundation taxa of coral reefs. The prolonged marine heatwave in Moorea, French Polynesia in 2019 resulted in some of the highest levels of thermal stress observed on these reefs for the past 30 years (Leichter et al., 2019; Pratchett et al., 2013) (Fig. S2). Here we show that this mass coral bleaching event disproportionately impacted the largest coral colonies. For *Pocillopora,* up to 76% of colonies ≥30 cm diameter died, compared with 17% of individuals <30 cm diameter. For

Acropora, up to 65% of colonies ≥30 cm diameter died, compared to 50% of individuals <30 cm diameter. In other words, colonies of *Pocillopora* and *Acropora* ≥30 cm diameter were ~3.5× and ~1.3×, respectively, more likely to die than colonies <30 cm diameter. This event reshaped typical size-mortality patterns, where smaller corals are more likely to die in a given year, and eliminated the major reproducers of two dominant coral taxa. Because large coral colonies are very fecund and disproportionately responsible for reproduction on coral reefs (Hall & Hughes, 1996), we estimate that this bleaching event reduced overall fecundity on these reefs by >58% for both *Pocillopora* and *Acropora.* Further, we show that 98% of coral recruits died during this heatwave, an order of magnitude decrease in survivorship as compared to years without thermal stress. Together, these results suggest that bleaching events may compromise recovery capacity of coral reefs by disproportionately impacting the life stages most critical for reef recovery, coral recruits and the largest, most fecund corals.

4.1. Impacts of marine heatwaves on the largest corals

Morphological and taxonomic differences in susceptibility to thermal stress drive variability in coral bleaching and mortality (Loya et al., 2001). This idea of ‘winners and losers’ among taxa in coral communities in response to heat stress is well known (Marshall & Baird, 2000; van Woesik, Sakai, Ganase, & Loya, 2011), where branching and plating taxa tend to bleach and die more frequently than massive and encrusting taxa (Loya et al., 2001). However, we show that even within taxa there are ‘winners and losers’ as colony size also drives major variability in response to thermal stress within taxa. We showed that larger colonies of *Pocillopora* spp. and *Acropora* spp. are significantly more likely to die from bleaching compared with smaller conspecifics. Past work has shown that juvenile corals are relatively resistant to bleaching compared to adults (Bena & Van Woesik, 2004; Depczynski et al., 2013; Loya et al., 2001), and small-scale field studies have found that coral colony size can be positively correlated with bleaching prevalence, severity, and mortality (Bena & Van Woesik, 2004; Depczynski et al., 2013; Pratchett et al., 2013; Shenkar et al., 2005). Here, we show that these relationships can manifest in landscape-scale patterns of coral mortality following a severe marine heatwave.

Although it was not the aim of our study to evaluate the mechanisms that drove size-dependent bleaching, it is likely that several mechanisms, which are not mutually exclusive, contributed to the size-dependent patterns of bleaching susceptibility and mortality. First, strong theoretical and empirical evidence suggests that differences in mass transfer rates can make larger corals more susceptible to bleaching during thermal stress (Nakamura & Woesik, 2001; van Woesik, Irikawa, Anzai, & Nakamura, 2012). One mechanism of coral bleaching is when harmful metabolites (oxygen radicals) produced by coral photosymbionts build up in coral tissues during periods of thermal stress (Downs et al., 2002; Lesser, Stochaj, Tapley, & Shick, 1990). Mass transfer rates govern corals' ability to exchange metabolites with the surrounding seawater, and these rates vary with size and morphology for marine invertebrates (Bena & Van Woesik, 2004; Nakamura & Woesik, 2001; Patterson, 1992; van Woesik et al., 2012). Therefore, due to lower mass transfer rates, larger coral colonies may be less likely to shed these harmful metabolites formed during thermal stress, resulting in more severe bleaching and mortality (van Woesik et al., 2012). Additionally, smaller corals are often relatively flat and have a low height to diameter ratio compared to larger, highly branched colonies of the same taxa. Flatter morphologies typically have higher rates of mass transfer than branching morphologies, and this could contribute to higher bleaching resistance in smaller corals (Loya et al., 2001). It is also possible that ontogenetic differences in Symbiodiniaceae communities (Coffroth, Santos, & Goulet, 2001; McIlroy, Cunning, Baker, & Coffroth, 2019) or efficiency of photosynthetic pathways (Edmunds & Gates, 2004) make smaller corals more resistant to thermal stress.

Another mechanism that likely contributed to size-dependent bleaching is differential bleaching susceptibility among cryptic species of *Pocillopora* (Burgess, Johnston, Wyatt, Leichter, & Edmunds, 2021). Corals in the genus *Pocillopora* exhibit significant phenotypic plasticity with many species being morphologically indistinguishable in the field (Johnston et al., 2017). Molecular identification of *Pocillopora* corals in Moorea suggests that at the time of the bleaching event, large individuals may have been disproportionately represented by thermally-sensitive cryptic species that experienced higher rates of mortality than other cryptic species (Burgess et al., 2021). Differences in thermal sensitivity among cryptic species of *Pocillopora* likely played a role in driving the size-dependent bleaching and mortality during this event (Burgess et al., 2021). Size-dependent bleaching may have also occurred within *Pocillopora* species, and this pattern has been reported for several species in other genera (Brandt, 2009; Shenkar et al., 2005). Several of these mechanisms are likely operating in concert to drive the size-dependent patterns in morality we saw where the largest individuals of the two dominant genera were nearly completely extirpated.

It is possible that the patterns we observed were driven in part by mass coral settlement events following past disturbances in Moorea. From 2007-2009, the reefs around Moorea experienced a severe COTS outbreak followed by a cyclone in 2010 that resulted in landscape-scale loss of nearly all corals on the outer reef (Adam et al., 2011; Kayal, Lenihan, Pau, Penin, & Adjeroud, 2011). Following these disturbances, Moorea's reefs returned to pre-disturbance coral cover in less than a decade, which was largely driven by high rates of coral recruitment (Holbrook et al., 2018). These catastrophic disturbances from 2007-2010 removed the existing population size-structure and genetic diversity, and recovery was likely driven by the establishment and success of just a few cohorts of new individuals that grew to reach large size classes at the same time. If coral size is a strong driver of variation in bleaching susceptibility, as our data shows, then reefs that were dominated by large individuals, especially if they were of bleaching-sensitive cryptic species, would have been particularly vulnerable to marine heatwaves that could cause another mass-mortality event. Furthermore, bleaching events that eliminate entire size classes of large individuals may set the stage for sequential catastrophic disturbances from bleaching as cohorts of corals that are relatively uniform in size grow into the bleaching sensitive size class at the same time.

4.2. Vulnerability of coral recruits to thermal stress

Coral recruitment is an essential first step for recovery of coral populations following catastrophic disturbances, and processes that inhibit recruitment or recruit survival can create bottlenecks that slow or prevent coral recovery. Low rates of recruitment are common following severe bleaching events (Aronson, Precht, Toscano, & Koltes, 2002; Burt & Bauman, 2020; Roth, Koksal, & Van Woesik, 2010), and past work has suggested that this is driven by the breakdown of stock-recruitment relationships due to the loss of reproductive adults (Hughes et al., 2019). However, it is also possible that recruits are scarce after bleaching events if recruits already present on the benthos have high-rates of mortality during periods of thermal stress. Our data are the first to suggest that the paucity of coral recruits following bleaching events may be influenced by near complete loss of entire cohorts of newly-settled coral recruits in addition to loss of the largest, most fecund corals during these events. To our knowledge this is the first published data on survivorship of coral recruits *in situ* during a marine heatwave.

Coral recruits have high-rates of early post-settlement mortality because they are highly vulnerable to predation (Christiansen, Ward, Harii, & Tibbetts, 2009; Gallagher & Doropoulos, 2017), competition (Arnold & Steneck, 2011), and stressors such as sedimentation and pollution (Babcock & Smith, 2002; Negri et al., 2005). Limited data from laboratory experiments (Fourney & Figueiredo, 2017; Nozawa & Harrison, 2007) and our unique data from *in situ* recruits show that marine heatwaves may also be a significant source of post-settlement mortality. Why coral recruits experience such high mortality during thermal stress (98% in our study) is uncertain. Most coral recruits of broadcast spawning corals (which typically account for >90% of recruits in Moorea (Edmunds, 2018)) begin life as aposymbiotic larvae that acquire symbionts from the environment (horizontal transmission) as larvae or early after settlement. Some evidence suggests that depriving coral recruits of symbionts in the first ~7 months post-settlement can substantially reduce their propensity to acquire symbionts later (McIlroy & Coffroth, 2017). It is possible that severe thermal stress that occurs early in ontogeny for coral recruits impairs the ability of recruits to acquire symbionts, which would adversely affect survival. Other work has shown that the respiration rate of coral recruits increases substantially at higher temperatures, suggesting that as temperatures increase coral recruits will have higher metabolic rates and therefore will require more energy to meet their metabolic needs (Edmunds, 2005). In the context of a prolonged marine heatwave, higher energy demands may be detrimental to coral recruits, especially if recruits have low densities of symbionts and therefore are receiving less photosynthetically-derived energy. Regardless of the mechanisms, high rates of mortality in coral recruits during marine heatwaves will have far reaching consequences for coral population dynamics and will probably slow coral recovery following bleaching events and other climate-driven perturbations.

4.3. Consequences for coral reproduction

Corals are modular, colonial organisms that become reproductively mature once they reach a size threshold, beyond which fecundity increases with colony size (Hall & Hughes, 1996). Size-specific fecundity makes large, mature colonies disproportionality important for reproduction. We showed that large colonies were also the most likely to die during the 2019 bleaching event, and we estimated that the size-specific patterns in mortality that we documented will reduce fecundity by >60% for *Pocillopora* spp. and *Acropora* spp. on these reefs (Fig. 5). This major reduction in the abundance of reproductive corals, and the near complete extirpation of large colonies will greatly reduce the number of coral larvae produced. Fewer larvae could slow reef recovery, especially if most of the larvae available to these reefs are self-seeded as opposed to arriving from other sources, which may be the case for *Pocillopora* on reefs around Moorea (Edmunds et al., 2016).

When large colonies are lost to bleaching there will be a major shift in the reproductive burden from large to small colonies, and this will likely have more severe effects on fecundity that our estimates did not capture. For example, larger colonies can produce larger eggs per polyp, therefore giving offspring more stored energy and a better chance of survival, than smaller conspecifics (Baird & Marshall, 2002), a relationship that we did not account for in our estimates of fecundity. Additionally, the sex allocation (volume of eggs and sperm produced) of corals can vary substantially with colony size, where larger colonies invest more energy in producing eggs (Hall & Hughes, 1996). Thus, truncating the size distribution of corals may result in a higher ratio of sperm to eggs produced by the remaining corals. The energetic costs associated with bleaching stress and recovery can also cause the surviving corals to reduce (Fine, Zibrowius, & Loya, 2001) or stop gamete production (Szmant & Gassman, 1990) for years following bleaching events (Levitan, Boudreau, Jara, & Knowlton, 2014). Thus, this bleaching event will likely have substantially more negative effects on fecundity than we estimate, likely creating a substantial bottleneck to coral recovery. If the size-dependent bleaching mortality that we observed in Moorea is a widespread pattern, dampening of fecundity caused by the loss of large individuals will be a significant impact to the resilience of coral reefs worldwide.

One challenge for our study was that we necessarily had to analyze our data at the genus level due to the inability to differentiate cryptic species in the field and the challenge in identifying recently dead, algal-covered corals past genus level. While grouping taxa at the genus level is not ideal, it is commonly done across the coral literature (as well as in other systems where visual taxonomy is challenging) because understanding patterns of mortality at the genus level is often ecologically meaningful for understanding the community and landscape-scale consequences of coral bleaching events. Loss of the largest corals, regardless of the species, will result in a substantial decrease in the number of coral larvae produced by the coral community, and therefore significantly fewer larvae will be available to reseed the reef.

4.4. Cascading impacts of losing the largest corals

The loss of the largest corals and subsequent shifts to higher relative abundance of smaller individuals will drastically alter the reefscape, likely triggering cascading impacts on other reef taxa that rely on corals for habitat (Hughes et al., 2018). Immediately following bleaching events, the loss of live coral cover can cause substantial declines in fishes and invertebrates that rely directly on live coral for food and shelter (Wilson, Graham, Pratchett, Jones, & Polunin, 2006). The loss of structural complexity, a long-term consequence of bleaching-induced coral mortality, can also trigger severe declines in fish and invertebrate abundance and diversity beyond those taxa that directly rely on corals (Adam et al., 2014; Pratchett et al., 2008). Corals create structural complexity that moderates competition and predation among reef inhabitants, and as it is lost, fish abundance, diversity, and functional redundancy also declines (Pratchett, Hoey, Wilson, Messmer, & Graham, 2011; Pratchett et al., 2008). Large corals are disproportionately important for the provisioning of habitat for reef inhabitants (Abele & Patton, 1976), therefore the loss of the largest corals during a marine heatwave will likely result in the reorganization of fish and invertebrate communities that could not be predicted based on the magnitude of loss in coral abundance alone.

In summary, our study reveals that a marine heatwave not only caused mass coral bleaching and mortality, but that it reversed typical size-mortality relationships, causing near complete loss of the largest individuals of the dominant taxa. As marine heatwaves and coral bleaching events become more frequent and intense, they may truncate the size distribution of bleaching-sensitive coral taxa, resulting in persistent shifts in coral population size structure skewed toward small individuals. Importantly, the asymmetric loss of large individuals can have more adverse effects on the persistence of populations than does the loss of juveniles or earlier life stages (Edmunds & Elahi, 2007; Heppell, Crowder, & Crouse, 1996; Hixon, Johnson, & Sogard, 2014; Vardi, Williams, & Sandin, 2012). Large corals, which typically have low mortality rates and high fecundity rates, are disproportionately important for seeding reef recovery and for creating habitat structure for other taxa.

The higher sensitivity of large corals to bleaching-induced mortality parallels the disproportionate loss of other large foundation species, like trees during droughts. Large trees, like large corals, may be more sensitive to the effects of climate change because they are more likely to experience severe changes in physiological processes during extreme events (Rowland et al., 2015). The disproportionate loss of large, ecologically-important individuals of foundation taxa due to climate change will have cascading impacts on ecosystems. By fundamentally reshaping typical demographic patterns, climate change-driven disturbances may slow recovery rates of foundation species, ultimately reorganizing the assemblages that depend on them for habitat.

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References

Abele, L. G., & Patton, W. K. (1976). The size of coral heads and the community biology of associated decapod crustaceans. *Journal of Biogeography*, *3*(1), 35–47. https://doi.org/10.2307/3038097

Adam, T. C., Brooks, A. J., Holbrook, S. J., Schmitt, R. J., Washburn, L., & Bernardi, G. (2014). How will coral reef fish communities respond to climate-driven disturbances? Insight from landscape-scale perturbations. *Oecologia*, *176*(1), 285–296. https://doi.org/10.1007/s00442-014-3011-x

Adam, T. C., Schmitt, R. J., Holbrook, S. J., Brooks, A. J., Edmunds, P. J., Carpenter, R. C., & Bernardi, G. (2011). Herbivory, connectivity, and ecosystem resilience: Response of a coral reef to a large-scale perturbation. *PLoS ONE*, *6*(8). https://doi.org/10.1371/journal.pone.0023717

Anderegg, W. R. L., Berry, J. A., Smith, D. D., Sperry, J. S., Anderegg, L. D. L., & Field, C. B. (2012). The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences*, *109*(1), 233–237. https://doi.org/10.1073/pnas.1107891109

Anderegg, W. R. L., Kane, J. M., & Anderegg, L. D. L. (2013). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, *3*(1), 30–36. https://doi.org/10.1038/nclimate1635

Arnold, S. N., & Steneck, R. S. (2011). Settling into an Increasingly Hostile World: The Rapidly Closing "Recruitment Window" for Corals. *PLoS ONE*, *6*(12), e28681. https://doi.org/10.1371/journal.pone.0028681

Aronson, R. B., Precht, W. F., Toscano, M. A., & Koltes, K. H. (2002). The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology*, *141*(3), 435–447. https://doi.org/10.1007/s00227-002-0842-5

Babcock, R., & Smith, L. (2002). Effects of sedimentation on coral settlement and survivorship. In *Proceedings of the Ninth International Coral Reef Symposium, Bali, 23-27 October 2000,* (Vol. 1, pp. 245–248).

Baird, A. H., & Marshall, P. A. (2002). Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series*, *237*, 133–141.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bena, C., & Van Woesik, R. (2004). The impact of two bleaching events on the survival of small coral colonies (Okinawa, Japan). *Bulletin of Marine Science*, *75*(1), 115–125.

Bennett, A. C., McDowell, N. G., Allen, C. D., & Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, *1*(10), 15139. https://doi.org/10.1038/nplants.2015.139

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/http://dx.doi.org/10.1016/j.tree.2008.10.008

Brandt, M. E. (2009). The effect of species and colony size on the bleaching response of reef-building corals in the Florida Keys during the 2005 mass bleaching event. *Coral Reefs*, *28*(4), 911–924. https://doi.org/10.1007/s00338-009-0548-y

Brown, B. E., & Phongsuwan, N. (2012). Delayed mortality in bleached massive corals on intertidal reef flats around Phuket, Andaman Sea, Thailand. *Phuket Mar. Biol. Cent. Res. Bull.*, *48*(April 2010), 43–48.

Burgess, S. C., Johnston, E. C., Wyatt, A. S. J., Leichter, J. J., & Edmunds, P. J. (2021). Response diversity in corals: hidden differences in bleaching mortality among cryptic Pocillopora species. *Ecology*, *102*(6). https://doi.org/10.1002/ecy.3324

Burt, J. A., & Bauman, A. G. (2020). Suppressed coral settlement following mass bleaching in the southern Persian/Arabian Gulf. *Aquatic Ecosystem Health and Management*, *23*(2), 166–174. https://doi.org/10.1080/14634988.2019.1676024

Carroll, A., Harrison, P., & Adjeroud, M. (2006). Sexual reproduction of Acropora reef corals at Moorea, French Polynesia. *Coral Reefs*, *25*(1), 93–97. https://doi.org/10.1007/s00338-005-0057-6

Christiansen, N. A., Ward, S., Harii, S., & Tibbetts, I. R. (2009). Grazing by a small fish affects the early stages of a post-settlement stony coral. *Coral Reefs*, *28*(1), 47–51. https://doi.org/10.1007/s00338-008-0429-9

Coffroth, M., Santos, S., & Goulet, T. (2001). Early ontogenetic expression of specificity in a cnidarian-algal symbiosis. *Marine Ecology Progress Series*, *222*, 85–96. https://doi.org/10.3354/meps222085

Depczynski, M., Gilmour, J. P., Ridgway, T., Barnes, H., Heyward, A. J., Holmes, T. H., … Wilson, S. K. (2013). Bleaching, coral mortality and subsequent survivorship on a West Australian fringing reef. *Coral Reefs*, *32*(1), 233–238. https://doi.org/10.1007/s00338-012-0974-0

Dietzel, A., Bode, M., Connolly, S. R., & Hughes, T. P. (2020). Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1936), 20201432. https://doi.org/10.1098/rspb.2020.1432

Downs, C. A., Fauth, J. E., Halas, J. C., Dustan, P., Bemiss, J., & Woodley, C. M. (2002). Oxidative stress and seasonal coral bleaching. *Free Radical Biology and Medicine*, *33*(4), 533–543. https://doi.org/10.1016/S0891-5849(02)00907-3

Edmunds, P. J. (2005). Effect of elevated temperature on aerobic respiration of coral recruits. *Marine Biology*, *146*(4), 655–663. https://doi.org/10.1007/s00227-004-1485-5

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), 1–11. https://doi.org/10.1038/s41598-018-34686-z

Edmunds, P. J. (2020). Moorea Coral Reef LTER. 2020. MCR LTER: Coral Reef: Long-term Population and Community Dynamics: Corals, ongoing since 2005. knb-lter-mcr.4.38 https://doi.org/10.6073/pasta/10ee808a046cb63c0b8e3bc3c9799806

Edmunds, P. J., & Elahi, R. (2007). The demographics of a 15-year decline in cover of the Caribbean reef coral Montastraea annularis. *Ecological Monographs*, *77*(1), 3–18. https://doi.org/10.1890/05-1081

Edmunds, P. J., & Gates, R. D. (2004). Size-Dependent Differences in the Photophysiology of the Reef Coral Porites astreoides. *The Biological Bulletin*, *206*(2), 61–64. https://doi.org/10.2307/1543536

Edmunds, P. J., Leichter, J. J., Johnston, E. C., Tong, E. J., & Toonen, R. J. (2016). Ecological and genetic variation in reef-building corals on four Society Islands.

Limnology and Oceanography, *61*(2), 543–557. https://doi.org/10.1002/lno.10231

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., … Webster, J. R. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, *3*(9), 479–486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2

Fine, M., Zibrowius, H., & Loya, Y. (2001). Oculina patagonica: a non-lessepsian scleractinian coral invading the Mediterranean sea. *Marine Biology*, *138*(6), 1195–1203. https://doi.org/10.1007/s002270100539

Fourney, F., & Figueiredo, J. (2017). Additive negative effects of anthropogenic sedimentation and warming on the survival of coral recruits. *Scientific Reports*, *7*(1), 1–8. https://doi.org/10.1038/s41598-017-12607-w

Gallagher, C., & Doropoulos, C. (2017). Spatial refugia mediate juvenile coral survival during coral–predator interactions. *Coral Reefs*, *36*(1), 51–61. https://doi.org/10.1007/s00338-016-1518-9

Gilmour, J. P., Smith, L. D., Heyward, A. J., Baird, A. H., & Pratchett, M. S. (2013). Recovery of an Isolated Coral Reef System Following Severe Disturbance. *Science*, *340*(6128), 69–71. https://doi.org/10.1126/science.1232310

Halekoh, U., & Højsgaard, S. (2014). A Kenward-Roger Approximation and Parametric Bootstrap Methods for Tests in Linear Mixed Models - The R Package pbkrtest. *Journal of Statistical Software*, *59*(9), 1–32. https://doi.org/10.18637/jss.v059.i09

Hall, V. R., & Hughes, T. P. (1996). Reproductive strategies of modular organisms: comparative studies of reef- building corals. *Ecology*, *77*(3), 950–963. https://doi.org/10.2307/2265514

Heppell, S. S., Crowder, L. B., & Crouse, D. T. (1996). Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications*, *6*(2), 556–565. https://doi.org/10.2307/2269391

Hixon, M. A., Johnson, D. W., & Sogard, S. M. (2014). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, *71*(8), 2171–2185. https://doi.org/10.1093/icesjms/fst200

Holbrook, S. J., Adam, T. C., Edmunds, P. J., Schmitt, R. J., Carpenter, R. C., Brooks, A. J., … Briggs, C. J. (2018). Recruitment Drives Spatial Variation in Recovery Rates of Resilient Coral Reefs. *Scientific Reports*, *8*(1), 7338. https://doi.org/10.1038/s41598-018-25414-8

House, J. E., Brambilla, V., Bidaut, L. M., Christie, A. P., Pizarro, O., Madin, J. S., & Dornelas, M. (2018). Moving to 3D: relationships between coral planar area, surface area and volume. *PeerJ*, *6*(2), e4280. https://doi.org/10.7717/peerj.4280

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., … Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, *359*(6371), 80–83. https://doi.org/10.1126/science.aan8048

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., … Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373–377. https://doi.org/10.1038/nature21707

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Chase, T. J., Dietzel, A., … Woods, R. M. (2019). Global warming impairs stock–recruitment dynamics of corals. *Nature*, *568*(7752), 387–390. https://doi.org/10.1038/s41586-019-1081-y

Hughes, Terence P., & Connell, J. H. (1987). Multiple stressors on coral reefs: A long-term perspective. *The American Naturalist*, *129*(6), 818–829. https://doi.org/10.1086/284677

Johnston, E. C., Forsman, Z. H., Flot, J. F., Schmidt-Roach, S., Pinzón, J. H., Knapp, I. S. S., & Toonen, R. J. (2017). A genomic glance through the fog of plasticity and diversification in Pocillopora. *Scientific Reports*, *7*(1), 1–11. https://doi.org/10.1038/s41598-017-06085-3

Kayal, M., Lenihan, H. S., Brooks, A. J., Holbrook, S. J., Schmitt, R. J., & Kendall, B. E. (2018). Predicting coral community recovery using multi-species population dynamics models. *Ecology Letters*, *21*(12), 1790–1799. https://doi.org/10.1111/ele.13153

Kayal, M., Lenihan, H. S., Pau, C., Penin, L., & Adjeroud, M. (2011). Associational refuges among corals mediate impacts of a crown-of-thorns starfish Acanthaster planci outbreak. *Coral Reefs*, *30*(3), 827–837. https://doi.org/10.1007/s00338-011-0763-1

Kotb, M. M. A. A., Hanafy, M. H., & Monir, T. (2018). Synchronized spawning and fecundity of Acropora species in the Red Sea. *Indian Journal of Geo-Marine Sciences*, *47*(10), 2032–2041.

LaJeunesse, T. C., Parkinson, J. E., Gabrielson, P. W., Jeong, H. J., Reimer, J. D., Voolstra, C. R., & Santos, S. R. (2018). Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. *Current Biology*, *28*(16), 2570–2580. https://doi.org/10.1016/j.cub.2018.07.008

Leichter, J. J., Seydel, K., & Gotschalk, C. (2019). MCR LTER: Coral Reef: Benthic Water Temperature, ongoing since 2005 ver 13. Environmental Data Initiative. https://doi.org/doi:10.6073/pasta/ea6a89415b1d9118d441235723c1a23f

Lenihan, H., Ake, H., & Winslow, E. (2019). MCR LTER: Coral Reef: Long-Term Coral Population and Community Dynamics: Annual Island Wide Coral Demography Survey 2011 ongoing ver 4. https://doi.org/https://doi.org/10.6073/pasta/92e72c8c91056f4d89a11a1b67b2c373

Lesser, M. P. (2011). Coral bleaching: causes and mechanisms. In *Coral reefs: an ecosystem in transition* (pp. 405–419). Springer.

Lesser, M. P., Stochaj, W. R., Tapley, D. W., & Shick, J. M. (1990). Coral Reefs effects of irradiance, ultraviolet radiation, and temperature. *Coral Reefs*, *8*(4), 225–232. Retrieved from http://www.springerlink.com/index/R8P6113W6L328215.pdf

Levitan, D. R., Boudreau, W., Jara, J., & Knowlton, N. (2014). Long-term reduced spawning in Orbicella coral species due to temperature stress. *Marine Ecology Progress Series*, *515*, 1–10. https://doi.org/10.3354/meps11063

Lindenmayer, D. B., Laurance, W. F., & Franklin, J. F. (2012). Ecology: Global decline in large old trees. *Science*, *338*(6112), 1305–1306. https://doi.org/10.1126/science.1231070

Liu, G., Strong, A. E., & Skirving, W. (2003). Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. *Eos, Transactions American Geophysical Union*, *84*(15), 137–141. https://doi.org/10.1029/2003EO150001

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., & Van Woesik, R. (2001). Coral bleaching: The winners and the losers. *Ecology Letters*, *4*(2), 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

Marshall, P. A., & Baird, A. H. (2000). Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs*, *19*(2), 155–163. https://doi.org/10.1007/s003380000086

Marti-Puig, P., Forsman, Z. H., Haverkort-Yeh, R. D., Knapp, I. S. S., Maragos, J. E., &

Toonen, R. J. (2014). Extreme phenotypic polymorphism in the coral genus Pocillopora; micro-morphology corresponds to mitochondrial groups, while colony morphology does not. *Bulletin of Marine Science*, *90*(1), 211–231. https://doi.org/10.5343/bms.2012.1080

McIlroy, S. E., & Coffroth, M. A. (2017). Coral ontogeny affects early symbiont acquisition in laboratory-reared recruits. *Coral Reefs*, *36*(3), 927–932. https://doi.org/10.1007/s00338-017-1584-7

McIlroy, S. E., Cunning, R., Baker, A. C., & Coffroth, M. A. (2019). Competition and succession among coral endosymbionts. *Ecology and Evolution*, *9*(22), 12767–12778. https://doi.org/10.1002/ece3.5749

Muller-Landau, H. C., Condit, R. S., Chave, J., Thomas, S. C., Bohlman, S. A., Bunyavejchewin, S., … Ashton, P. (2006). Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecology Letters*, *9*(5), 575–588. https://doi.org/10.1111/j.1461-0248.2006.00904.x

Nakamura, T., & Woesik, R. Van. (2001). Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event, *212*(2), 301–304.

Negri, A., Vollhardt, C., Humphrey, C., Heyward, A., Jones, R., Eaglesham, G., & Fabricius, K. (2005). Effects of the herbicide diuron on the early life history stages of coral. *Marine Pollution Bulletin*, *51*(1–4), 370–383. https://doi.org/10.1016/j.marpolbul.2004.10.053

Nozawa, Y., & Harrison, P. L. (2007). Effects of elevated temperature on larval settlement and post-settlement survival in scleractinian corals, Acropora solitaryensis and Favites chinensis. *Marine Biology*, *152*(5), 1181–1185. https://doi.org/10.1007/s00227-007-0765-2

Oxenford, H. A., Roach, R., & Brathwaite, A. (2008). Large scale coral mortality in Barbados: a delayed response to the 2005 bleaching episode. *Proceedings of the 11th International Coral Reef Symposium*, *16*(16), 505–509.

Patterson, M. R. (1992). A mass transfer explanation of metabolic scaling relations in some aquatic invertebrates and algae. *Science*, *255*(5050), 1421–1423. https://doi.org/10.1126/science.255.5050.1421

Penin, L., Michonneau, F., Baird, A., Connolly, S., Pratchett, M., Kayal, M., & Adjeroud, M. (2010). Early post-settlement mortality and the structure of coral assemblages. *Marine Ecology Progress Series*, *408*, 55–64. https://doi.org/10.3354/meps08554

Pinzón, J. H., Sampayo, E., Cox, E., Chauka, L. J., Chen, C. A., Voolstra, C. R., & Lajeunesse, T. C. (2013). Blind to morphology: Genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (Pocillopora, Scleractinia). *Journal of Biogeography*, *40*(8), 1595–1608. https://doi.org/10.1111/jbi.12110

Pratchett, M. S., Hoey, A. S., Wilson, S. K., Messmer, V., & Graham, N. A. J. (2011). Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity*, *3*(3), 424–452. https://doi.org/10.3390/d3030424

Pratchett, M. S., McCowan, D., Maynard, J. A., & Heron, S. F. (2013). Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. *PLoS ONE*, *8*(7), 1–10. https://doi.org/10.1371/journal.pone.0070443

Pratchett, M. S., Munday, P. L., Wilson, S. K., Graham, N. A. J., Cinner, J. E., Bellwood, D. R., … McClanahan, T. R. (2008). Effects of climate-induced coral bleaching on coral-reef fishes-ecological and economic consequences. *Oceanography and Marine Biology*, *46*, 251–296. https://doi.org/10.1201/9781420065756.ch6

Price, N. (2010). Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. *Oecologia*, *163*(3), 747–758. https://doi.org/10.1007/s00442-010-1578-4

Raudenbush, S. W., Yang, M. L., & Yosef, M. (2000). Maximum Likelihood for Generalized Linear Models with Nested Random Effects via High-Order, Multivariate Laplace Approximation. *Journal of Computational and Graphical Statistics*, *9*(1), 141–157. https://doi.org/10.1080/10618600.2000.10474870

Richmond, R., & Hunter, C. (1990). Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Marine Ecology Progress Series*, *60*, 185–203. https://doi.org/10.3354/meps060185

Roth, L., Koksal, S., & Van Woesik, R. (2010). Effects of thermal stress on key processes driving coral-population dynamics. *Marine Ecology Progress Series*, *411*, 73–87.

Rowland, L., Da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira, A. A. R., … Meir, P. (2015). Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, *528*(7580), 119–122. https://doi.org/10.1038/nature15539

Shenkar, N., Fine, M., & Loya, Y. (2005). Size matters: bleaching dynamics of the coral Oculina patagonica. *Marine Ecology Progress Series*, *294*(2001), 181–188.

Speare, K. E., Adam, T. C., Winslow, E. M., Lenihan, H. S., & Burkepile, D. E. (2021). MCR LTER: Coral Reefs: Coral bleaching and mortality in July 2019; data for Speare et al. 2021 Global Change Biology. https://doi.org/https://doi.org/10.6073/pasta/f59968d039de006909c5c92c51c3919c.

Stimson, J. S. (1978). Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. *Marine Biology*, *48*(2), 173–184. https://doi.org/10.1007/BF00395017

Szmant, A. M., & Gassman, N. J. (1990). The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral Montastrea annularis. *Coral Reefs*, *8*(4), 217–224. https://doi.org/10.1007/BF00265014

Thomas, S. C. (1996). Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. *Oikos*, *76*(1), 145–154.

Tsounis, G., & Edmunds, P. J. (2016). The potential for self-seeding by the coral Pocillopora spp. in Moorea, French Polynesia. *PeerJ*, *2016*(11), e2544. https://doi.org/10.7717/peerj.2544

Van Nieuwstadt, M. G. L., & Sheil, D. (2005). Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *Journal of Ecology*, *93*(1), 191–201. https://doi.org/10.1111/j.1365-2745.2004.00954.x

van Woesik, R., Irikawa, A., Anzai, R., & Nakamura, T. (2012). Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. *Coral Reefs*, *31*(3), 633–639. https://doi.org/10.1007/s00338-012-0911-2

van Woesik, R., Sakai, K., Ganase, A., & Loya, Y. (2011). Revisiting the winners and the losers a decade after coral bleaching. *Marine Ecology Progress Series*, *434*, 67–76. https://doi.org/10.3354/meps09203

Vardi, T., Williams, D. E., & Sandin, S. A. (2012). Population dynamics of threatened elkhorn coral in the northern Florida Keys, USA. *Endangered Species Research*, *19*(2), 157–169. https://doi.org/10.3354/esr00475

Wickham, H. (2010). *ggplot2: elegant graphics for data analysis (Use R!)*. Springer New York, NY.

Wilson, S. K., Graham, N. A. J., Pratchett, M. S., Jones, G. P., & Polunin, N. V. C. (2006). Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Global Change Biology*, *12*(11), 2220–2234. https://doi.org/10.1111/j.1365-2486.2006.01252.x

Figures

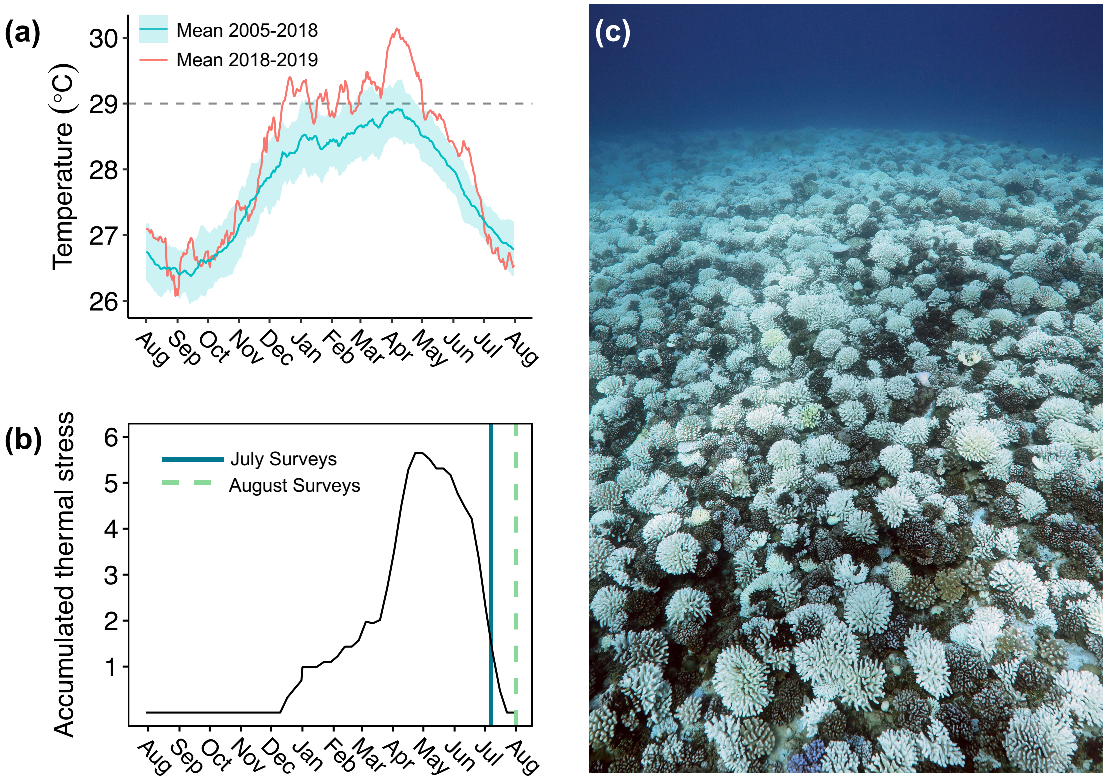

Photo: Andrew Thurber

Figure 1. Long-term ocean temperature trends and thermal stress events in Moorea. A) Long-term ocean temperature trends vs. temperatures in 2018-2019 on the outer reef of Moorea, measured *in situ* using thermistors mounted on the reef at 10 m depth at six sites around the island. Data from a subset of four of the six sites (at least one from each of the three sides of the island) had continuous data throughout 2018-2019, and therefore we considered only those four sites in our analysis of temperature trends for this year. Mean ocean temperature from 2005-2018 is shown in blue and shading is ± one standard deviation. B) Accumulated thermal stress in 2018-2019. C) The severely bleached coral community at 10 m depth on the outer reef in early May 2019. Photo credit Andrew Thurber.

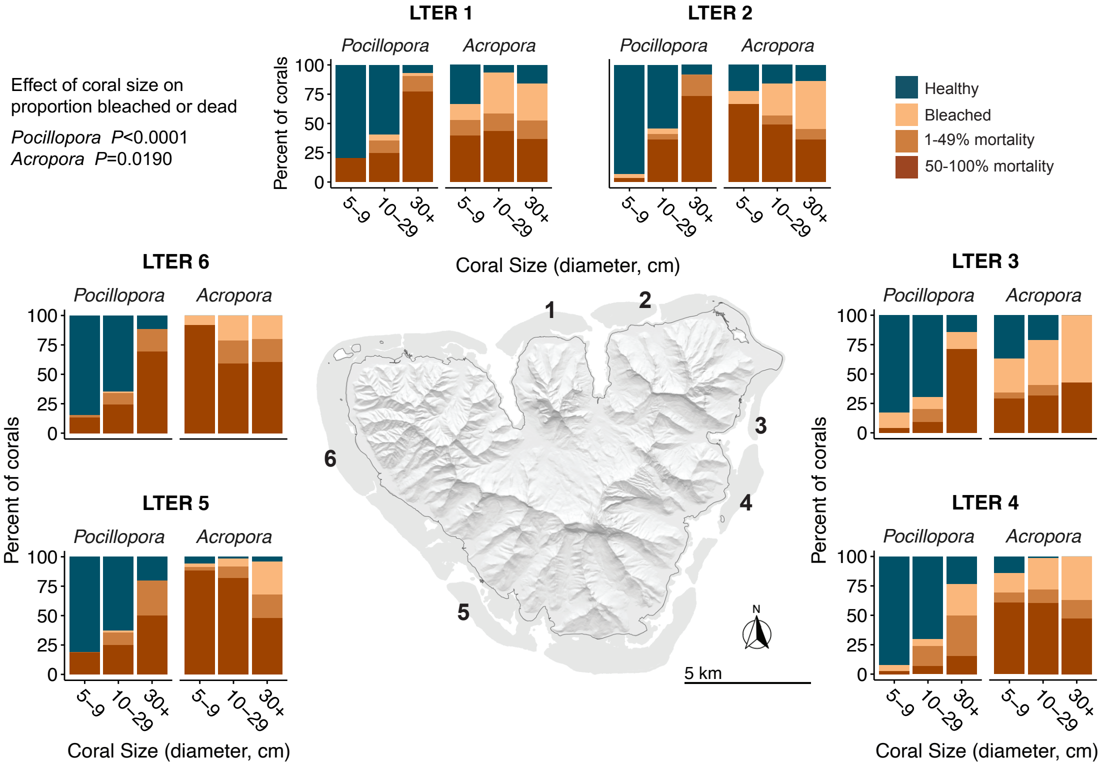

Figure 2. Island-wide patterns of coral bleaching and mortality. The proportion of individuals of the two dominant genera (*Pocillopora* and *Acropora*) that appeared to be healthy, were bleached, or had 1-49% mortality or 50-100% mortality. Data on bleaching and mortality were collected for >2,200 individual colonies by divers *in situ* at six sites on the outer reef of Moorea. Numbers on the map indicate the location of each of the six sites on the outer reef.

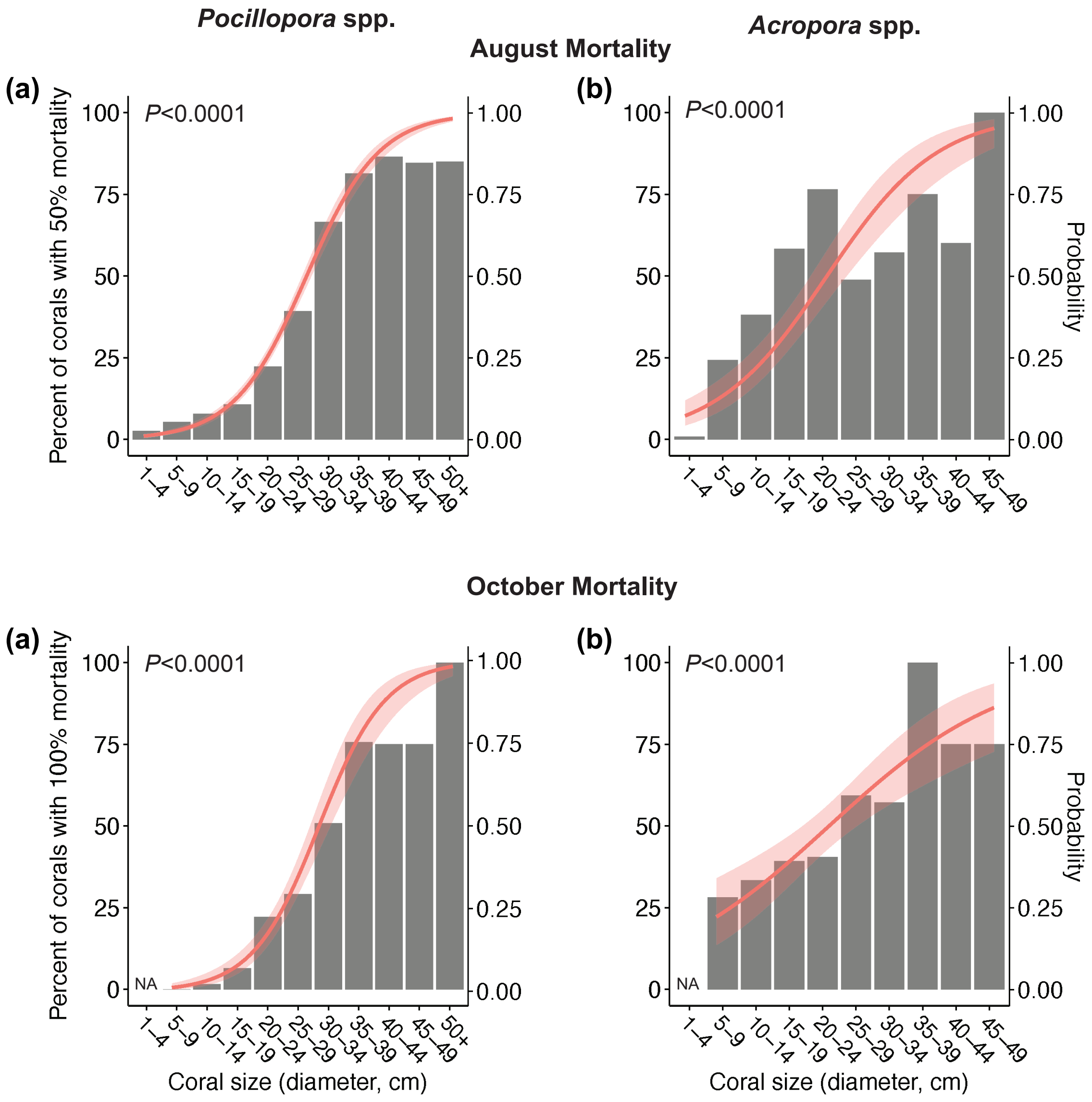

Figure 3. Relationships between coral colony size and probability of mortality during the 2018-2019 bleaching event. The percent of individuals of *Pocillopora* and *Acropora* in each size class with at least (A,B) 50% mortality and (C,D) 100% mortality following the bleaching event. The red line is the probability of having at least 50% mortality (A,B) or 100% mortality (C,D) via logistic regression. P- values from logistic regression.

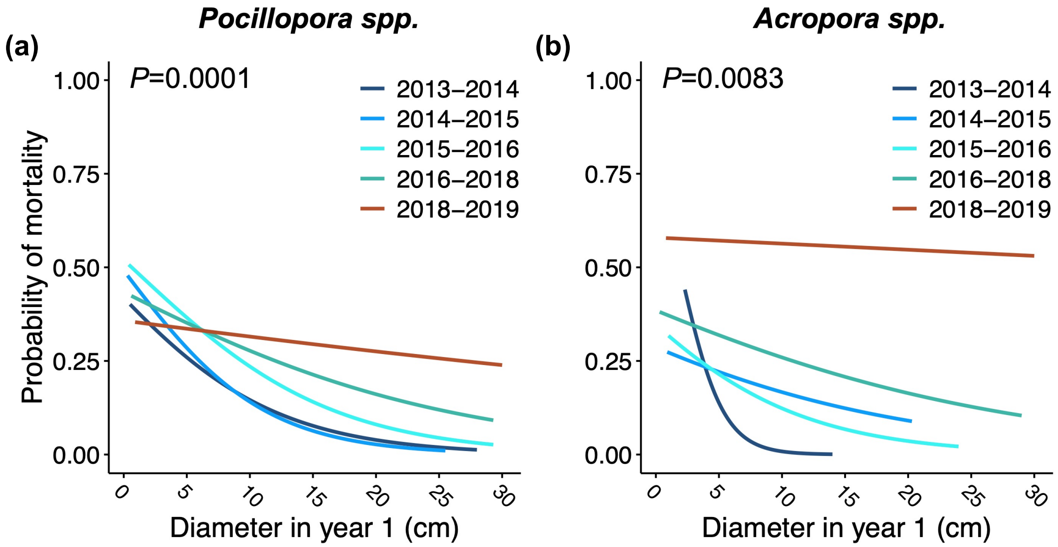

Figure 4. Relationship between coral colony size and annual mortality patterns in low thermal stress years (2013-2018) and a high thermal stress year (2018-2019). Annual mortality curves for A) *Pocillopora* and B) *Acropora* from 2013-2019. The x-axis is colony size in year 1 and the y-axis is the probability of mortality from year 1 to year 2. P-values are for the Size x Year Type interaction in the generalized linear mixed model comparing low vs. high thermal stress years. Note that coral mortality was not sampled in 2017 so the 2016-2018 line represents mortality over two years.

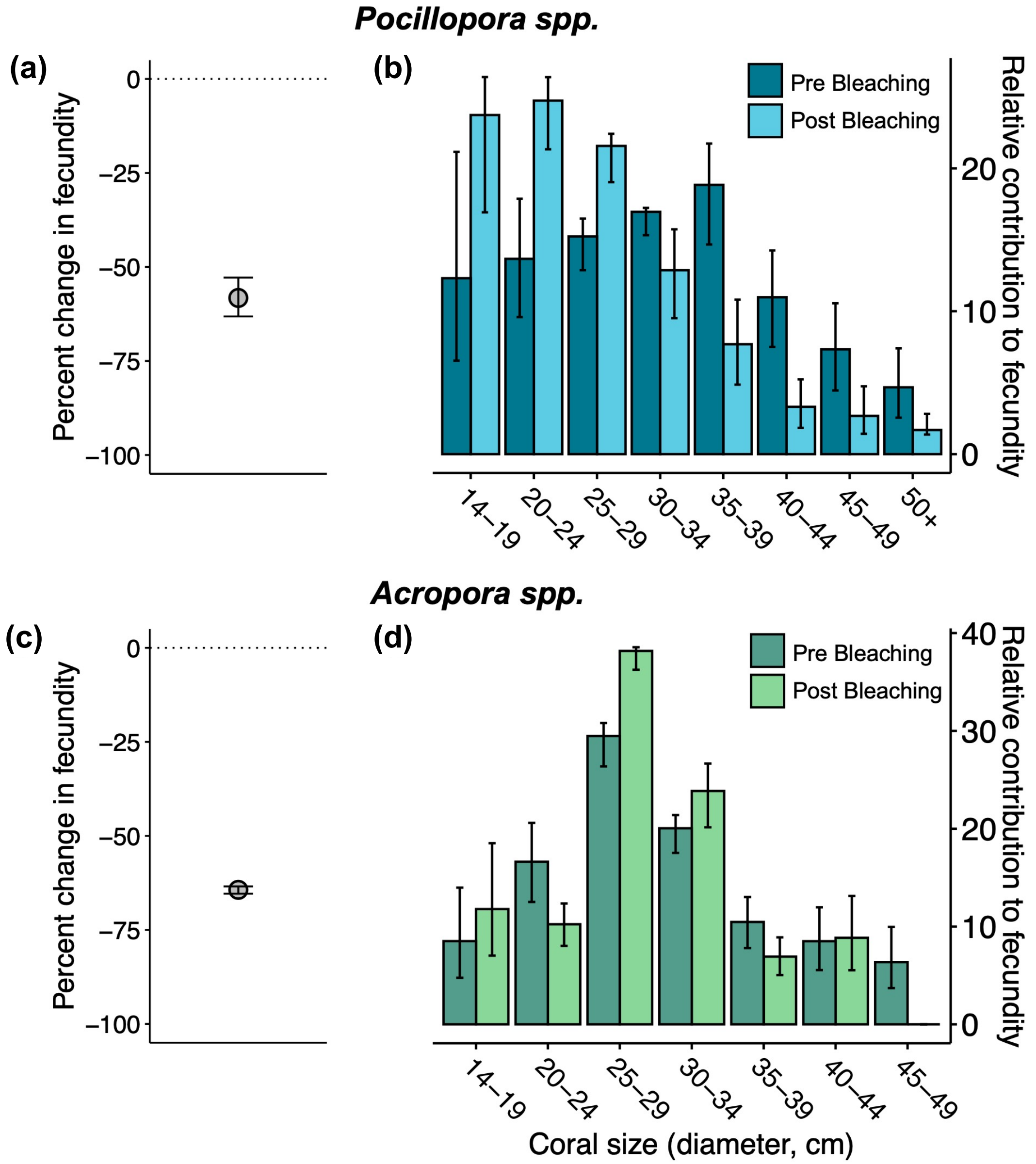

Figure 5. Fecundity estimates for *Pocillopora* and *Acropora* before and after the bleaching event. Estimated change in genus-level fecundity ± 95% confidence intervals for *Pocillopora* and *Acropora,* respectively (A and C). The relative contribution to total fecundity ± 95% confidence intervals (Pre and Post Bleaching) for each size class of individuals for *Pocillopora* and *Acropora,* respectively (B and D). Data from the August 2019 bleaching and mortality surveys were used to estimate

population fecundity (A-D). All fecundity estimates were standardized to the area surveyed, therefore, differences between pre and post bleaching fecundity reflect changes in fecundity based on the loss of corals in each size class.

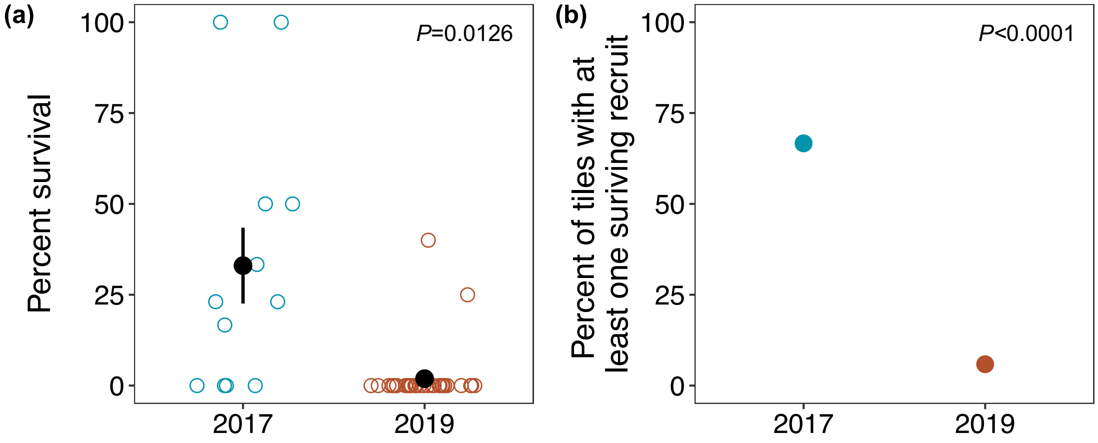

Figure 6. Survivorship of coral recruits under high thermal stress during the marine heatwave compared to a year with low thermal stress. A) Survival of coral recruits (individuals 1-3 mm in diameter and <1 year old) in 2017 (a year with low thermal stress) and during the marine heatwave of 2019. Colored data points are mean survival per settlement tile (n=12 tiles in in 2017 and n=34 tiles in 2019). Black points (lines are ±SE) are the overall mean survival calculated from individual tile means for March – July of 2017 and 2019. P-value from two tailed t-test. B) Percent of tiles with at least one surviving coral recruit in 2017 and 2019. P-value from contingency test.

Appendix

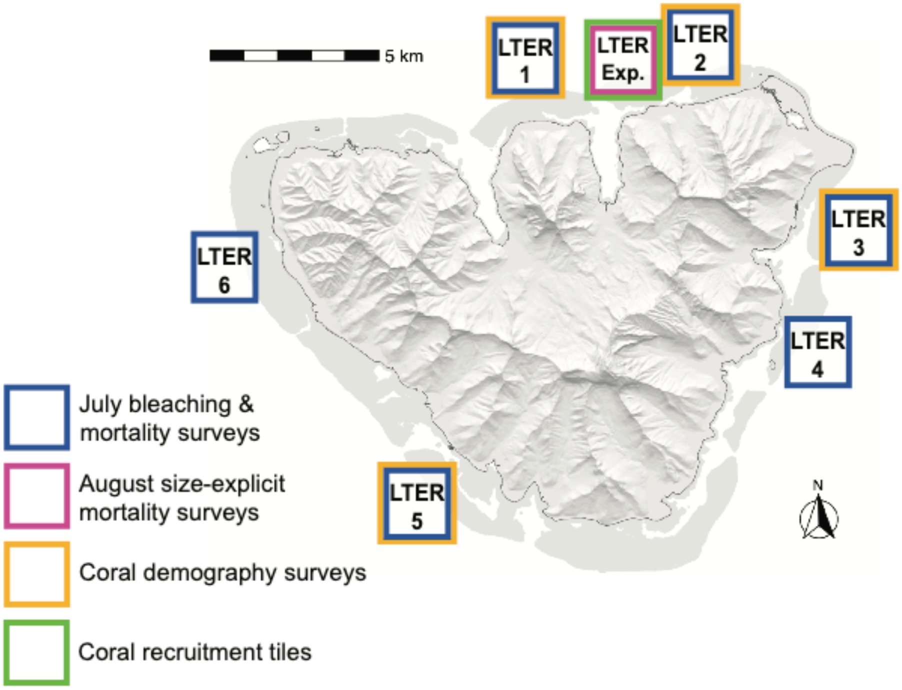

Figure S1. A map of the island of Mo'orea and the location of each site surveyed. Colors surrounding site markers denote the datasets collected at each site.

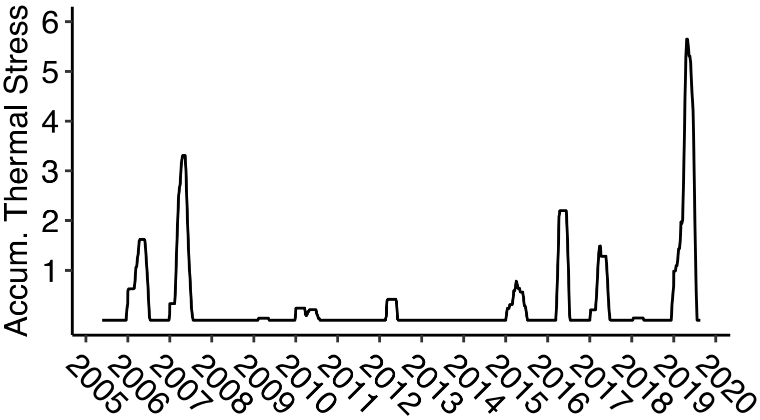

Figure S2. History of accumulated thermal stress throughout the 14-year MCR LTER time series.

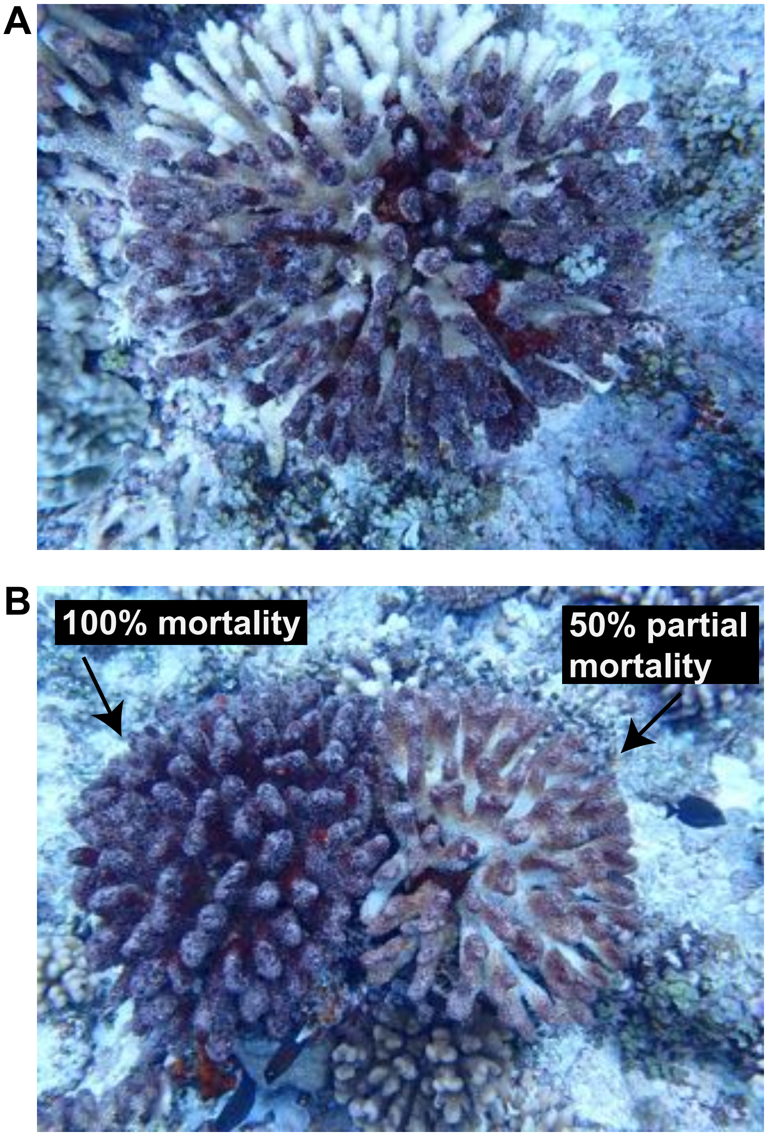

Figure S3. Partial mortality of coral colonies. A,B) Examples of *Pocillopora* that had 50% partial mortality (recent mortality) at the time of our surveys (August 2019). In B) there are two recently dead corals. The coral on the left has 100% mortality and the coral on the right has 50% mortality.

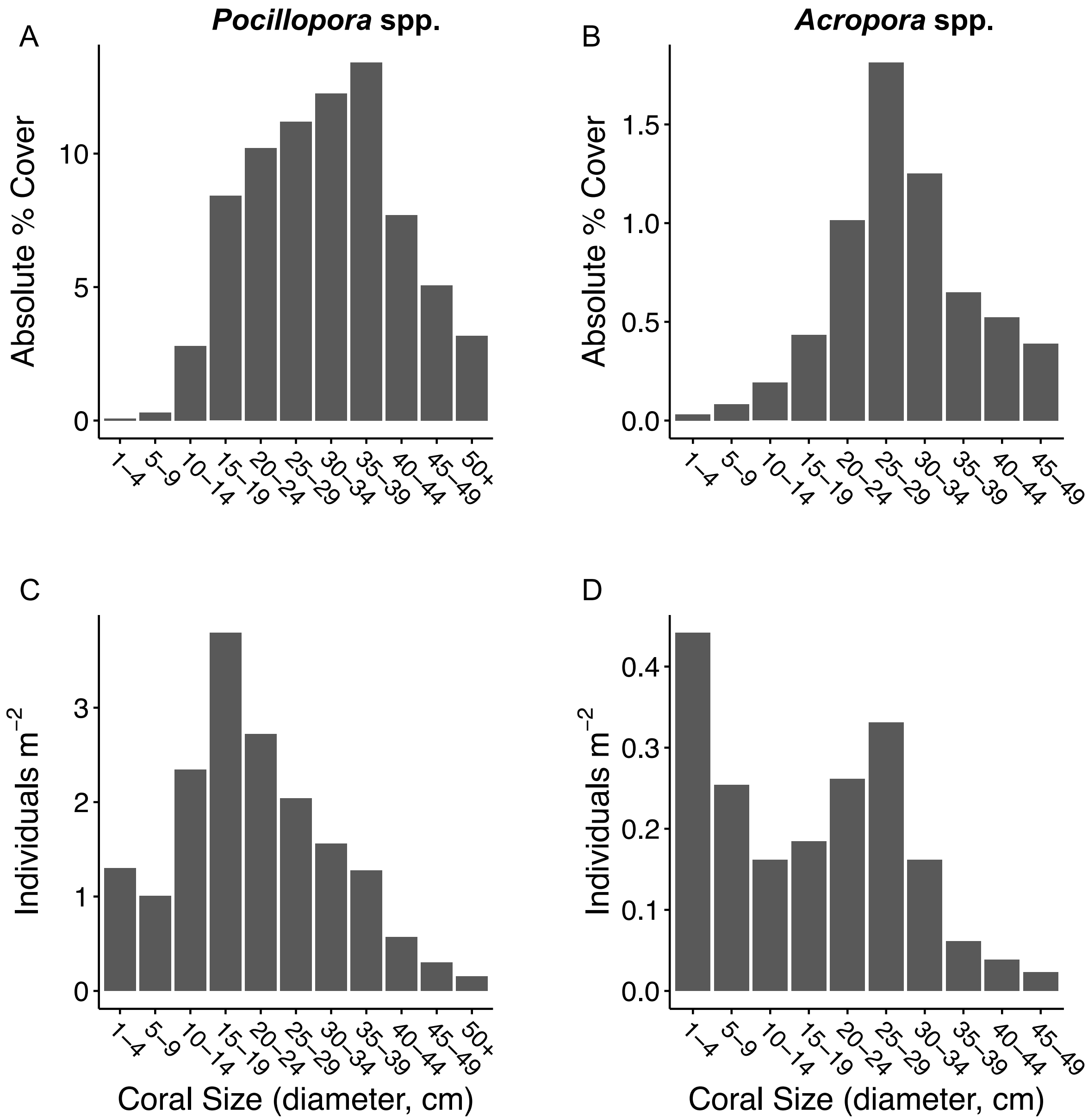

Figure S4. *Pocillopora* and *Acropora* abundance. The percent coral cover of each size class of A) *Pocillopora* spp. and B) *Acropora* spp. and the size frequency distributions of C) *Pocillopora* spp. and D) *Acropora* spp.

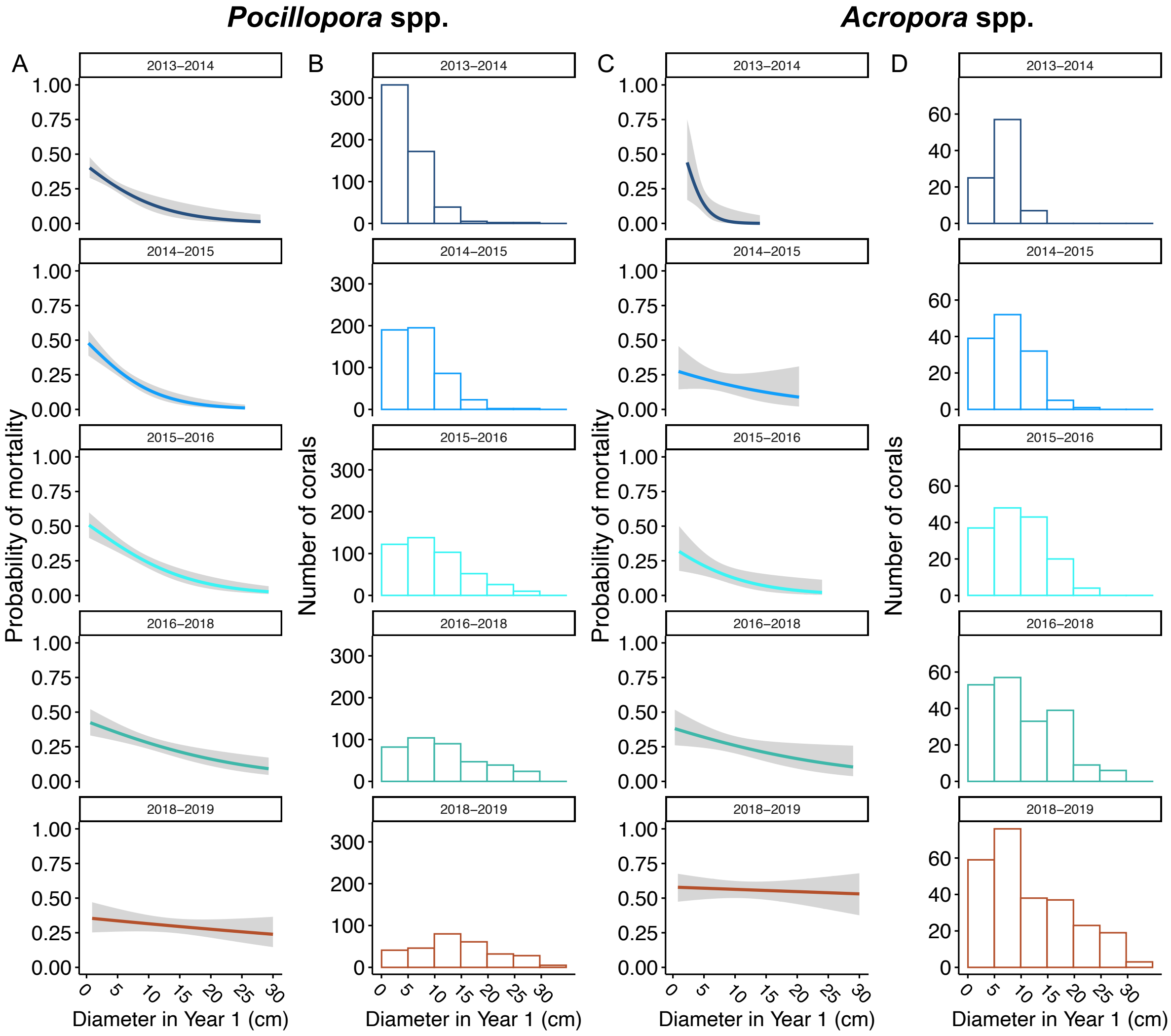

Figure S5. Relationship between coral colony size and annual mortality and colony size-frequency distributions for each year. A,C) The relationship between colony size and the probability of annual mortality for *Pocillopora* and *Acropora*, respectively. Shaded bands are 95% confidence intervals. B,D) Size frequency distributions of corals in year 1 for each survey interval for *Pocillopora* and *Acropora*, respectively. We restricted the data analysis of this dataset to corals ≤30 cm diameter.

Table S1. The number of corals surveyed in each size class in August and October 2019

	Pocillopora spp.		*Acropora* spp.	
	August 2019	**October 2019**	**August 2019**	**October 2019**
1-4 cm	345	NA	117	NA
5-9 cm	131	9	34	32
10-14 cm	305	61	21	24
15-19 cm	493	140	25	28
20-24 cm	354	99	35	42
25-29 cm	265	72	44	54
30-34 cm	203	60	21	28
35-39 cm	166	37	8	12
40-44 cm	74	8	5	8
45-49 cm	39	4	3	4
50+ cm	20	2	NA	NA

Table S2. Equations and parameter estimates for fecundity calculations

Estimating colony planar surface area from colony diameter

$PSA=d^x$

Where d is colony diameter (cm) and PSA is planar surface area (cm^2)

Genus	**Species**	**x**	**x, standard error**	**Source**
Pocillopora	spp.	1.8701	0.0055	Derived in this study
Acropora	*spp.*	1.8233	0.0047	Derived in this study

Estimating colony live surface area from planar surface area

$LSA = e^{(\alpha + \beta \ln(PSA))}$

where LSA is live surface area (cm^2)

Genus	**Species**	**α**	**standard error**	**β**	**standard error**	**Source**
Pocillopora	spp.	1.024	0.8363	1.118	0.1651	House et al. 2018
Acropora	spp.	1.024	0.8363	1.118	0.1651	House et al. 2018

Estimating colony fecundity from live surface area

$F=LSA*F_{const}$

Genus	**Species**	**F_{const}**	**F_{const}, standard error**	**Units**	**Source**
Pocillopora	spp.	6327	1882	$\text{eggs}^{-1}\text{cm}^{-2}\text{yr}^{-1}$	Calculated in Tsounis and Edmunds 2016
Acropora	spp.	276	110	$\text{oocytes}^{-1}\text{cm}^{-2}\text{yr}^{-1}$	Mean fecundity of 11 *Acropora* species; data from Kotb et al. 2018

Table S3. Results of mixed effects models using likelihood ratio tests to test the effects of caging, nutrient enrichment, and coral disturbance on percent recruit survival

Response	**Treatment**	**p**	**df**
Percent recruit survival	Herbivore exclusion (4 levels: 2.5cm holes, 5cm holes, 15cm holes, open)	0.08	3
	Nutrient Enrichment (2 levels: enriched with osmocote, or unenriched)	0.83	2
	Coral Disturbance (adult corals removed, adult corals present)	0.51	2

II. Early life stage bottlenecks determine rates of coral recovery following severe disturbance

1. Introduction

Disturbances that reduce the abundance of foundation organisms are increasing in frequency and intensity with global climate change. Understanding why some communities recover quickly whereas others recovery slowly or never recover is key to understanding drivers of community resilience. Following disturbances, recovery rates of foundation species can be shaped by a combination of biotic and abiotic factors. Top-down pressure is an important driver of recovery following disturbance in many communities and can either accelerate or slow community recovery. For example, in rocky intertidal communities top-down pressure by herbivores can increase rates of recovery of algae by controlling the abundance of early successional species that preempt space (Aquilino & Stachowicz, 2012). In contrast, intense top-down pressure by grazing sea urchins in kelp forests can slow or prevent kelp recovery by inhibiting the reestablishment of kelp recruits (Filbee-Dexter & Scheibling, 2014; Watanabe & Harrold, 1991). Differences in abiotic factors such as temperature, water availability, and light across environmental gradients like latitude, elevation, or depth can also shape the recovery of foundation organisms. For example, higher elevation forests can recover more quickly after forest fires compared to low elevation forests because lower temperatures and higher water availability at higher elevations promote tree recruitment and growth (Lippok et al., 2013). Further, kelp forests recover more slowly from disturbance at lower latitudes compared to higher latitudes because higher water temperatures at lower latitudes decrease the physiological performance of kelp recruits

(Wernberg et al., 2010). Understanding how biotic forcing such as top-down pressure, and abiotic factors shape community recovery dynamics is key to understanding community resilience.

Many of the factors that regulate recovery rates of foundation organisms after disturbance do so by influencing the supply and recruitment of new individuals. The establishment of new individuals is the essential first step of recovery and bottlenecks that limit recolonization after disturbance can create roadblocks to recovery, whereas factors that promote recolonization can expedite recovery (Castorani et al., 2015; Holbrook et al., 2018; Wijdeven & Kuzee, 2000). First, the supply of new individuals (i.e. seedlings, larvae, propagules) to a disturbed community can dictate rates of recovery. In kelp forests, for example, high rates of propagule supply driven by connectivity with other populations promotes the settlement and recovery of kelp following disturbance (Castorani et al., 2015). Further, differences in the survival of newly established spat or propagules can dictate patterns of recruitment. For example, grazing herbivores can cause incidental mortality of newly settled coral spat and limit rates of recruitment on coral reefs (Penin et al., 2010). Rates of community recovery can be strongly influenced by processes that shape the recruitment of foundations species and can be further modulated by the survival and growth of new recruits.

Once new individuals recruit to a population, biotic and abiotic factors can dictate the survivorship and growth of the newly established individuals and influence rates of recovery. Differences in abiotic conditions across environmental gradients such as depth, latitude, or elevation can dictate the success of newly established recruits. For example, low latitude kelp forests recover more slowly than high latitude reefs because kelp recruits have lower physiological performance in warmer water, which slows the rate of kelp growth and recovery (Wernberg et al., 2010). Additionally, lower temperatures and higher water availability can increase seedling success at higher elevations compared to low elevations (Gworek, Vander, & Brussard, 2007). Top-down forcing by consumers is an important biotic factor that can have context dependent effects on the rates of reestablishment of foundation species. Herbivores can accelerate the recovery rate of algal communities by controlling the abundance of early successional species (Aquilino & Stachowicz, 2012), but they can also inhibit recovery by consuming newly-established recruits of the recovering foundation organisms, such as in kelp forests where urchins consume kelp recruits (Dean, Schroeter, & Dixon, 1984; Steneck et al., 2002). Further, biotic and abiotic forces can interact to dictate rates of community, such as in rocky intertidal communities where wave exposure and top-down pressure by consumers interactively shape recovery rates of barnacle and mussel communities (Bryson, Trussell, & Ewanchuk, 2014). Understanding the relative importance of the supply of new individuals and their success and how they are shaped by biotic and abiotic factors is key to understanding how foundation organisms recover from major disturbances.

Moorea, French Polynesia (17 º 30'S, 149º50'W) is a high volcanic island surrounded by a shallow lagoon and outer reef. Coral reefs on the outer reef around Moorea experienced an outbreak of the corallivorous crown-of-thorns sea star, *Acanthaster planci,* (COTS) from 2007 to 2009, followed by a Category 4 cyclone in 2010. These disturbances resulted in a severe decline in coral cover island-wide from ~46% in 2005 to <1% in 2010 (island-wide averages, Supp. Figure 1). Reefs around Moorea rapidly recovered from these disturbances, with some reefs exceeding pre-disturbance coral cover within five years (Supp. Figure 1). Although there was widespread recovery of stony corals, there was significant heterogeneity in the rate of recovery between sites and depths. 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 number of corals that recruited after the disturbances (Holbrook et al., 2018). Here we investigate the drivers of variation in coral recovery between depths using a combination of time-series data and *in situ* experiments. First, we used time-series data on coral settlement from settlement tiles deployed *in situ* to ask we asked whether differences in the supply and settlement of corals explained differences in rates of coral recovery between depths. Second, we used annual photoquadrats to quantify coral recruitment at 10 and 17m and used these recruitment data to ask whether the number of corals that recruited to reefs at 10 and 17m drove differences in recovery rates. Third, we used the same annual photoquadrats to track the fate of individual coral recruits and estimate rates of coral mortality. We used these data on coral recruit mortality to ask whether differences in mortality of newly-recruited corals drove differences in recovery. And fourth, we measured coral size in pairs of consecutive years to estimate rates of coral growth. We used these data to ask whether coral growth rates differed among depths and whether differences in growth drove different rates of recovery.

2. Methods

2.1. Study Location

Moorea, French Polynesia (17°30′S, 149°50′W) is a high volcanic island with an outer reef that surrounds a wide, shallow patch reef lagoon. Reefs around Moorea have been monitored extensively as part of the Moorea Coral Reef Long Term Ecological Research time series program (MCR LTER) since 2005. The MCR LTER collects data annually on benthic communities at six sites on the outer reef, with two sites on each side of the island. We focused our study at two sites on the north shore of Moorea (LTER 1 and LTER 2) because these sites had the greatest differences in coral recovery rates between depths (10 and 17 m, see Supp. Fig. 1). Fieldwork to collect the MCR LTER time series data and our field experiments was conducted from the Richard B. Gump South Pacific Research Station on Moorea.

2.2. Patterns of coral decline and recovery

At each of the six MCR LTER sites, one permanently marked 50 m transect was established at two depths, 10 and 17 m, to collect data on the abundance of benthic organisms. Each transect is photographed annually in 40 fixed locations using a digital camera in an underwater housing attached to a 50×50 cm quadrat affixed with a ruler with centimeter markings. Photoquadrats are analyzed to quantify the percent cover of benthic organisms using 200 random point IDs using either CPCe software (through 2014) or the CoralNet web-based application (2015-2018). Stony corals are identified to genus. To assess changes in the abundance of stony corals throughout the time series, we calculated the average percent cover of stony corals (scleractinians and *Millepora*) of the 40 photoquadrats at each site-depth combination for each year of the time series from 2005-2018. At LTER 1 and 2 we also calculated the relative abundance of the three most abundant coral genera, *Pocillopora, Acropora,* and *Porites,* for each year of the time series.

2.3. Coral settlement

Coral settlement was quantified during two time periods (late January/early February-late August/early September and late August/early September - late January/early February) annually at 10 and 17 m at LTER 1 and LTER 2. At the start of each time period 15 or 16 terracotta coral settlement tiles (15×15×1 cm) were deployed at each site-depth combination. Tiles were secured to the benthos horizontally with the grooved side facing down using threaded stainless steel posts and hex nuts. Tiles were preconditioned in the lagoon for several months prior to each deployment. At the end of each time period, tiles were collected and replaced with new tiles. Tiles were brought to the lab where they were soaked in bleach, dried, and scored for coral settlers using microscopy (~40× magnification). Coral settlers were identified to family. Because coral recovery was driven primarily by the increase in abundance of *Pocillpora* following the disturbances, we only analyzed data on the settlement of corals in the family Pocilloporidae. For each tile, we summed the number of Pocilloporidae settlers during the two sampling time periods to calculate the total number of Pocilloporidae settlers per tile per year. Then we analyzed this data on the number of Pocillporidae settlers per tile per year using a mixed effects model. We asked whether the settlement of Pocilloporidae corals differed between depths using a mixed effects model with fixed effects of depth, year, and the depth×year interaction, and a random effect of site using the *‘lme4’* package in R version 4.1.0.

2.4. Coral recruitment, survival and growth

Rates of the recruitment, survival and growth of corals in the genus *Pocillopora* were quantified by tracking the fate of individual corals that appeared in the annual time series photoquadrats. Surveys conducted *in situ* by divers indicated that no coral recruits were visible on the benthos in August 2010 but that recruits were visible by 2011 (Holbrook et al. 2018), therefore we quantified demographic rates of corals starting in 2011. We quantified the demographic rates of corals in 13 photoquadrats at LTER 1 10 m, 26 photoquadrats at LTER 1 17 m, 18 photoquadrats at LTER 2 10 m, and 28 photoquadrats at LTER 2 17 m. We searched each photoquadrat for new *Pocillopora* coral recruits and gave each recruit in the photo a unique identifying number. In each consecutive year, we searched the photoquads for coral recruits that were visible in the photo from the previous year and new recruits that appeared since the previous year. Thus, each coral was only counted as a new recruit once in the time series. This analysis yielded a total of 1,605 *Pocillopora* recruits in our dataset. For each site and depth, we calculated the mean number of new coral recruits in each photoquadrat each year (recruits m^{-2} $year^{-1}$). We then analyzed our data on the number of recruits per quadrat per year using a mixed effects model. We asked whether the recruitment of *Pocillopora* corals differed between depths using a mixed effects model with fixed effects of depth, year, and the depth×year interaction, and a random effect of site using the *'lme4'* package.

In each pair of consecutive years, we assessed the annual mortality of each coral in our dataset. The probability of mortality of corals decreases with coral age and size, and therefore 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 recruitment differed between depths. First, we calculated the proportion of coral recruits that died the first year after recruitment for each quadrat for each year in the time series (e.g., 2012 mortality was the proportion of corals that were first identified in the 2011 photos and were dead in the 2012 photos). We asked whether the annual mortality of coral recruits differed between depths using a mixed effects model with fixed effects of depth, year, and the depth×year interaction, and a random effect of site using the *'lme4'* package. We only analyzed mortality data only until 2015 (e.g., recruits arriving by 2014) because recruitment declined precipitously throughout the time series at both sites and depths and many photoquadrats had no new coral recruits after 2014.

The COTS outbreak from 2007-2009 killed nearly all corals on the outer reef and Cyclone Oli in 2010 broke and removed the majority of the coral skeletons from the reef substrate, resulting in patchy substrate types with a mix of rubble, remnants of dead branching coral skeletons, and hard consolidated substrate. We hypothesized that coral recruitment rates may differ on different substrate types, and that the mortality of coral recruits may differ by substrate type. For each coral recruit in our dataset, we classified the substrate type that it settled on as: 1) hard substrate, 2) dead coral skeletons still attached to the substrate ('dead skeletons'), or 3) remnants of dead coral skeletons that were unattached to the substrate ('rubble'). We then calculated the proportion of corals that settled on each substrate type for each quadrat, and the proportion of corals on each substrate type that died in the first year after recruitment. We hypothesized that recruit mortality may be higher on rubble than on other substrate types because unattached rubble moves with ocean swell and may poor settlement habitat for corals. Our data on the proportion of corals that died on each substrate type were not independent so we only analyzed data on the proportion of corals that recruited to rubble. We asked whether the proportion of corals that settled on rubble and died differed between depths using a t-test.

To quantify the annual growth of corals we measured corals that were visible in photos in consecutive years using imageJ software. For each year that a coral was visible, we traced the perimeter of the coral, calculated planar surface area, and measured the widest 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 many corals were omitted from the growth dataset in later years. Additionally, corals that died were omitted from the growth dataset starting in the first year that they appeared dead and in all later years. We estimated the growth of the coral between consecutive years by calculating the difference in planar surface area between consecutive years. Most corals grew throughout the time series, but some corals shrank due to partial colony mortality and fragmentation. To analyze our data on coral growth, we first calculated the average change in planar surface per coral between consecutive years for each quadrat. We then averaged mean coral growth across each pair of years in the time series to calculate average annual coral growth (cm^{-2} yr^{-1}). We asked whether the change in planar surface area of corals differed between depths using a mixed effects model with fixed effects of depth, year, and the depth×year interaction, and a random effect of site using the *'lme4'* package. We only analyzed data through 2016 because by 2017 and 2018 the majority of corals were partially out of the frame of the photoquadrat, and therefore estimates of change in planar surface area in later years are biased toward smaller colonies because smaller colonies are less likely to be partially out of the photoquadrats.

2.5. Evaluating the demographic drivers of coral recovery

We compared results of our demographic data on coral settlement, recruitment, survivorship, and growth to the patterns of coral community recovery between depths. There was significant variation in coral recruitment and post-recruitment survival, but not coral settlement or growth, between depths (See Results). Therefore, we focused our analysis on the relationships between coral recruitment and coral recovery. We were interested in understanding how much variation in the recovery rate of corals could be explained by variation in the number of corals that recruited. First, we calculated the recovery rate (% cover year^{-1}) for each quadrat. Some quadrats reached minimum coral cover in 2010 and some reached minimum coral cover in 2011, therefore, quadrats had a recovery phase of either 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. For each photoquadrat, we first identified the year of minimum coral cover, which was 2010 or 2011 for nearly all photoquadrats. Some photoquadrats had two years of minimum coral cover (for example, 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 as the response variable in a mixed effects model to evaluate the relationship between coral recruitment and the rate of coral recovery. We analyzed our data on the recovery rate of corals at the quadrat level using a mixed effects model with the number of recruits as the fixed effect and a random effect that combined depth and site.

We also used the same coral recovery dataset described above to explore possible relationships between the recovery rate of corals and coral growth. For each quadrate we calculated mean annual coral growth rates between each pair of consecutive years in the time series (e.g. mean coral growth from 2013-2014 was the mean change in area of corals in a quadrat from 2013 to 2014). Then for each quadrat we averaged mean annual growth rates across all years in our time series of coral growth data from 2011-2016. This generated a mean annual growth rate (cm^2 yr^{-1}) for each quadrat which we used as a predictor variable in our data analysis. We analyzed our data on rates of coral recovery using a mixed effects model with a fixed effect of mean annual growth rate and a random effect of site and depth.

2.6. Testing the effects of top-down pressure on coral settlement

Our data analysis indicated that the number of corals that recruit was a strong predictor of the recovery rate of corals (See Results). Our data also showed that there was no difference in the number of corals that settled between depths. Together, these results suggest that a demographic bottleneck between settlement and the time that coral recruits are visible on the benthos influences differences in the recruitment of corals between 10 and 17 m. To explore possible mechanisms that could drive differences in the survival of coral settlers between 10 and 17 m we conducted a reciprocal transplant experiment.

At one site on the outer reef (S17° 28.386' W149° 49.059’) between LTER 1 and LTER 2 we deployed 26 limestone coral settlement tiles per depth at 10 and 17 m for one year to accumulate naturally-settled coral recruits. Coral settlement tiles were secured to the benthos using a stainless steel post drilled into the reef substrate and secured with a washer and two hex nuts. Our past work has shown that top-down pressure by herbivorous fishes has a strong influence on the number of corals that settle on tiles (K.E. Speare, *unpublished data*). We hypothesized that differences in top-down pressure by herbivores may drive differences in the number of corals that settle and survive until they reach a size when they are visible as coral recruits. We excluded herbivorous fishes from half of the tiles at each depth using 15×15×15 cm exclosures constructed out of plastic coated wire mesh with 2.5 cm openings that prevented herbivorous fishes from accessing the tiles. A total of 13 tiles were deployed in each depth × herbivore exclusion treatment for a total of 52 coral settlement tiles. Tiles were deployed in July 2017 and retrieved in July 2018 to count coral recruits. Tiles were brought to the lab while keeping them submerged in seawater during transport and held at the lab in a flow-through seawater table for ~24hr while being scored for coral recruits. This method has been used in the past without significant handling effects on the survivorship of coral settlers (Penin et al. 2010). Tiles were searched under a microscope for coral settlers at 20-40× magnification. For each coral settler, we mapped its location onto a high-resolution digital photograph of the tile. Coral settlers are notoriously difficult to identify while alive because their skeletal structures are not visible. Therefore, we did not identify coral settlers to family and instead collected data on all coral settlers. We analyzed data on the number of coral settlers per tile using a two-way ANOVA with fixed effects of depth and herbivore exclusion.

2.7. Investigating differences in coral settler mortality between depths

Tiles in the herbivore exclusion treatment had significantly more coral settlers than uncaged tiles (See Results). Therefore, to maximize the number of coral settlers per tile we only used tiles from the herbivore exclusion treatment in the reciprocal transplant experiment. We only used tiles that had at least one coral settler and on average tiles had 5.9 coral settlers, but ranged from 1 to 23 coral settlers. We assigned each tile to one of four groups and made the number of coral settlers per group as even as possible. Each group of tiles was either transplanted back to its original depth or transplanted to the opposite depth, which created four treatments: 1) 10 m to 10 m, 2) 10 m to 17 m, 3) 17 m to 17 m, and 4) 17 m to 10 m. We transplanted the coral settlement tiles back to the reef for 21 days. At the end of the experiment we collected the tiles and brought them back to the field station, keeping the tiles submerged in seawater. We again searched the tiles for coral settlers using microscopy, and used the digital maps of coral settler locations to look for the previously mapped coral settlers. We scored each coral settler as either dead or alive. For coral settlers that died we assigned each settler into a category based on the condition of its skeleton, or lack thereof. Dead coral settlers whose skeletons appeared intact and had no visible physical damage were scored as ‘intact’, settlers with some physical damage, such as damage to the skeletal structure, were scored as ‘damaged’, and settlers that were no longer present and had no remnants of skeleton left on the tile were scored as ‘disappeared’. For each coral settlement tile we calculated the calculated the mean percent mortality of coral settlers. We then used a mixed effects model to ask whether transplant treatment explained variation in the percent mortality of coral settlers on each tile. Because our data on the skeletal condition of dead coral settlers are non-independent, we only analyzed differences in the percent of settlers that were ‘disappeared’ using a t-test.

3. Results

3.1. Patterns of coral decline and recovery

Prior to the COTS outbreak and Cyclone Oli the percent cover of stony corals at the two sites on the north shore of Moorea (LTER 1 and 2) peaked in 2005 at 39.3% and 46.6% at 10 and 17m, respectively (Fig. 1A). At the peak of coral cover in 2005 reefs were not dominated by any one genus of corals and the relative abundance of *Acropora, Porites,* and *Pocillopora* was 29.5%, 22.6%, and 39.9% at 10m, and 25.2%, 28.3%, and 29.3% at 17m. Reefs at 17m reached a minimum coral cover of 0.9% in 2010 and reefs at 10m reached a minimum of 1.1% coral cover in 2011. Reefs at 10m recovered faster than reefs at 17m and the mean annual rate of recovery of coral cover was 9.7% yr^{-1} and 4.1% yr^{-1} at 10 and 17m, respectively. Reefs at 10m surpassed pre-disturbance coral cover by 2015, whereas reefs at 17m had not returned to pre-disturbance coral cover by 2018. Reefs at 10m and 17m reached peak coral cover of 71.3% and 30.1% respectively, for the timeframe that we considered ending in 2018. Recovery on the outer reef was driven by the rapid recruitment and increase in abundance of corals in the genus *Pocillopora* (Holbrook et al., 2018) and by 2018 the relative abundance of the three most abundant coral genera, *Acropora, Porites,* and *Pocillopora* was similar at 10 and 17m (Fig. 1B). In 2018 corals in the genus *Pocillopora* accounted for 76.1% and 66.2% of all coral cover at 10 and 17 m, respectively, whereas *Acropora* accounted for 4.5% and 4.4% of coral cover and *Porites* accounted for 6.2% and 13.9% of coral cover at 10 and 17m, respectively.

3.2. Coral settlement

Coral recovery on the outer reef was driven by the increase in abundance of corals in the genus *Pocillopora* therefore we only considered the settlement of corals in the family Pocilloporidae in our analysis of coral settlement. In our analysis of Pocilloporidae settlement the interaction between depth and year was not significant (P=0.070, mixed effects model) and the effect of depth was not significant (P=0.464, mixed effects model, Fig. 2A). There was a significant effect of year on the number of Pocilloporidae settlers (P<0.0001, mixed effects model). Pocilloporidae settlement peaked in 2011 for both depths, with an average of 6.6 and 8.3 settlers tile^{-1} at 10 and 17m, respectively. This peak in coral settlement occurred at approximately the same time as minimum coral cover for reefs at both depths. Settlement declined between 2011 and 2015 and on average there was less than 1 Pocilloporidae settler per tile in 2014 and 2015.

3.3. Coral recruitment, survival and growth

In our analysis of coral recruitment, there was a significant depth×year effect on the number of new *Pocillopora* recruits (P<0.0001, mixed effects model, Fig. 2B). Coral recruitment peaked in 2012, one year after the peak in settlement of Pocilloporidae corals. On average there were 58.3 and 16.8 new *Pocillopora* recruits m^{-2} on reefs at 10 and 17 m in 2012. Recruitment declined from 2012 to 2018 as the percent cover of corals increased at both depths. The minimum recruitment of new *Pocillopora* corals occurred in 2018 with an average of 0.0 and 5.7 new recruits m^{-2} at 10 and 17m, respectively.

When we analyzed data on coral recruit mortality there were significant effects of depth and year on the percent of recruits that died (P=0.006 and P=0.007 for depth and year, respectively, mixed effects model, Fig. 3A) but no interaction between depth and year (P=0.675, mixed effects model). Annual coral recruit mortality was lowest from 2011-2012 and increased moderately until 2014-2015, the last pair of years for which we analyzed mortality data. Annual recruit mortality was higher at 17m than at 10m. From 2011-2012 the 6.1% of recruits died at 10m compared to 23.9% of recruits that died at 17m. By 2014-2015, 32.4% and 41.7% of recruits died at 10m and 17m, respectively. There was a significant effect of depth on the proportion of coral recruits that died on rubble (P<0.0001, t-test, Fig. 3B). Across all pairs of years that we considered in our analysis of recruit mortality, only 9.5% of all recruits that died at 10m were settled on rubble, whereas 33.5% of recruits that died at 17m were settled on rubble.

We estimated coral growth as the change in planar surface area between consecutive years (‘growth’ hereafter). In our analysis of annual coral growth there was a significant interaction between depth and year (P=0.034, mixed effects model, Fig. 4). Mean coral growth was lowest from 2011-2012 and increased throughout the time series. On average corals grew by 2.3 $cm^2 yr^{-1}$ and 3.4 $cm^2 yr^{-1}$ from 2011-2012 at 10 and 17m, respectively, and by 2015-2016 corals grew by 17.8 $cm^2 yr^{-1}$ and 28.1 $cm^2 yr^{-1}$ at 10 and 17m, respectively.

3.4. Evaluating the demographic drivers of coral recovery

Patterns of coral settlement did not differ between depths and therefore did not match patterns of variation in recovery rate between depths. However, the number of *Pocillopora* corals that recruited to reefs differed significantly on reefs at 10 and 17m, particularly in the first three years after reefs reached minimum coral cover (2011-2013). The number of *Pocillopora* recruits in each quadrat was a strong predictor of the recovery rate of each quadrat ($P<0.0001$, mixed effects model, Fig. 5A). The mean growth rate of *Pocillopora* corals in a quadrat was not a significant predictor of the recovery rate of each quadrat ($P=0.156$, mixed effects model, Fig. 5B).

3.5. Investigating the differences in coral settler mortality between depths

After one year of deployment, tiles in cages that excluded herbivores had 5.9 coral settlers tile^{-1} on average, whereas tiles that were not in cages had 2.3 coral settlers tile^{-1}. On average tiles at 10m had 3.8 coral settlers tile^{-1} whereas tiles at 17m had 4.4 coral settlers tile^{-1}. Caging that excluded herbivores had a significant effect on the number of coral settlers on each tile, but there was no effect of depth (caging $P<0.001$, depth $P=0.648$, ANOVA, Fig. 6A). There was a significant effect of depth on the number of coral settlers that survived on each tile ($P=0.002$, mixed effects model, Fig. 6B). More coral settlers died on tiles at 17m compared to tiles at 10m, and on average, 86.4% of coral settlers died at 17m whereas 55.2% of coral settlers died at 10m. Depth had a significant effect on the number of dead coral settlers that were categorized as “removed” on tiles at 17m compared to tiles at 10m ($P<0.0001$, t-test, Fig. 6C).

4. Discussion

Following catastrophic disturbances that reduced coral cover on the outer reef of Moorea to <1%, corals recovered more quickly on reefs at 10m compared to reefs at 17m. In 2011, the year after reefs reached minimum coral cover, there was a large peak in settlement of Pocilloporidae corals, but settlement did not differ between depths, indicating that differences in the supply and settlement of coral larvae did not drive differences in coral recovery. Following the peak in coral settlement in 2011 there was massive recruitment of *Pocillopora* corals on the outer reef, but recruitment was ~3.5 times higher at 10m compared to 17m. The number of corals that recruited to a given quadrat strongly predicted the rate of coral recovery, indicating that recruitment was the major driver of differences in recovery rates between depths on the outer reef. We also showed that the mortality of coral recruits at 17m was twice the rate of recruit mortality at 10m. At 17m three times as many recruits died on rubble compared to reefs at 10m, suggesting that differences in recruit mortality were driven in part by differences in substrate types between depths. These results suggest that the recruitment and survivorship of coral recruits together drove differences in recovery rates on the outer reef of Moorea. Finally, we investigated post-settlement bottlenecks that may have driven lower rates of recruitment on deeper reefs. We show that rates of mortality of newly-settled corals exposed to fishes are higher on deeper reefs compared to shallow reefs, suggesting that top-down pressure by herbivorous and or corallivorous fishes is an important mechanism structuring coral recruitment dynamics.

Our major finding that differences in coral recruitment drove rates of coral recovery following disturbance is congruent with past work in this system that showed that differences in recruitment drove differences in rates of recovery at 10m depth around the island of Moorea (Holbrook et al., 2018). Holbrook et al. suggested that differences in the supply of coral larvae around the island of Moorea may have led to different rates of coral settlement and ultimately recruitment. However, it is unlikely that this same mechanism also drove differences in recruitment between depths in our study. We found no differences in settlement between depths, but 3.5× higher recruitment at 10m compared to 17m, suggesting that post-settlement effects that create a bottleneck between the time that corals settle and when they grow large enough to be visible on the benthos as recruits drives differences in rates of coral recruitment. Our experiment with coral settlement tiles showed that rates of coral settlement were more than double when fishes were excluded. Further, rates of coral settler mortality on tiles that were exposed to fishes were significantly higher at 17m compared to 10m. Finally, our repeated surveys of coral settlement tiles exposed to herbivores showed that at 17m coral recruits were more likely to have disappeared and were less likely to be intact than coral recruits on tiles at 17m. Together these results suggest that top-down pressure by fishes, either through herbivory or predation, creates a bottleneck between settlement and recruitment, and that this bottleneck may be substantially stronger on deeper reefs compared to shallower reefs. Past work has shown that top down pressure by herbivorous fishes, particularly by grazing parrotfishes (Penin et al., 2010), is a major driver of mortality of newly-settled corals (Evensen et al. *in press*., Christiansen et al. 2009, Doropoulos et al. 2012, Doropoulos 2016). Our data showing that rates of mortality of newly-settled corals is higher and that coral recruits are more likely to disappear at 17m compared to 10m suggests that top-down pressure may be an important mechanism structuring recruitment on reefs in Moorea.

It is also likely that higher mortality of coral recruits contributed to differences in rates of coral recovery on deeper reefs compared to shallower reefs. Our work showed that the mortality of coral recruits was moderately higher at 17m compared to 10m. There could be several mechanisms driving this pattern. Data from the time series photos showed that the survival of coral recruits in the first year after recruitment was on average 20% higher at 10m compared to 17m, and our data suggests that these differences in recruit mortality may be driven in part by lower survivorship on dead coral skeletons at 17m compared to 10m. Top-down pressure by consumers may also have been a significant source of mortality to coral recruits. Consumers can damage and kill coral recruits either through direct predation (Adam et al. *in review*) or incidental mortality by fish feeding on algae, and it's possible that the effects of top-down pressure differ by depth. It's also likely that differences in mortality between depths were driven by differences in rates of mortality of recruits on different substrate types, particularly on rubble, which is likely poor habitat for coral recruits because it moves and turns over frequently. Although we report modest differences in recruit mortality between depths, it is possible that our method of data collection underestimated true rates of mortality of small coral recruits. It is likely that we are missing some recruits in the photos because they are too small to be seen in the photographs but then die before the next annual pictures are taken. Therefore, the mortality of the smallest coral recruits may be substantially higher than we estimate and contribute to the differences in rates of recruitment that we document from the time series photo data.

Surprisingly, differences in coral growth rates did not drive differences in rates of coral recovery on deep vs shallow reefs. Coral growth rates decline with depth for many species of corals (Baker & Weber, 1975; Huston, 1985) because coral calcification rates decline as light attenuates with depth (Buddemeier, Maragos, & Knutson, 1974; Marubini, Barnett, Langdon, & Atkinson, 2001). Therefore, it's reasonable to hypothesize that corals would grow slower at 17m than 10m, however we did not observe differences in *Pocillopora* growth rates with depth (Fig. 4). One likely explanation is that the higher density of coral recruits at 10m compared to 17m led to decreased individual growth rates of corals in high densities. Several experimental studies have shown that coral growth can increase with density for small corals (Kopecky, Cook, Schmitt, & Stier, 2021; Shantz, Stier, & Idjadi, 2011), but as corals grow and begin to interact with neighboring corals, competition with other corals can substantially decrease coral growth rates (Romano, 1990; Tanner, 1997). It is possible that higher densities of corals at 10m resulted in lower growth rates of corals than if coral density was lower. Other studies have also shown that high densities of adult corals reduces coral recruitment in Moorea, indicating that density dependence is an important mechanism structuring coral community dynamics in this system (Edmunds, 2018; Edmunds, Nelson, & Bramanti, 2018). Another mechanism that could have contributed to equivalent coral growth rates across depths is differences in *Pocillopora* assemblage structure across depths. Recent work in Moorea has shown that different cryptic species of *Pocillopora* corals may differ in their relative abundance across depths on the outer reef (Johnston, Wyatt, Leichter, & Burgess, 2021). It is possible that the cryptic species that are common on deeper reefs are uniquely well adapted for this lower light habitat and have comparable growth rates to the coral assemblages on neighboring shallower reefs. Regardless of the mechanism that drove similar growth rates at both depths, it is clear that differences in growth rates did not drive differences in coral community recovery on these reefs.

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References

Adam, T. C., Holbrook, S. J., Burkepile, D. E., Speare, K. E., Brooks, A. J., Ladd, M. C., … Schmitt, R. J. (n.d.). Priority effects in coral-macroalgae interactions can drive alternative community paths in the absense of top-down control. *Ecology*.

Aquilino, K. M., & Stachowicz, J. J. (2012). Seaweed richness and herbivory increase rate of community recovery from disturbance. *Ecology*, *93*(4), 879–890. https://doi.org/10.1890/11-0457.1

Baker, P. A., & Weber, J. N. (1975). Coral growth rate: Variation with depth. *Earth and Planetary Science Letters*, *27*(1), 57–61. https://doi.org/10.1016/0012-821X(75)90160-0

Bryson, E. S., Trussell, G. C., & Ewanchuk, P. J. (2014). Broad-scale geographic variation in the organization of rocky intertidal communities in the Gulf of Maine. *Ecological Monographs*, *84*(4), 579–597. https://doi.org/10.1890/13-1106.1

Buddemeier, R. W., Maragos, J. E., & Knutson, D. W. (1974). Radiographic studies of reef coral exoskeletons: Rates and patterns of coral growth. *Journal of Experimental Marine Biology and Ecology*, *14*(2), 179–199. https://doi.org/10.1016/0022-0981(74)90024-0

Castorani, M. C. N., Reed, D. C., Alberto, F., Bell, T. W., Simons, R. D., Cavanaugh, K. C., … Raimondi, P. T. (2015). Connectivity structures local population dynamics: A long-term empirical test in a large metapopulation system. *Ecology*, *96*(12), 3141–3152. https://doi.org/10.1890/15-0283.1

Christiansen, N. A., Ward, S., Harii, S., & Tibbetts, I. R. (2009). Grazing by a small fish affects the early stages of a post-settlement stony coral. *Coral Reefs*, *28*(1), 47–51. https://doi.org/10.1007/s00338-008-0429-9

Dean, T. A., Schroeter, S. C., & Dixon, J. D. (1984). Effects of grazing by two species of sea urchins (Strongylocentrotus franciscanus and Lytechinus anamesus) on recruitment and survival of two species of kelp (Macrocystis pyrifera and Pterygophora californica). *Marine Biology*, *78*(3), 301–313. https://doi.org/10.1007/BF00393016

Doropoulos, C. (2016). Characterizing the ecological trade- - offs throughout the early ontogeny of coral recruitment, *86*(1), 20–44.

Doropoulos, Christopher, Ward, S., Marshell, A., Diaz-Pulido, G., & Mumby. (2012). Interactions among chronic and acute impacts on coral recruits: the importance of size-escape thresholds. *Ecology*, *93*(10), 2131–2138.

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), 1–11. https://doi.org/10.1038/s41598-018-34686-z

Edmunds, P. J., Nelson, H. R., & Bramanti, L. (2018). Density-dependence mediates coral assemblage structure. *Ecology*, *99*(11), 2605–2613. https://doi.org/10.1002/ecy.2511

Evensen, N. R., Id, O., Doropoulos, C., Id, O., Gouezo, M., Id, O., … Wales, N. S. (n.d.). *Benthic micro- and macro-community succession and coral recruitment under overfishing and nutrient enrichment*. https://doi.org/10.1002/ecy.3536

Filbee-Dexter, K., & Scheibling, R. E. (2014). Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series*, *495*, 1–25. https://doi.org/10.3354/meps10573

Gworek, J. R., Vander, S. B., & Brussard, P. F. (2007). Changes in biotic interactions and climate determine recruitment of Jeffrey pine along an elevation gradient, *239*, 57–68. https://doi.org/10.1016/j.foreco.2006.11.010

Holbrook, S. J., Adam, T. C., Edmunds, P. J., Schmitt, R. J., Carpenter, R. C., Brooks, A. J., … Briggs, C. J. (2018). Recruitment Drives Spatial Variation in Recovery Rates of Resilient Coral Reefs. *Scientific Reports*, *8*(1), 7338. https://doi.org/10.1038/s41598-018-25414-8

Hughes, T. P., & Connell, J. H. (1987). Population dynamics based on size or age? A reef-coral analysis. *American Naturalist*, *129*(6), 818–829. https://doi.org/10.1086/284677

Huston, M. (1985). Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reefs*, *4*(1), 19–25. https://doi.org/10.1007/BF00302200

Johnston, E. C., Wyatt, A. S. J., Leichter, J. J., & Burgess, S. C. (2021). Niche differences in co-occurring cryptic coral species (Pocillopora spp.). *Coral Reefs*. https://doi.org/10.1007/s00338-021-02107-9

Kopecky, K. L., Cook, D. T., Schmitt, R. J., & Stier, A. C. (2021). Effects of corallivory and coral colony density on coral growth and survival. *Coral Reefs*, *40*(2), 283–288. https://doi.org/10.1007/s00338-021-02076-z

Lippok, D., Beck, S. G., Renison, D., Gallegos, S. C., Saavedra, F. V., Hensen, I., & Schleuning, M. (2013). Forest recovery of areas deforested by fire increases with elevation in the tropical Andes. *Forest Ecology and Management*, *295*, 69–76. https://doi.org/10.1016/j.foreco.2013.01.011

Marubini, F., Barnett, H., Langdon, C., & Atkinson, M. J. (2001). Dependence of calcification on light and carbonate ion concentration for the hermatypic coral Porites compressa. *Marine Ecology Progress Series*, *220*, 153–162. https://doi.org/10.3354/meps220153

Penin, L., Michonneau, F., Baird, A., Connolly, S., Pratchett, M., Kayal, M., & Adjeroud, M. (2010). Early post-settlement mortality and the structure of coral assemblages. *Marine Ecology Progress Series*, *408*, 55–64. https://doi.org/10.3354/meps08554

Romano, S. L. (1990). Long-term effects of interspecific aggression on growth of the reef-building corals Cyphastrea ocellina (Dana) and Pocillopora damicornis (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, *140*(1–2), 135–146. https://doi.org/10.1016/0022-0981(90)90087-S

Shantz, A. A., Stier, A. C., & Idjadi, J. A. (2011). Coral density and predation affect growth of a reef-building coral. *Coral Reefs*, *30*(2), 363–367. https://doi.org/10.1007/s00338-010-0694-2

Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation*, *29*(4), 436–459. https://doi.org/10.1017/S0376892902000322

Tanner, J. E. (1997). Interspecific competition reduces fitness in scleractinian corals. *Journal of Experimental Marine Biology and Ecology*, *214*(1–2), 19–34. https://doi.org/10.1016/S0022-0981(97)00024-5

Watanabe, J. M., & Harrold, C. (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*(2), 125–141. https://doi.org/10.3354/meps071125

Wernberg, T., Thomsen, M. S., Tuya, F., Kendrick, G. A., Peter, A., & Toohey, B. D. (2010). Decreasing resilience of kelp beds along a latitudinal temperature gradient : potential implications for a warmer future. *Ecology Letters*, 685–694.

https://doi.org/10.1111/j.1461-0248.2010.01466.x

Wijdeven, S. M. J., & Kuzee, M. E. (2000). Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration Ecology*, *8*(4), 414–424. https://doi.org/10.1046/j.1526-100X.2000.80056.x

Figures

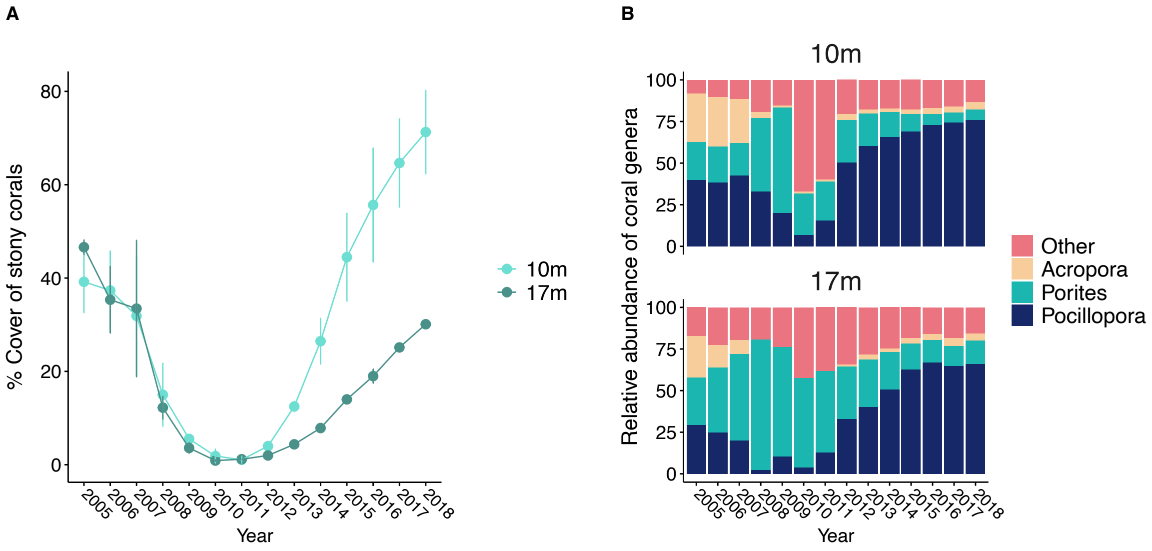

Figure 1. A) Patterns of coral decline and recovery on the outer reef at 10 and 17m between 2005 and 2018. Data points are the percent cover of stony corals averaged between sites (LTER 1 and LTER 2) for each depth. B) The relative abundance of the three most abundant coral taxa, *Acropora, Porites,* and *Pocillopora*, and Other (all other genera) throughout the time series at 10 and 17m. Data are mean relative abundance averaged between sites (LTER 1 and LTER 2) for each depth.

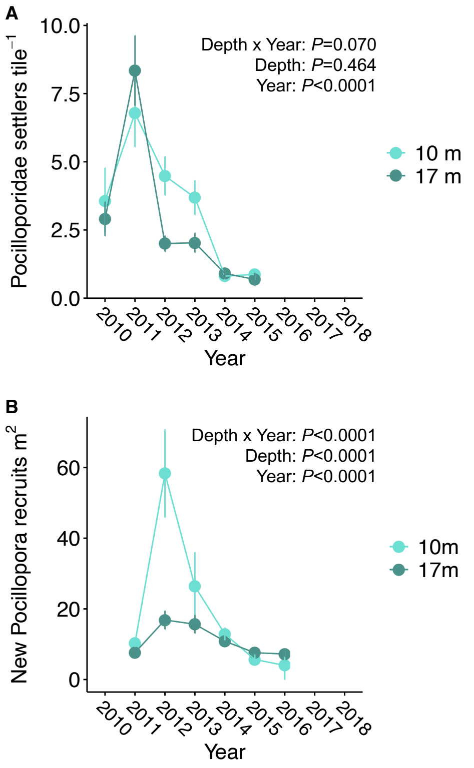

Figure 2. The A) settlement of Pocilloporidae corals on settlement tiles at 10 and 17m. Data points are the mean number of Pocilloporidae settlers tile^{-1} year^{-1} averaged between sites for each depth. Statistics are from the mixed effects model. B) Annual rates of recruitment of *Pocillopora* corals at 10 and 17m. Data points are the mean number of *Pocillopora* recruits m^{-2} year^{-1} averaged between sites for each depth. Statistics are from the mixed effects model.

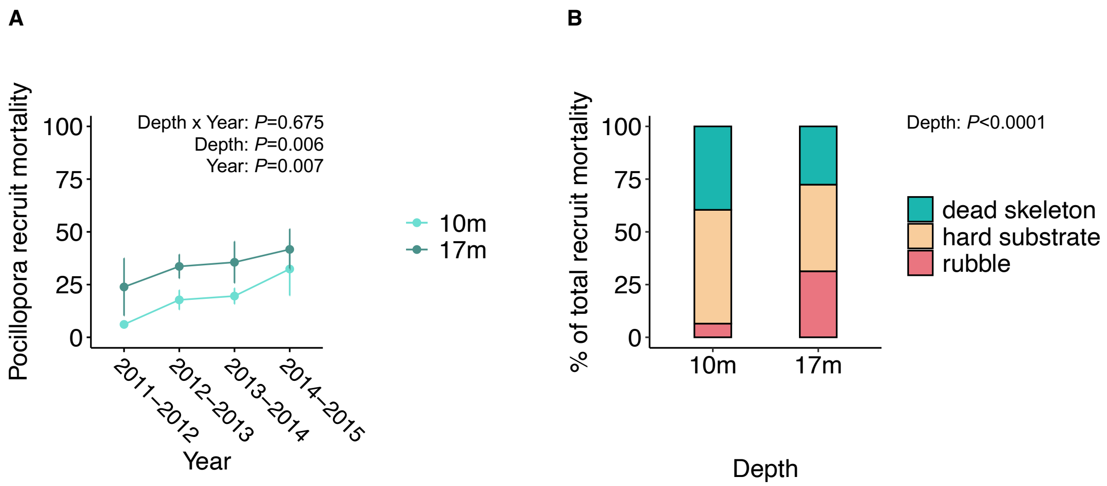

Figure 3. A) Annual rates of *Pocillopora* recruit mortality at 10 and 17m. Data points are the mean number of recruits that died per quadrat, averaged across sites for each depth. Statistics are from the mixed effects model. B) Percent of total recruit mortality that occurred on each substrate category averaged across sites for each depth. Statistics are from the t-test asking whether there are differences between depths in the prpoportion of recruits that died on rubble.

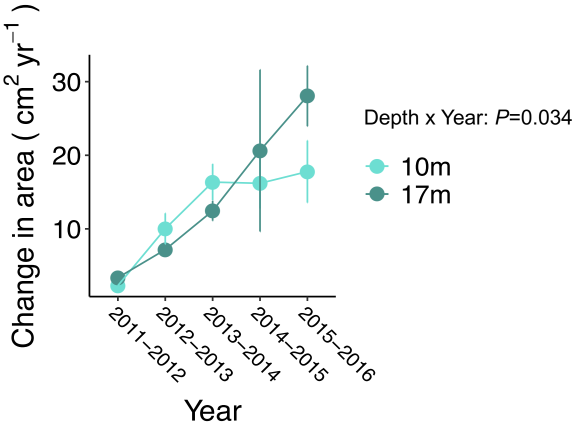

Figure 4. Mean coral growth between pairs of consecutive years at 10 and 17m. Statisitcs are the results of a mixed effects model.

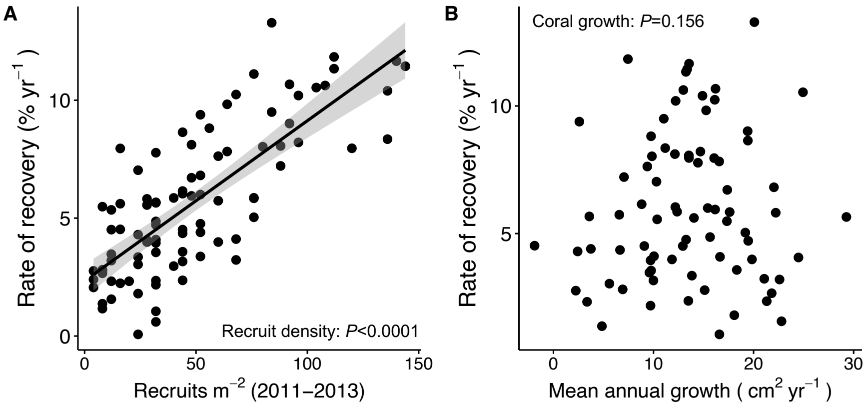

Figure 5. A) Relationship between the rate of coral recovery (% yr^{-1}) and the number of corals that recruited from 2011-2013 (recruits m^{2}). Data points are individual quadrats from permanent transects at LTER 1 and LTER 2 at 10 and 17m. Statistics are from the mixed effects model. B) The relationship between the rate of coral recovery and the mean annual growth (cm^{2} yr^{-1}) of corals in each quadrat from 2011-2016. Data points are individual quadrats from the permanent transects at LTER 1 and LTER 2 at 10 and 17m. Statistics are from the mixed effects model.

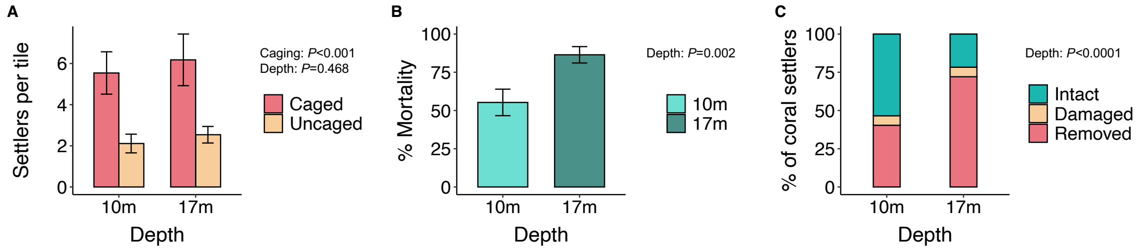

Figure 6. A) Differences in the number of coral settlers on tiles where herbivores were excluded (caged, pink) and where herbivores were not excluded (uncaged, yellow) at 10 and 17m. Data are the mean number of settlers per tile. Statistics are from the ANOVA. B) Mean percent mortality of coral settlers on tiles at 10 and 17m. Data are the average percent mortality per tile. Statisitcs are from the mixed effects model. C) The percent of dead coral settlers that were classified as each "intact", "damaged", or "removed". Statistics are results of a t-test comparing the effect of depth on the percent of coral recruits that were classified as "removed".

Appendix

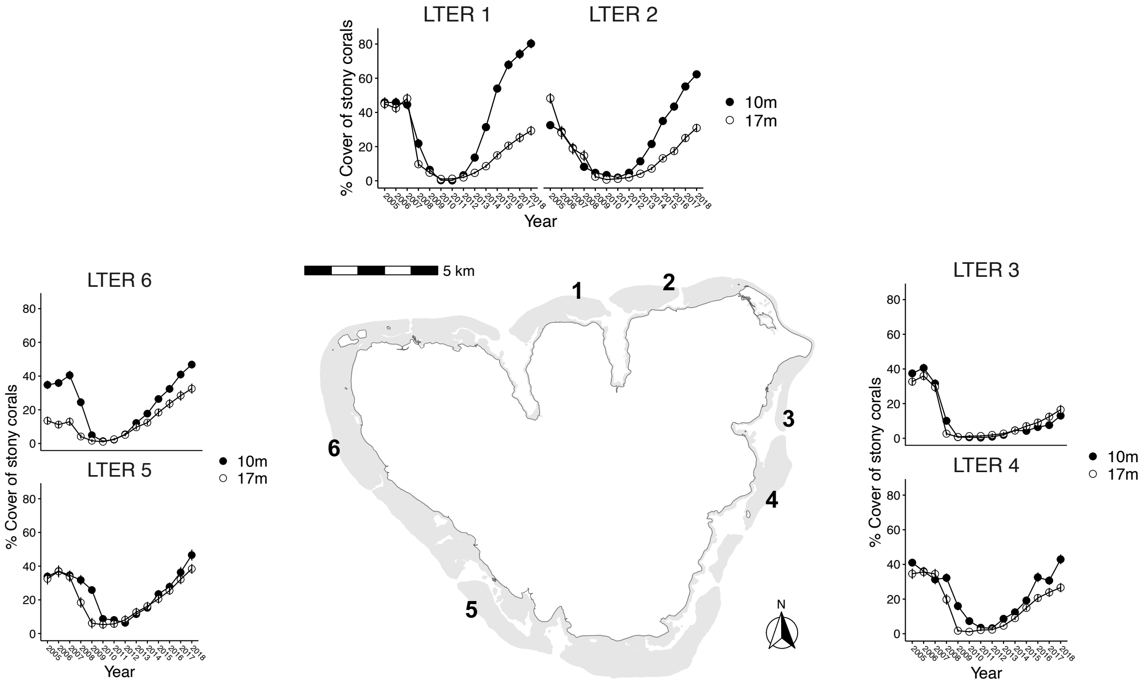

Figure S1. Patterns of coral decline and recovery at the six LTER sites around Moorea. Dark circles represent sites at 10m where open circles represent sites at 17m

III. Sediment associated with algal turfs inhibits the settlement of two endangered coral species

1. Introduction

Coral cover has declined steeply on reefs across the Caribbean since at least the 1970's as a result of recurrent large-scale bleaching events, disease outbreaks, overfishing, and nutrient pollution (Gardner et al., 2003; Jackson et al., 2014). As coral cover has declined there has been a regional collapse of important reef-building corals in the genera *Acropora* and *Orbicella* driven by a combination of disease outbreaks (Aronson and Precht, 2001) and multiple widespread bleaching events (Wilkinson and Hodgson, 1999; Wilkinson and Souter, 2008). Although disease and bleaching are likely responsible for the decline of *Acropora* and *Orbicella*, failure to recover is likely driven by lack of recruitment (Hughes and Tanner, 2000) or bottlenecks at early life history stages (Bak and Engel, 1979; Edmunds, 2007). The establishment of new individuals via recruitment is essential for coral recovery and necessitates better understanding of processes that promote or inhibit recruitment.

One potential bottleneck in recruitment may be long-term changes to benthic communities as corals decline and anthropogenic stressors such as overfishing, nutrient pollution, and sedimentation impact benthic habitat quality. As coral cover has declined across the Caribbean, macroalgae and algal turfs – short, productive communities of filamentous algae (also termed 'epilithic algal communities') (Connell et al., 2014) – have increased in abundance (Schutte et al., 2010; Jackson et al., 2014). These shifts in benthic community composition may be influencing settlement and recruit success and eroding the potential for recruitment of new corals. In addition to sufficient larval supply, successful coral recruitment depends on the availability of suitable settlement substrate and the survival of newly settled corals (Arnold et al., 2010). Selection of a suitable settlement location is key to this process and can strongly influence survivorship and growth (Price, 2010; Ritson-Williams et al., 2010). Thus, coral larvae display complex behavioral responses to environmental cues, often preferring to settle near some taxa, such as certain species of crusotose coralline algae (CCA) (Ritson-Williams et al., 2014, 2016), while avoiding many species of macroalgae and cyanobacteria, as well as some species of CCA (Kuffner and Paul, 2004; Kuffner et al., 2006; Paul et al., 2011; Ritson-Williams et al., 2014). Although the negative effects of macroalgae on coral larval settlement have been well-documented (Kuffner et al., 2006; Paul et al., 2011), we know much less about the role of turf algae in influencing coral settlement (Birrell et al., 2005, 2008).

Abundant turf algae is often considered to be indicative of healthy reefs with high grazing pressure (Carpenter, 1986; Hay, 1997); however, the characteristics of turf algae communities (length, density, community composition) can differ greatly based on grazing pressure and sedimentation. Short, productive algal turfs are common under higher grazing regimes, but increases in sediment loading can reduce grazing pressure and shift the community to long, sediment-laden algal turfs (Goatley et al., 2016) that are low preference for herbivorous fishes (Gordon et al., 2016; Tebbett et al., 2017). These types of long, thick algal turfs that trap sediment are likely poor settlement habitat for coral larvae (Birrell et al., 2005) and may pose a physical barrier to potentially settling corals. However, there have been few experimental tests on the effects of algal turfs on coral settlement (Birrell et al., 2005), and we know little about how sediment-laden algal turfs influence the abundance of young corals on reefs, despite their increasing abundance.

Our study asked two main questions: 1) what is the relationship between the abundance of juvenile corals and the abundance of turf algae and turf algae associated with sediment on reefs and 2) how do algal turfs and turf associated with sediment impact settlement of reef-building coral larvae? We conducted this work in the upper Florida Keys, USA where coral cover is low and turf algae is abundant. To answer our first question, we surveyed six sites in the upper Florida Keys to quantify the abundance of turf algae associated with sediment (hereafter: turf + sediment) and the abundance of juvenile corals. To answer our second question, we used laboratory settlement assays to test the effects of turf algae and turf + sediment on larval settlement of *Acropora palmata* and *Orbicella faveolata*, two ecologically important, but endangered, reef-building species. Prior to the start of our experiments we conditioned settlement tiles in the field for two years to cultivate natural communities of algal turfs and turf + sediment to use as settlement substrate in our experiments. First, we tested the effects of turf algae and turf + sediment on settlement of *A. palmata* and *O. faveolata* larvae. We then conducted a second experiment to isolate the effects of turf algae without sediment on coral settlement. Finally, we assayed coral settlement over a gradient of turf cover to understand how the abundance of algal turf covering the benthos affects coral settlement.

2. Methods

2.1. Field Surveys

In 2015 we surveyed six spur-and-groove fore-reef sites on SCUBA in the upper Florida Keys (GPS coordinates Table S1) to investigate the relationship between the abundance of juvenile corals (<4 cm diameter) and the percent cover of turf algae and turf +

sediment. We assessed the benthic community along eight, 50 m transects at each site, with a 50 x 50 cm quadrat placed every other meter. In each quadrat we took digital photographs (Olympus Tough TG-4 camera) which were later used to calculate percent cover using Coral Point Count with Excel extension (Kohler and Gill, 2006). The benthic cover categories that we used were: crustose coralline algae (CCA), gorgonians, sand, scleractinian corals, sediment, sponges, upright macroalgae, turf algae, turf algae + sediment, and other (unidentifiable substrate, bare space, zooanthids, cyanobacteria, and fire coral). Searching for coral recruits and juveniles on natural substrate is time intensive; we therefore identified and sized juvenile corals to the lowest taxonomic resolution possible (typically genus but species when possible) in a 25 x 25 cm subset of each 50 x 50 cm quadrat. We averaged coral count data as well as percent cover data by site. We investigated the relationship between juvenile coral abundance and the percent cover of turf algae, turf + sediment, and crustose coralline algae (CCA) using Pearson correlation. All statistical analyses described throughout the manuscript were performed in R (Version 3.4.2)(R Core Team, 2017), and graphs were made using the ggplot2 package (Wickham, 2010).

2.2. Gamete Collection and Rearing of Coral Larval

We collected spawned gamete bundles of *A. palmata* and *O. faveolata* from parent colonies in the upper Florida Keys during the annual spawning period in August of 2016 and 2017 and immediately transported them to our field laboratory in Key Largo. Gametes of each species were fertilized and reared in an outdoor laboratory according to Miller (2014). Competent larvae of both *A. palmata* and *O. faveolata* were obtained in 2016. *A. palmata* had poor fertilization in 2017, therefore only *O. faveolata* larvae were available for settlement assays that year. We conducted daily, independent competency assays to ensure that a high proportion (e.g. >30% per 24 h for *O. faveolata*, >10% for *A. palmata*) of larvae were inclined to settle and metamorphose in response to a positive settlement cue (chip of reef rubble) throughout the duration of the settlement experiments. Based on these observations, we began settlement experiments 9 days after gamete fertilization for *A. palmata* and 6 days after gamete fertilization for *O. faveolata*. Successive experiments for each species used larvae that were two days older than the previous, since it was only possible to conduct one 48 hr experiment at a time due to limited space in the seawater system.

2.3. Cultivation of Algal Turf Communities for Settlement Assays

We used 10 × 10 × 2 cm coral limestone tiles as settlement substrate for all experiments. Coral limestone tiles (Keystone Productions, Coral City, FL) contain natural millimeter scale structural complexity that closely mimics the natural limestone foundation of coral reefs as they were quarried from Floridian Pleistocene reef formations. Limestone tiles were attached to PVC-coated mesh with cable ties and nailed to the benthos near Pickles Reef (80°24.964'W, 24°59.087'N) where they stayed for two years. Communities of turf algae, CCA, sponges, and macroalgae that are similar to the communities on the natural substrate developed on the tiles.

Immediately prior to the start of the settlement assays (<24 hrs) we collected and transported tiles from the reef to the lab, taking care not to dislodge sediment particles. We subdivided the large tiles into 2 × 2 × 1 cm (L × W × H) settlement tiles using a tile saw. We cut each tile such that one side of each tile contained the algal community on the exterior of the tile, and the other five sides were fresh-cut limestone. Therefore, each tile had only one pre-conditioned surface. Past experiments have shown that many larvae settle on the undersides of settlement substrate (Price, 2010; Raimondi and Morse, 2000; Arnold and Steneck, 2011), but our objective was to understand how larvae respond to the algal communities on the tile surfaces. Therefore, we coated each of the five bare limestone sides with a thin layer of paraffin wax to make these sides unavailable to larvae, leaving only the side with the algal community available for larvae to settle. Our preliminary experiments showed that larvae will settle near but not on top of wax, making it a suitable barrier to prevent larvae from avoiding the algal communities of interest by settling on the bare limestone surfaces.

2.4. Settlement Experiments with Coral Larvae

We carried out settlement experiments in a temperature-controlled recirculating water system with seawater collected from a nearby fore reef. We used clear acrylic cylindrical chambers (1L volume) as experimental settlement chambers in which the bottom end was covered with 120μ mesh and the top end was open to the air. Settlement chambers were submerged halfway in the recirculating water system with the mesh end down, which allowed water to flow in and out of the chambers but did not allow larvae to escape.

We put one settlement tile and 20 or 30 larvae (for *A. palmata* or *O. faveolata,* respectively) in each settlement chamber for 48 hours. At the end of each settlement experiment, we counted the number of settled larvae on each tile using fluorescence microscopy. Individuals were classified as 'settlers' only if they displayed visible signs of settlement (attachment to the substrate) and metamorphosis (i.e., transition from pear shaped to flat/disc shape). Each of the following settlement experiments was carried out using this protocol.

Experiment 1: *Turf vs. Turf + sediment Experiment:* In this experiment, we compared larval settlement on substrates dominated by turf versus turf + sediment. The turf + sediment tiles were left unmanipulated and were dominated by turf algae (a mix of red, green, and brown filamentous algae), with no macroalgae, and covered in 1-3mm of sediment. For the turf only treatment, we selected tiles that were dominated by filamentous turf algae but had no macroalgae, removed sediment by gently shaking each tile underwater, and then brushed each tile with a soft paintbrush to remove any remaining sediment. We conducted this experiment in 2016 with simultaneous, independent settlement assays for coral larvae of *A. palmata* and *O. faveolata* with 15 replicates of each treatment. Percent larval settlement was calculated for each replicate. The data were not normally distributed (via visual inspection of histogram and QQ plots), therefore we assessed differences in percent settlement between treatments for each coral species using a non-parametric Mann-Whitney U test.

Experiment 2: *Turf Removal Experiment:* We conducted this experiment in 2017 using *O. faveolata* larvae. We asked whether removing turf algae increases coral larval settlement. When selecting tiles for this experiment we selected tiles most similar in terms of percent cover and community composition of turf. We were interested in the effects of turf algae on coral settlement, but we also acknowledged that other aspects of the tile community, such as small patches of CCA, may also influence settlement. Therefore, we utilized a repeated measures design to assay coral settlement on the same tiles, with and without turf algae. Each settlement tile was assigned an identification number and used in two settlement trials for this experiment. For each settlement tile, we also quantified the percent cover of CCA, turf algae, and turf + sediment using a dissecting microscope.

In trial A, we assayed coral settlement on turf and turf + sediment tiles (n = 15 per treatment) using the same methods as the previous experiment. After the tiles were scored for settled larvae, we discarded the turf + sediment tiles and used only the turf tiles in Trial B. For each turf tile, we removed all turf algae with tweezers under a dissecting microscope and removed all settled larvae from the tiles with a scalpel and a syringe. Then for trial B, we conducted a second settlement assay with a new set of larvae on the same tiles after the turf algae were removed. This experimental design allowed us to compare settlement on the same tile both with and without the effect of turf algae. We tested the difference between settlement on turf vs. turf + sediment (trial A) using a non-parametric Mann-Whitney U test. We used a paired t-test, with "tile number" as the pairing factor, to assess the effect of turf algae removal by comparing settlement on the turf tiles from trial A with the settlement on those same tiles in trial B after turf was removed.

During both trial A and trial B, we also assayed settlement on bare control tiles (n=14) which were limestone tiles conditioned in the same way as the turf tiles, but with all external community removed using a tile saw (i.e., completely bare limestone). Our intention was not to compare settlement between the turf tiles and the control tiles, but to use the control tiles to ensure that larval competency did not vary between trials A and B due to differences in the age of the larvae.

Experiment 3: *Turf Gradient Experiment:* Given that turf presence at moderate abundance had minor impacts on the settlement of coral larvae (see Results for Experiment 2), we wanted to test whether increasing turf density inhibits larval settlement. We took advantage of natural heterogeneity of the tile communities to assay coral larval settlement over a gradient of turf cover. We selected 28 tiles with turf cover ranging from 2-92%. All tiles initially had some sediment covering them (1-3mm) which we removed as described above. On some tiles, we used tweezers to slightly modify turf cover by removing some filaments to ensure a gradient of turf density. For each settlement tile, we also quantified the percent cover of CCA, turf algae, and turf + sediment using a dissecting microscope. We assayed coral settlement with *O. faveolata* larvae using the same methods as described previously. We assessed the relationship between percent cover of turf and the percent settlement on each tile using a simple linear regression. Additionally, we hypothesized that the percent cover of CCA may drive differences in percent settlement and assessed this relationship via simple linear regression.

3. Results

Field Surveys: Percent cover of turf algae ranged from 1.6-29.4% across all sites. Turf + sediment was abundant at all sites and ranged from 22.3-59.4% (Fig. 1). Although the relative proportions of turf and turf + sediment varied at each site, combined they were 38.1-67.6% of the benthic community. Mean sediment depth in the turf +sediment category at each site ranged from 2.04 – 6.83 mm (mean 4.6 mm). Coral cover was low across all sites (0.6-1.7% cover). Mean juvenile coral abundance ranged from 8.24-14.32 individuals m^{-2} across the different sites (Fig. 1B). We found a strong negative correlation between percent cover of turf + sediment and the abundance of juvenile corals at the site level (R = -0.92, df = 4, p = 0.009, Fig. 2A), but there was no relationship between the abundance of turf algae without sediment and the abundance of juvenile corals (R = 0.61, df = 4, p = 0.188, Fig. 2B).

Experiment 1: Turf vs. Turf + Sediment Experiment: A. palmata settlement was low overall and ranged from 0-15% across both settlement substrate treatments. Over 10 times more *A. palmata* larvae settled on the turf tiles than on the turf + sediment tiles (5.5 ± 1.6% and 0.5 ± 0.5%, respectively; Mann-Whitney U, W = 18.5, p = 0.008; Fig. 3A). Further, only one larva settled on all of the turf + sediment replicates combined, suggesting strong aversion to this substrate type. Settlement of *O. faveolata* larvae ranged from 0-43.3% across both settlement substrate treatments with settlement over 13 times higher on turf compared to turf + sediment tiles (16.0 ± 3.9% and 1.2 ± 0.6%, respectively; Mann-Whitney U, W = 45, p = 0.004; Fig. 3B,C).

Experiment 2: Turf Removal Experiment: Settlement on fresh-cut limestone tile surface replicates did not differ between Trials A and B (mean percent settlement was 3.1 ± 1.4% and 2.9 ± 1.7%, respectively; t-test, t = 0.113, df = 26, p = 0.911), confirming that changes in larval competency over time did not compromise our repeated measures design. In Trial A, *O. faveolata* settlement was significantly higher on turf compared to turf + sediment tiles (8.3 ± 2.9% and 0.1 ± 0.2%, respectively; Mann-Whitney U, W=59, p<0.001, Fig. 4A). However, there was no difference in settlement between tiles with turf (8.3 ± 2.9%; Trial A) and those same tiles once turf was removed (12.7 ± 3.2%; Trial B) (paired t-test, p = 0.109, t = -1.721, df = 13, Fig. 4B). In Trial A (before turf removal), the cover of turf on tiles ranged from 30-

98% (mean of 62.9 ± 6.6%). In Trial B (after turf removal), the percent cover of turf on the same tiles was 0%.

Most tiles contained small understory patches of CCA (0-20% cover) within the turf community. We explored the possibility that the settlement response to turf removal depended on the cover of CCA using a simple linear regression of the change in settlement for each tile [Settlement in Trial B – Settlement in Trial A] as a function of CCA cover. We did not find evidence that CCA cover influenced the settlement response to turf removal (linear regression, adjusted R-squared < 0.001, $p = 0.793$, Fig. S1A), or that initial turf cover influenced the response to turf removal (linear regression, adjusted R-squared < 0.001, $p = 0.783$, Fig. S1B).

Experiment 3: Turf Gradient Experiment: Cover of algal turf ranged from 2-92% across all tiles. Settlement of *O. faveolata* was variable and ranged from 0-23.3% but there was no relationship between settlement and cover of algal turfs (linear regression, adjusted R-squared < 0.001, $p = 0.547$, Fig. 5A). Percent cover of CCA on the tiles ranged from 0-40%, and there was a significant negative relationship between the percent cover of CCA and percent settlement of larvae (linear regression, adjusted R-squared $= 0.178$, $p = 0.012$, Fig. 5B).

4. Discussion

Here, we show that naturally-occurring sediment entrapped in reef algal turfs is likely a significant impediment to settlement and recruitment of coral larvae. In field surveys, sediment-laden turf was abundant (~ 20-60% cover) across all our sites in the Florida Keys and at most sites was more abundant than the more benign turf (without sediment) cover (Fig. 1A). There was a strong, negative relationship between the abundance of sediment-laden turf and juvenile coral abundance at the site level. In laboratory assays, *A. palmata* and *O. faveolata* larvae had significantly lower settlement on tiles with both turf algae and sediment than on tiles with only turf algae. *A. palmata* and *O. faveolata* larvae did settle among algal turfs without sediment, suggesting that algal turfs may have little impact on larval settlement. Further, we found that removing turf algae did not significantly increase settlement for *O. faveolata* larvae and that even the densest turf communities did not inhibit larval settlement. Similarly, in our field surveys, there was no relationship between turf abundance and juvenile coral abundance. There was a negative relationship between settlement in *O. faveolata* larvae and the abundance of crustose coralline algae (CCA), suggesting the CCA communities that develop in areas with significant sediment do not facilitate coral settlement. Together, our results from both field surveys and laboratory assays demonstrate that sediment-laden turf suppresses settlement for *A. palmata* and *O. faveolata* larvae.

4.1. Impacts of sediment on coral settlement

Our results are consistent with previous work showing that sediment and sediment-laden turf (turf + sediment) is detrimental to settling corals (Hogdson, 1990; Babcock and Davies, 1991; Babcock and Smith, 2002; Birrell et al., 2005; Jones et al., 2015). Past studies, however, have used artificially created turf communities (Birrell et al., 2005), non-calcium carbonate settlement substrate (Hogdson, 1990; Babcock and Smith, 2002), or artificially added sediment (Babcock and Davies, 1991; Birrell et al., 2005), making it more difficult to understand how naturally-occurring sediment impacts coral settlement.

We build on previous literature by using turf algal communities with naturally accumulated sediment that were cultivated *in situ* on a reef for two years. These tiles more accurately represent the benthic environment that settling larvae encounter compared to artificially created communities, which could change sediment cover, sediment grain size, or turf community composition relative to natural communities. Any of these changes could significantly alter larval settlement choices. Further, the mean sediment depth on the turf + sediment tiles (1-3 mm) that we used in our settlement experiments was lower than the mean sediment depth across the reef sites that we surveyed (2–7 mm). Thus, our results demonstrate that even little accumulation of sediment is detrimental to coral settlement and are a conservative estimate of how sediment loads on reefs in the Florida Keys likely impede coral settlement.

We showed that coral larvae were unable to settle on turf + sediment on upward facing surfaces where sediment naturally accumulates. In areas where sediment accumulates, sediment particles are thought to reduce coral settlement via a physical mechanism by preventing larvae from attaching to solid substrate (Hogdson, 1990). However, field studies have also reported lower rates of coral settlement at sites with high sediment loads as compared to sites with low sediment loads even on the undersides of settlement tiles, cryptic habitats that do not collect sediment (Babcock and Smith, 2002; Price, 2010). When considered with our results, previous data suggest that sediment broadly suppresses coral settlement, possibly through multiple mechanisms such as physically preventing attachment to substrate (Hogdson, 1990), reducing light (Jones et al., 2015), smothering and obscuring settlement cues (Jones et al., 2015), and by driving changes in the benthic community that reduce the abundance of positive cues (Steneck, 1997).

For example, we showed a negative relationship between coral settlement and the abundance of CCA. Some species of CCA are attractive to settling coral larvae (settlement inducers) whereas other taxa are avoided or have no effect on settlement (Ritson-Williams et al., 2010, 2014), and therefore CCAs within turf communities may influence settlement by attracting or deterring coral larvae. Unfortunately, it was not possible to identify these CCAs to determine whether they were known settlement-inducing or –deterring species because they were small and lacked reproductive structures necessary for identification (R. Steneck, personal comm.). However, the negative relationship that we found between coral settlement and CCA abundance in our Turf Gradient experiment (Fig. 5B) implies that the CCAs on our tiles were not settlement-inducing species. Since we cultivated these turf tiles in a sediment-laden habitat, the negative relationship that we found between CCA abundance and coral settlement suggests that the CCAs that do well in these sediment-laden habitats are not those that promote coral recruitment. Therefore, sediment may influence coral settlement by altering the benthic community composition (Steneck, 1997). Thus, sediment-laden reefs that have lost adult corals may struggle to recover if sediment reduces coral recruitment reef-wide, both in areas where sediment accumulates and in refuge areas that are sheltered from sedimentation.

4.2. Algal turf characteristics and impacts on coral settlement

Our experiments show that coral larvae are able to settle among algal turfs, but it is unclear how different types of turfs influence settlement. Turf algal communities are difficult to identify and poorly described taxonomically (Connell et al., 2014) making it difficult to compare the effects of turf algae across studies. However, some evidence suggests that qualitatively different turf communities, cultivated under different grazing regimes, can have different effects on coral settlement. For example, tall, dense algal turfs farmed by territorial damselfishes may strongly inhibit coral settlement (Arnold et al., 2010). In contrast, shorter, heavily grazed algal turfs may have little or no inhibitory effect on coral settlement (Birrell et al., 2005). We suggest that the characteristics of turf algae (taxonomic composition, canopy height, density) and grazing regimes may have profoundly different but almost completely unknown effects on coral settlement.

Interestingly, we did not find evidence that algal turf cover influences coral settlement, as hypothesized by others (Birrell et al., 2005, 2008), suggesting that the turfs used in our study were relatively benign compared to some other types of turfs used in other studies. Algal turfs may negatively influence coral settlement either by physically blocking larvae from accessing the substrate, or larvae may be deterred from turfs by negative settlement cues produced by turf algae (Birrell et al., 2008). In either case, we would hypothesize that removing turf algae or reducing turf algal cover would increase coral settlement. However, we found that removing algal turfs did not significantly increase coral settlement, and, in a separate experiment, we found no relationship between coral settlement and the abundance of turf algae.

The lack of impact of algal turfs on coral settlement may have occurred due to three, non-mutually exclusive, reasons. First, our turfs were relatively short (1.8-5.2 mm canopy height) compared to turfs that negatively influenced settlement in other studies (up to 8 mm, Birrell et al. 2005; up to 10 mm, Arnold et al. 2010), and turf height may strongly influence the ability of larvae to access hard substrate under and among algal turfs (Birrell et al., 2008). Second, our turfs were cultivated under natural grazing regimes and were likely qualitatively different than those that negatively influenced settlement in other experiments that were cultivated under very low grazing regimes (Birrell et al., 2005) or in the territories of turf-farming damselfish (Arnold et al., 2010). Third, it is also possible that coral larvae select for habitats at a smaller spatial scale than the scale at which we quantified turf cover (2×2 cm tiles). We hypothesize that, even on the tiles with abundant turf algae, larvae were able to find small areas clear of algal turfs to settle.

4.3. Implications for endangered *Acropora* and *Orbicella* spp.

Our study is the first to investigate the effects of turf algae and sediment on settlement of *A. palmata* and *O. faveolata*, two endangered but ecologically important coral species across the wider Caribbean. These once-dominant species have undergone massive declines since the late 20th century and have failed to recover across the Caribbean. Successful recovery necessitates substantial recruitment and survival of new individuals to adulthood; it is therefore paramount to resolve the habitat requirements and conditions that promote successful settlement and recruitment for these two species. Our results confirm the Endangered Species Act Critical Habitat requirements for *Acropora palmata* and *Acropora cervicornis*, which states that they require substrate clear of sediment, turf algae, and macroalgae for settlement (National Oceanic and Atmospheric Administration, 2008). Importantly, our results strongly suggest that substrate 'free of sediment' is an important characteristic of the habitat requirements for *Acropora.* Although the 'critical habitat' for *O. faveolata* has not yet been defined, 'sediment free' substrate is likely equally important for larval settlement of this species. *A. palmata* and *O. faveolata* typically have low recruitment rates by sexually produced larvae in nature (Hughes et al., 2000; Quinn and Kojis, 2005; Williams et al., 2008), and therefore their larvae may be particularly sensitive to unfavorable settlement habitat, such as the conservative sediment loads used in our study.

Recent work in the Florida Keys has reported substantial *Acropora* recruitment on settlement tiles across a wide geographic range, but a complete lack of juveniles on adjacent natural reef substrate (van Woesik et al., 2014). These data suggest that, at least for *Acropora spp.,* there is a significant supply of larvae to Florida reefs, but this does not translate to successful recruitment (van Woesik et al., 2014). We suggest that the widespread abundance of sediment-laden algal turfs may be severely reducing already infrequent recruitment events, and may pose a roadblock to recovery of these two important coral species. Although sediment seems to strongly impede coral settlement, in the absence of sediment, algal turfs did not affect coral settlement. These results are encouraging because they suggest that reducing sediment loads alone could have a positive effect on coral settlement, and possibly lessen the recruitment bottleneck for these two species.

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References

Arnold, S.N., Steneck, R.S., 2011. Settling into an Increasingly Hostile World: The Rapidly Closing "Recruitment Window" for Corals. PLoS One 6, e28681. https://doi.org/10.1371/journal.pone.0028681

Arnold, S.N., Steneck, R.S., Mumby, P.J., 2010. Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. Mar. Ecol. Prog. Ser. 414, 91–105. https://doi.org/10.3354/meps08724

Aronson, R.B., Precht, W.F., 2001. White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460, 25–38.

Babcock, R., Davies, P., 1991. Effects of sedimentation on settlement of Acropora millepora. Coral Reefs 9, 205–208.

Babcock, R., Smith, L., 2002. Effects of sedimentation on coral settlement and survivorship. Proceedings 9th International Coral Reef Symposium, Bali, Indonesia 23-27 October 2000, pp. 245–248.

Bak, R.P.M., Engel, M.S., 1979. Distribution, Abundance and Survival of Juvenile Hermatypic Corals (Scleractinia) and the Importance of Life History Strategies in the Parent Coral Community. Mar. Biol. 54, 341–352.

Birrell, C.L., McCook, L.J., Willis, B.L., 2005. Effects of algal turfs and sediment on coral settlement. Mar. Pollut. Bull. 51, 408–414. https://doi.org/10.1016/j.marpolbul.2004.10.022

Birrell, C.L., Mccook, L.J., Willis, B.L., Diaz-pulido, G.A., 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Ocean. Mar Biol Annu Rev 46, 25–63. https://doi.org/doi:10.1201/9781420065756.ch2

Carpenter, R.C., 1986. Partitioning Herbivory and Its Effects on Coral Reef Algal Communities. Ecol. Monogr. 56, 345–364.

Connell, S.D., Foster, M.S., Airoldi, L., 2014. What are algal turfs? Towards a better description of turfs. Mar. Ecol. Prog. Ser. 495, 299–307. https://doi.org/10.3354/meps10513

Edmunds, P.J., 2007. Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. Mar. Ecol. Prog. Ser. 341, 1–13.

Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-term region-wide declines in Caribbean corals. Science. 301, 958–960. https://doi.org/10.1126/science.1086050

Goatley, C.H.R., Bonaldo, R.M., Fox, R.J., Bellwood, D.R., 2016. Sediments and herbivory as sensitive indicators of coral reef degradation. Ecol. Soc. 21. https://doi.org/10.5751/ES-08334-210129

Gordon, S.E., Goatley, C.H.R., Bellwood, D.R., 2016. Low-quality sediments deter grazing by the parrotfish Scarus rivulatus on inner-shelf reefs. Coral Reefs 35, 285–291. https://doi.org/10.1007/s00338-015-1374-z

Hay, M.E., 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs 16, S67–S76. https://doi.org/10.1007/s003380050243

Hogdson, G., 1990. Tetracycline reduces sedimentation damage to corals. Mar. Biol. 104, 493–496.

Hughes, T., Baird, A., Dinsdale, E., Moltschaniwskyj, N., Pratchett, M., Tanner, J., Willis, B., 2000. Supply-Side Ecology Works Both Ways: The Link between Benthic Adults, Fecundity, and Larval Recruits. Ecology 81, 2241–2249. https://doi.org/10.2307/177111

Hughes, T.P., Tanner, J.E., 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81, 2250–2263.

Jackson, J.B.C., Donovan, M.K., Cramer, K.L., Lam, V. V., 2014. Status and Trends of Caribbean Coral Reefs. Gland Glob. Coral Reef Monit. Network, IUCN.

Jones, R., Ricardo, G.F., Negri, A.P., 2015. Effects of sediments on the reproductive cycle of corals. Mar. Pollut. Bull. 100, 13–33. https://doi.org/10.1016/j.marpolbul.2015.08.021

Kohler, K.E., Gill, S.M., 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. Comput. Geosci. 32, 1259–1269. https://doi.org/10.1016/j.cageo.2005.11.009

Kuffner, I.B., Paul, V.J., 2004. Effects of the benthic cyanobacterium Lyngbya majuscula on larval recruitment of the reef corals Acropora surculosa and Pocillopora damicornis. Coral Reefs 23, 455–458. https://doi.org/10.1007/s00338-004-0416-8

Kuffner, I.B., Walters, L.J., Becerro, M.A., Paul, V.J., Ritson-Williams, R., Beach, K.S., 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar. Ecol. Prog. Ser. 323, 107–117.

Miller, M.W., 2014. Post-settlement survivorship in two Caribbean broadcasting corals. Coral Reefs 33, 1041–1046. https://doi.org/10.1007/s00338-014-1177-7

National Oceanic and Atmospheric Administration, 2008. Endangered and Threatened Species; Critical Habitat for Threatened Elkhorn and Staghorn Corals [WWW Document]. Fed. Regist. URL https://www.federalregister.gov/documents/2008/11/26/E8-27748/endangered-and-threatened-species-critical-habitat-for-threatened-elkhorn-and-staghorn-corals

Paul, V., Kuffner, I., Walters, L., Ritson-Williams, R., Beach, K., Becerro, M., 2011. Chemically mediated interactions between macroalgae Dictyota spp. and multiple life-history stages of the coral Porites astreoides. Mar. Ecol. Prog. Ser. 426, 161–170. https://doi.org/10.3354/meps09032

Price, N., 2010. Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. Oecologia 163, 747–758. https://doi.org/10.1007/s00442-010-1578-4

Quinn, N.J., Kojis, B.L., 2005. Patterns of sexual recruitment of acroporid coral populations on the West Fore Reef at Discovery Bay , Jamaica. Rev. Biol. Trop. 53.

R Core Team, 2017. R: A language and environment for statistical computing.

Raimondi, P.T., Morse, A.N.C., 2000. The Consequences of Complex Larval Behavior in a Coral. Ecology 81, 3193–3211.

Ritson-Williams, R., Arnold, S.N., Paul, V.J., 2016. Patterns of larval settlement preferences and post-settlement survival for seven Caribbean corals. Mar. Ecol. Prog. Ser. 548, 127–138. https://doi.org/10.3354/meps11688

Ritson-Williams, R., Arnold, S.N., Paul, V.J., Steneck, R.S., 2014. Larval settlement preferences of Acropora palmata and Montastraea faveolata in response to diverse red algae. Coral Reefs 33, 59–66. https://doi.org/10.1007/s00338-013-1113-2

Ritson-Williams, R., Paul, V.J., Arnold, S.N., Steneck, R.S., 2010. Larval settlement preferences and post-settlement survival of the threatened Caribbean corals Acropora palmata and A. cervicornis. Coral Reefs 29, 71–81. https://doi.org/10.1007/s00338-009-0555-z

Schutte, V., Selig, E., Bruno, J., 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. Mar. Ecol. Prog. Ser. 402, 115–122. https://doi.org/10.3354/meps08438

Steneck, R.S., 1997. Crustose corallines, other algal functional groups, herbivores and sediments: complex interactions along reef productivity gradients, in: Proc 8th Int Coral Reef Symp. pp. 695–700.

Tebbett, S.B., Goatley, C.H.R., Bellwood, D.R., 2017. The effects of algal turf sediments and organic loads on feeding by coral reef surgeonfishes. PLoS One 12, 1–14. https://doi.org/10.1371/journal.pone.0169479

van Woesik, R., Scott, W.J., Aronson, R.B., 2014. Lost opportunities: Coral recruitment does not translate to reef recovery in the Florida Keys. Mar. Pollut. Bull. 88, 110–117. https://doi.org/https://doi.org/10.1016/j.marpolbul.2014.09.017

Wickham, H., 2010. ggplot2: elegant graphics for data analysis (Use R!). Springer New York, NY.

Wilkinson, C., Hodgson, G., 1999. Coral reefs and the 1997-1998 mass bleaching and mortality. Nat. Resour. 35, 16–25.

Wilkinson, C., Souter, D., 2008. Status of Caribbean coral reefs after bleaching and hurricanes in 2005. Glob. Coral Reef Monit. Netw.

Williams, D.E., Miller, M.W., Kraemer, K.L., 2008. Recruitment failure in Florida Keys Acropora palmata , a threatened Caribbean coral. Coral Reefs 27, 697–705. https://doi.org/10.1007/s00338-008-0386-3

Figures

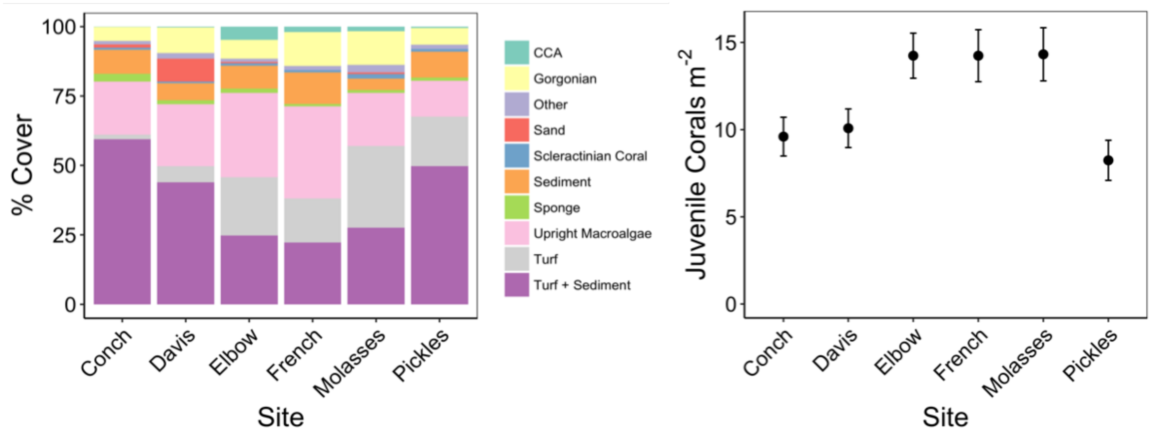

Fig. 1. A) Benthic community composition and B) mean juvenile coral abundance from field surveys at six reef sites in the upper Florida Keys.

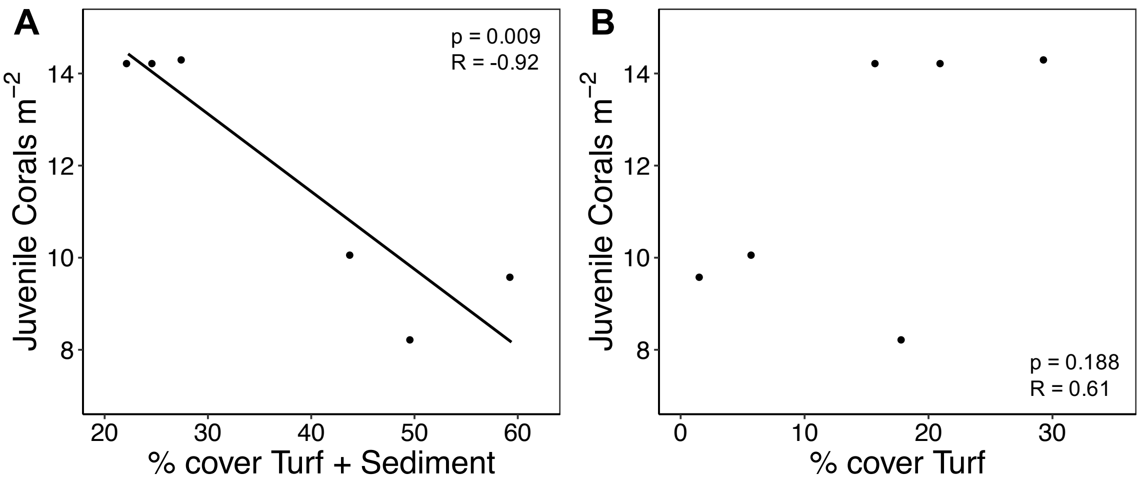

Fig. 2. The relationship between the abundance of all juvenile corals and percent cover of A) turf + sediment and B) turf. Statistics are from Pearson correlations.

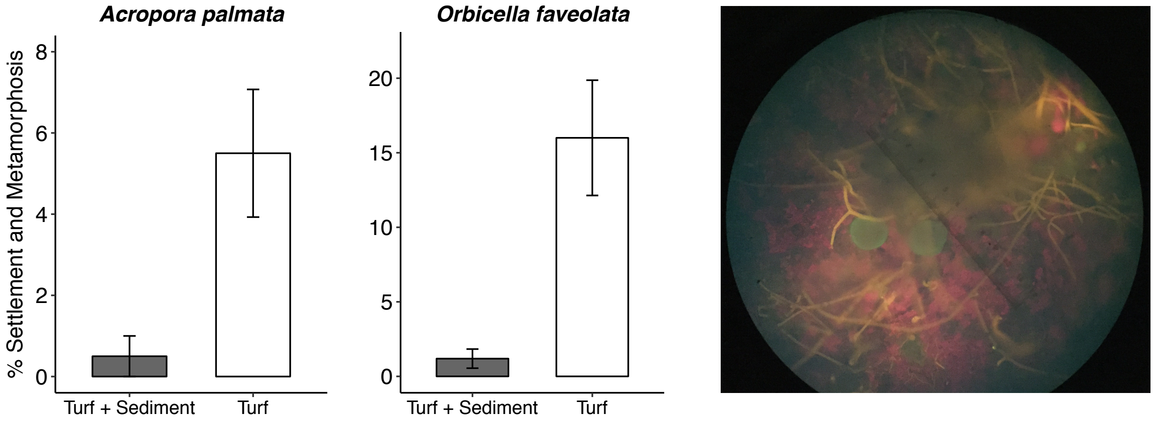

Fig. 3. Mean percent settlement and metamorphosis (±SE) of A) *Acropora palmata* and B) *Orbicella faveolata* larvae in response to Turf + Sediment and Turf in Experiment 1: *Turf vs. Turf + sediment Experiment*. Statistics from Mann-Whitney U test. C) *O. faveolata* settlers in the turf treatment, viewed with a fluorescent filter on the microscope. The settlers fluoresce green and are indicated with arrows, and the yellow filaments are turf algae.

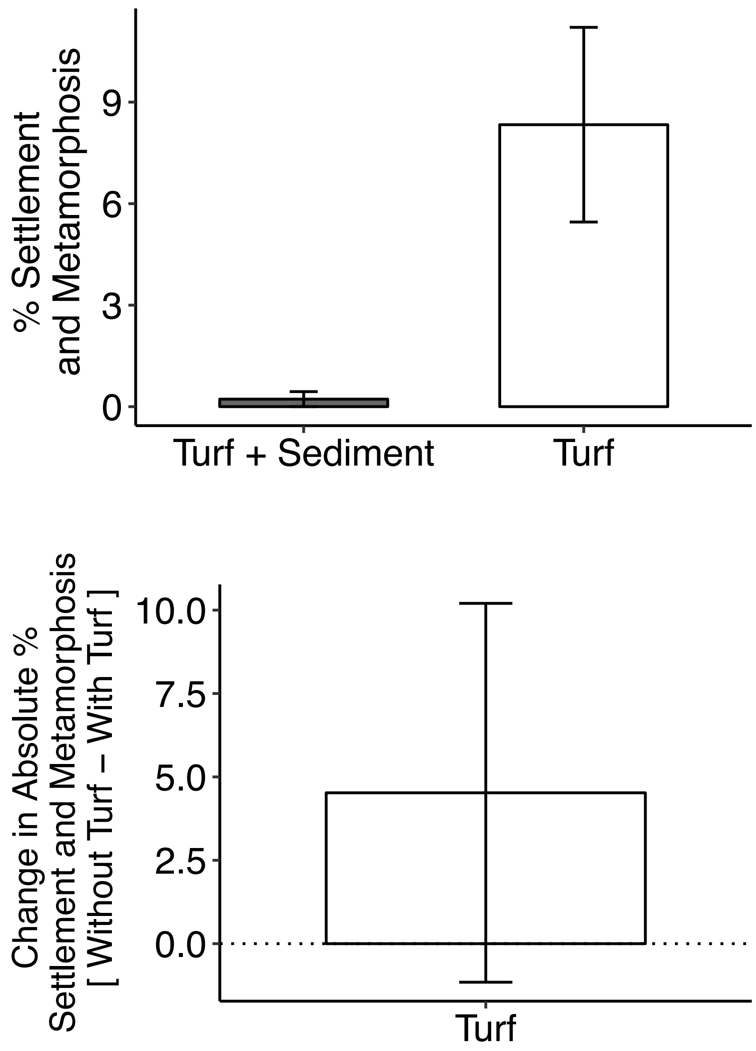

Fig. 4. A) Mean percent settlement and metamorphosis (±SE) of *Orbicella faveolata* larvae in response to Turf + Sediment and Turf in Experiment 2: *Turf Removal Experiment*. Statistics from Mann-Whitney U test. B) Change in absolute percent settlement (±95% confidence interval) on each tile after turf algae was removed. Statistics from paired t-test.

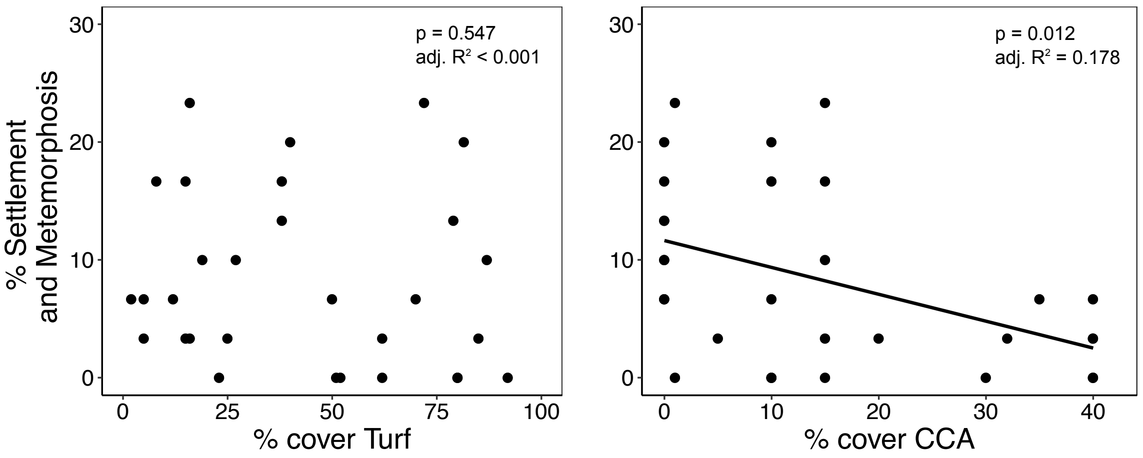

Fig. 5. Percent settlement and metamorphosis on each tile vs. A) percent cover of turf algae, and B) percent cover of CCA in Experiment 3: *Turf Gradient Experiment*. Statistics are results of simple linear regressions.

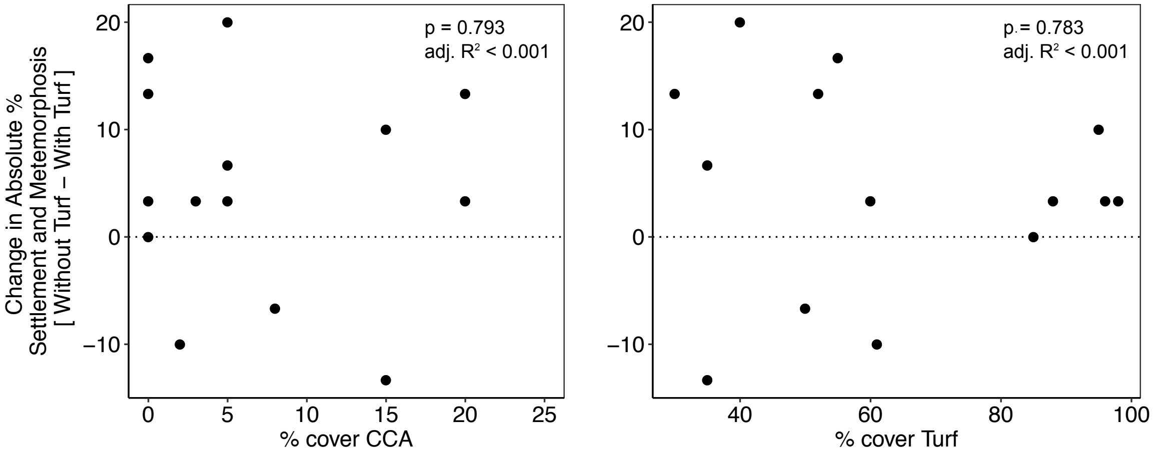

Fig. S1. The change in absolute percent settlement and metamorphosis on each tile vs. A) percent cover of CCA and B) percent cover of turf on each tile in Experiment 3: Turf Gradient Experiment. Statistics are results of simple linear regressions.

Appendix

Table S1: **Site Coordinates**

Site	**Lat. Long.**
Conch Reef	N 24 57.559, W 080 27.472
Davis Reef	N 24 55.834, W 080 30.350
Elbow Reef	N 25 13.632, W 080 26.076
French Reef	N 25 03.603, W 080 34.852
Molasses Reef	N 25 00.290, W 080 22.701
Pickles Reef	N 24 98.752, W 080 41.446

IV. Scale-dependent habitat selection by larvae of a reef-building coral

1. Introduction

When animals select habitats, they navigate heterogeneous landscapes to access resources and avoid risks (Senft et al., 1987). Mobile animals have the ability to continuously make decisions about their surroundings, allowing them to change their location to respond to changing environmental conditions. Further, the drivers of habitat selection change over an organism's life for many types of animals (Lecchini, Osenberg, Shima, St Mary, & Galzin, 2007; Pardieck, Orth, Diaz, & Lipcius, 1999; Richards, 1992). For example, many species of marine fishes utilize nursery microhabitats that offer protection from predators early in ontogeny but migrate to other habitats with greater food availability later in life (Deegan, 1990; Sponaugle & Cowen, 1996). In contrast, most sessile animals (e.g., barnacles, mussels, corals) have a motile phase early in ontogeny before they settle and become site-attached for the rest of their lives. Therefore, sessile animals typically have limited opportunities to select their habitat. Yet, these decisions shape their lifelong access to resources and exposure to risks such as competition and predation (Larsson & Jonsson, 2006) as well as influence their abundance and distribution of species (Baird, Babcock, & Mundy, 2003; Connell, 1985; Raimondi & Morse, 2000).

Because selection for settlement habitat is such a consequential process for sessile animals, the propagules of many taxa display complex responses to abiotic and biotic cues in the environment that provide information about habitat quality and shape individuals' propensity to settle (Connell, 1985; Raphael Ritson-Williams et al., 2009). For example, in rocky intertidal communities, the larvae of barnacles can perceive cues left on the substrate by predatory whelks and avoid these areas to reduce their future risk of predation (L. E. Johnson & Strathmann, 1989). Similarly, coral larvae avoid settling near macroalgae which likely reduces their risk of competition early in ontogeny (Raphael Ritson-Williams, Arnold, & Paul, 2020). In addition to biotic cues, the larvae of barnacles also perceive abiotic cues including water flow and actively avoid settling in high flow habitats where flow rates exceed speeds that are suboptimal for suspension feeding (Larsson & Jonsson, 2006). Further, coral larvae avoid low oxygen habitats which are likely unsuitable for post-settlement growth and survival (Jorissen & Nugues, 2021). It is well understood that biotic and abiotic cues shape the habitat selection by the larvae of sessile organisms, but we have a poor understanding of the scale at which these larvae respond to cues in potential habitats.

The spatial scale at which organisms respond to their environment and make decisions depends on the scale at which organisms perceive and interact with their habitat (Jackson & Fahrig, 2012; D. H. Johnson, 1980; Wiens, 1976). Some have suggested that there is a specific scale at which a species responds to its habitat (termed the 'species characteristic selection scale' (Holland, Bert, & Fahrig, 2004)). These scales have been identified for many species across a wide range of taxa (Fisher, Anholt, & Volpe, 2011; Stuber, F. Gruber, & Fontaine, 2018; Stuber & Fontaine, 2019). For some groups of animals, such as terrestrial mammals, body size is a predictor of the scale at which species choose habitats, where species with larger body size select habitats at larger spatial scales than smaller-bodied species (Fisher et al., 2011). However, making generalizable predictions across taxa about the scale at which species respond to the environment remains challenging (Stuber et al., 2018), likely because most species make decisions at more than one spatial scale. A growing body of evidence suggests that animals respond to habitat characteristics at multiple spatial scales (Holland & Yang, 2016) and that they make decisions hierarchically with different drivers of selection operating at different scales (Rettie & Messier, 2000). For example, large mobile animals, such as ungulates, often avoid predators at large spatial scales and make finer-scale choices based on food availability (Dussault et al., 2005; C. J. Johnson, Parker, Heard, Michael, & Gillinghamt, 2002).

In contrast to highly mobile animals that make decisions continuously throughout their lives, sessile animals, such as marine invertebrates, have only one opportunity to select their habitat. During the mobile phase, the propagules ('larvae') of marine invertebrates can travel tens to thousands of kilometers from their origins before settling in a new location (Álvarez-Noriega et al., 2020; Connolly & Baird, 2010). A combination of biological and physical processes dictates the movement of larvae, and passive physical processes, such as currents, generally drive the movement of larvae at large spatial scales, and increasingly more active processes determine larval movement at fine spatial scales (Pawlik, 1992). For example, larvae of marine invertebrates can use a combination light (Mundy & Babcock, 1998), sound (Vermeij, Marhaver, Huijbers, Nagelkerken, & Stephen, 2010), water flow (Larsson & Jonsson, 2006), and other abiotic cues to locate potential settlement sites. Biological cues from other benthic taxa can further mediate the settlement behavior of larvae, often resulting in correlations (both positive and negative) between the abundance of those taxa and the number of newly recruited individuals (Jenkins, 2005; Price, 2010). Although we have identified some of the major drivers of habitat selection for many species of marine invertebrates, few studies explicitly investigate the scale at which these drivers influence habitat selection (but see Walters 1992) or how larvae respond to multiple habitat characteristics simultaneously (but see Elmer et al. 2018).

Corals are sessile marine invertebrates and during settlement coral larvae balance both positive and negative settlement cues (Raphael Ritson-Williams et al., 2009). For example, some coral larvae prefer to settle on or near certain species of crustose coralline algae (CCA) (Harrington, Fabricius, De'Ath, & Negri, 2004; R. Ritson-Williams, Arnold, Paul, & Steneck, 2014; Tebben et al., 2015), but strongly avoid many species of fleshy macroalgae (Birrell, Mccook, Willis, & Harrington, 2008; Kuffner et al., 2006; Paul et al., 2011). The decisions that larvae make are a crucial step in the life cycle of corals because they determine their future competitors and success as adults. For example, larvae that settle on preferred CCA have significantly higher rates of survival than larvae that settle on avoided species of CCA, which can overgrow and outcompete coral recruits (Harrington et al., 2004; Price, 2010). However, most studies on habitat selection by coral larvae and the larvae of other marine invertebrates are artificial in that they ask whether coral larvae will settle near individual taxa. Rarely, do these studies give larvae realistic choices that they encounter in nature. When larvae settle on coral reefs, they make decisions within the broader reef community, balancing avoiding negative cues and selecting for positive cues. These decisions are complex and most work on coral settlement ignores the simultaneous push and pull of good and bad cues. Further, we know little about the scale at which coral larvae, or marine invertebrate larvae in general, respond to positive and negative cues to make the final decision to settle.

In our study, we investigated the settlement decisions of coral larvae within the landscape of complex benthic communities across several spatial scales. First, we pre-conditioned settlement tiles on a coral reef for two years to allow natural communities of benthic taxa to develop. We then used these tiles in an experiment examining the settlement choices in larvae of the reef building coral *Orbicella faveolata.* We gave coral larvae the opportunity to settle on tiles for 48 hours and then used high resolution digital photographs to make made digital maps of locations where each larva settled relative to benthic taxa. We then used these maps to evaluate relationships between the abundance of benthic taxa and the settlement of coral larvae. Specifically, we asked four questions: Questions 1) and 2) Does benthic community composition influence the likelihood of coral settlement or the number of larvae that settle? Which taxa positively or negatively influence the willingness of larvae to settle or the number of larvae that settle? Questions 3 and 4) When larvae do settle, which taxa do coral larva select for or avoid? And at which scales do they select for or avoid these taxa?

2. Methods

2.1. Gamete Collection and Rearing of Coral Larvae

We collected spawned gamete bundles of *O. faveolata* from parent colonies in the upper Florida Keys during the annual spawning period in August of 2017 and immediately transported them to our field laboratory in Key Largo, FL. Gametes of each species were fertilized and reared in an outdoor laboratory according to Miller (2014). We conducted daily, independent competency assays to ensure that a high proportion (e.g. >30% per 24 h) of larvae were inclined to settle and metamorphose in response to a positive settlement cue (chip of reef rubble) before starting the settlement experiments. Based on these observations, we began settlement experiments 6 days after fertilization of *O. faveolata* gametes.

2.2. Cultivation of Benthic Communities for Settlement Assays

We used 10 × 10 × 2 cm coral limestone tiles (Keystone Productions, Coral City, FL) as settlement substrate. Coral limestone tiles closely mimic the natural limestone foundation of coral reefs as they were quarried from Floridian Pleistocene reef formations. Limestone tiles were attached to plastic-coated mesh with cable ties and nailed to the benthos near Pickles Reef (80°24.964'W, 24°59.087'N) where they were conditioned for two years. Communities of turf algae, CCA, sponges, and macroalgae developed on the tiles, and these communities were very similar to the communities on the adjacent natural substrate.

Immediately prior to the start of the settlement experiment (<24 hrs) we collected tiles from the reef and transported them to our field lab on Key Largo. Our objective was to understand how coral larvae select settlement habitat at small spatial scales. Therefore, we subdivided the large tiles into smaller tiles 2.5 × 2.5 × 1 cm (L × W × H) settlement tiles using a tile saw. We cut the tiles such that one side of each tile contained the community on the exterior of the tile and the other five sides were fresh-cut limestone. Therefore, each tile had only one pre-conditioned surface. Past experiments have shown that many larvae settle on the undersides of settlement substrate (Price, 2010; Raimondi and Morse, 2000; Arnold and Steneck, 2011), but our objective was to understand how larvae respond to the benthic communities on the tile surfaces. Therefore, we coated each of the five bare limestone sides with a thin layer of paraffin wax to make these sides unavailable to larvae, leaving only one preconditioned side available for larvae to settle, a method that we have previously used for coral settlement experiments (Speare et al. 2019). Our preliminary experiments showed that larvae will settle near but not on top of paraffin wax, making it a suitable barrier to prevent larvae from avoiding the algal communities of interest by settling on the bare limestone surfaces.

Subdividing the preconditioned settlement tiles resulted in ~100, 2.5 × 2.5 × 1 cm tiles to choose from for this settlement experiment. Coral larvae strongly avoid many species of fleshy macroalgae (Birrell et al., 2008; Kuffner et al., 2006), and we wanted to avoid very strong negative settlement cues, therefore we selected tiles with minimal amounts of fleshy macroalgae. There were small amounts of several taxa of fleshy macroalgae on some of the tiles (in the genera *Valonia, Acetabularia,* and *Dictyota*) but each taxa accounted for <2% of the tile community. Our objective was to investigate the settlement decisions of larvae in different communities, therefore we selected 30 tiles that encompassed gradients in abundance of red filamentous algae, CCA, small boring sponges, green filamentous algae, and bare space. Prior to the start of the experiment we took high resolution digital photographs of each of the 30 settlement tiles (Olympus Stylus Tough TG-4) while the tiles were submerged in seawater. Digital photographs of the tiles were used to quantify the community composition on each tile and to map the location of coral settlers.

2.3. Settlement Experiment with Coral Larvae

We carried out our settlement experiment in a temperature-controlled recirculating water system with seawater collected from a nearby fore reef. We used clear acrylic cylindrical chambers (1L volume) as experimental settlement chambers in which the bottom end was covered with 120µ mesh and the top end was open to the air. Settlement chambers were submerged halfway in the recirculating water system with the mesh end down, which allowed water to flow in and out of the chambers but did not allow larvae to escape.

We put one settlement tile and 30 larvae in each settlement chamber for 48 hours. At the end of the settlement experiment, we counted the number of settled larvae on each tile using fluorescence microscopy. Individuals were classified as ‘settlers’ only if they displayed visible signs of settlement (attachment to the substrate) and metamorphosis (i.e., transition from pear shaped to flat/disc shape). For each settler we digitally mapped its location onto the digital photograph of each tile (Preview for Mac OS). This method allowed us to generate a location for each settler using an x,y coordinate system that corresponds to pixels of the image of each tile.

2.4. Quantifying Community Composition of Settlement Tiles

We used the digital photographs of the tiles to quantify benthic community composition of each tile by manually identifying points using CoralNet software (Beijbom et al., 2015). Points were overlaid in a uniform grid on the tile photographs. Because the dimensions (the length of each side) of each settlement tile were slightly different (mean ± SD of all side lengths 2.4 ± 0.3 cm), for each tile, we adjusted the number of rows and columns of points so that the point density for each tile was 100 points cm^{-2}. We manually identified the community member under each point using functional groups (e.g., sponge, calcareous invertebrates, etc., See Supplementary Table 1 for descriptions of community members). Each of the points was associated with an x,y coordinate that corresponds to the location of that pixel of the digital photograph, making our benthic composition data spatially explicit.

2.5. Data Analysis

Questions 1) and 2) Does benthic community composition influence the likelihood of coral settlement or the number of larvae that settle? Which taxa positively or negatively influence the willingness of larvae to settle or the number of larvae that settle?

Statistical analyses were performed in R version 3.6.2 (R Core Team, 2017). First, we asked whether the community composition of tiles was associated with the likelihood that a tile had at least one settler or differences in the number of settlers. For each tile, the percent cover of each community member was calculated as the proportion of points identified as each community member relative to the total number of points on the tile. Using the R package *vegan* (Oksanen et al., 2013) we first calculated compositional dissimilarities using Bray-Curtis dissimilarity matrix. We then used two-dimensional nonmetric multidimensional scaling (2D-NMDS) to visualize differences in tile community composition. We grouped tiles based on whether or not they had at least one coral settler, and then asked whether tile community composition differed between tiles that had at least one *O. faveolata* settler, and those that had no settlers using a permutational analysis of variance (PERMANOVA, *adonis* function in *vegan* (Oksanen et al., 2013)). We used linear regression to assess the relationship between the number of settlers on each tile and each tile's position along MDS1 and MDS2. Then to determine which community members drove dissimilarity between tiles with at least one coral settler and those with no coral settlers we used a SIMPER analysis (Clarke, 1993).

Questions 3 and 4) When larvae do settle, which taxa do coral larva select for or avoid? And at which scales do they select for or avoid these taxa?

Next, we asked whether coral larvae selected for or against certain taxa at scales smaller than the scale of the tile. To do this we first determined community composition in concentric circular neighborhoods (hereafter ‘neighborhoods’) of 1-7 mm radius around each settler. For each neighborhood of a given radius we calculated community composition by computing the distance between the location of the settler and the location of every point id on that tile. Points whose distance from the settler was less than or equal to the circle radius were stored and used to determine the community composition of that neighborhood. This process was repeated for each size neighborhood for each settler (7 neighborhood sizes per settler). The high density of points identified on each tile (100 points cm^{-2}) allowed us to evaluate community composition at these small spatial scales (see Table 2 for the number of points identified in each size neighborhood).

We were interested in understanding whether coral larvae were selecting for settlement neighborhoods that differed in community composition compared to the tile as a whole. Using the data on community composition of neighborhoods and community composition of whole tiles we carried out a compositional analysis of habitat use, which compares the proportional use of habitat characteristics (percent cover of community members) compared to their availability (Aebischer, Robertson, & Kenward, 1993) using the *compana* function within the *adehabitatHS* package (Calenge, 2006). We carried out separate compositional analyses of habitat use for each size neighborhood (Fig. 3B, Supp. Table 2). Some of the coral settlers were located near the edge of the tile such that a large portion of the neighborhood circle was off of the tile. We restricted the compositional analyses of habitat use to only include settlers for which at least 90% of their neighborhood was on the tile (See Supp. Table 2 for the number of point IDs in each size neighborhood and the number of settlers included in data analysis for each size circle). Because neighborhood area increases as neighborhood radii increases, more of the larger radii neighborhoods were at least partially off the edge of the tile than the smaller radii neighborhoods, and therefore the number of settler neighborhoods included in the data analysis decreased as neighborhood size increased.

To evaluate the possibility that decreasing sample size (number of neighborhoods) with increasing neighborhood size influenced our results, we downsampled the number of settler neighborhoods in our data analysis to a common sample size across all neighborhood sizes (n=19 neighborhoods) and reran the compositional analysis of habitat use using the downsampled dataset. We used a bootstrapping procedure (100 iterations) to repeatedly select a random subset of the data (downsample) and ran the compositional analysis of habitat use to generate a mean p-value and 95% confidence interval for each size neighborhood. To evaluate the possibility that sampling small areas of the tiles (neighborhoods) returned significant results in the compositional analysis of habitat use due to randomness inherent in sampling small areas of the tile, we also carried out a separate 'control' analysis using randomly selected areas on the tiles. For each size neighborhood we randomly selected locations on the settlement tiles using a random number generator. We selected the same number of random locations for each size neighborhood as we used in the compositional analysis of habitat use for the settler neighborhoods (See Supp. Table 2). We then conducted the compositional analysis of habitat use for the randomly selected neighborhoods as described above.

Lastly, we evaluated selection for or against individual members of the tile community using Strauss' Linear Selection Index (L): $L = r_i - p_i$ where r_i is the proportional cover of community member *i* within a neighborhood, and p_i is the proportional cover of community member *i* on the tile. Therefore, positive values of the selection index, L, reflect selection for a given community member relative to its abundance, whereas negative values of L reflect avoidance of a given community member. Tiles that had 0% cover of a given community member, *i,* were omitted from the data analysis for that community member because it is impossible to select for or against a community member that is not present. We calculated the selection index for each community member within each neighborhood size and averaged selectivity indices by community member and neighborhood size and calculated 95% confidence intervals.

3. Results

Questions 1 and 2) Does benthic community composition influence the likelihood of coral settlement or the number of larvae that settle? Which taxa positively or negatively influence the willingness of larvae to settle or the number of larvae that settle?

Of the 30 settlement tiles in this experiment, 23 tiles had at least one settler (Fig 1A). We found that tiles that had at least one coral settler had significantly different community composition compared to tiles that had no coral settlers (PERMANOVA, tile community composition ~ tiles with or without coral settlers, df=1, F=4.87, P=0.01, R^2=0.15). On average, tiles with settlers had 22.3% more bare substrate, but 15.1% less red thick filamentous algae, 11.0% less CCA, and 4.8% less red fine filamentous algae compared to tiles with no settlers (Fig. 1B). Bare substrate, red thick filamentous algae, CCA, and red fine filamentous algae combined to account for 70.7% of the dissimilarity between tiles with at least one settler and tiles with no corals settlers (SIMPER, Table 1).

There was also a significant effect of community composition on the number of coral larvae that settled, which ranged between 0 and 7 settlers (mean of 2.5) on each settlement tile. There was a significant negative relationship between the number of settlers per tile and the MDS1 axis (linear regression, *P*=0.016, adjusted R^2=0.163, Fig. 2A), but no relationship between the number of settlers and the MDS2 axis (linear regression, *P*=0.194, adjusted R^2=0.026, Fig. 2B). The major taxa driving separation along MDS 1 were bare substrate, green fine filamentous algae, red thick filamentous algae and CCA (Fig. 1A). The negative relationship between density of coral larvae and MDS 1 showed more larvae settled on tiles dominated by green fine filamentous algae and bare substrate and fewer larvae settled as tiles became dominated by red thick filamentous algae and CCA.

Questions 3 and 4) When larvae do settle, which taxa do coral larva select for or avoid? And at which scales do they select for or avoid these taxa?

The compositional analysis of habitat use revealed that coral larvae selected neighborhoods that were significantly different from the community composition of the whole tile (i.e. the 'available' habitat) for neighborhoods of 1-6 mm radii (*P*-values given in Fig 3B). These results were robust to downsampling. When we conducted the same composition analysis of habitat use with neighborhoods that were selected by a random number generator (the control analysis), we did not detect significant differences from the whole tile for any of the different size neighborhoods (Fig. 3C). This result confirms that the significant habitat selection that we observed was not driven by randomness associated with sampling small areas of the tiles.

When we compared the abundance of individual benthic taxa within each neighborhood to its abundance on the tile, we found that larvae exhibited strong preferences for or against individual community members and that these preferences often changed across neighborhood sizes (Fig. 4). Strauss' Linear Selection Index showed that generally, larvae exhibited stronger preferences for or against individual community members for smaller radii neighborhoods compared to larger neighborhoods. For small neighborhoods larvae strongly avoided red thick filamentous algae (1 mm radii), sediment (1-2 mm radii), and sponges (1-2, 4-5 mm radii). They also avoided red fine filamentous algae across most neighborhoods (1, 4-6 mm radii). Larvae also showed a trend towards a preference for bare space within 1-2 mm radii neighborhoods, but this effect was not significant. Larvae also preferred green fine filamentous algae across most neighborhoods (3-6 mm radii). For larger neighborhoods larvae showed some preference for macroalgae (5-6 mm radii).

4. Discussion

Here we show that benthic communities strongly influence the complex decisions coral larvae make when selecting habitat to settle. In our experiment, tiles that had at least one *O. faveolata* settler had significantly different community composition than tiles with no settlers. Red filamentous algae and CCA were abundant on tiles with no settlers while bare substrate was abundant on tiles with settlers. The overall density of settlers on tiles was higher on tiles abundant with green filamentous algae and bare substrate, but lower on tiles abundant with red filamentous algae and CCA. At finer spatial scales (the scale of millimeters within tiles), coral settlers avoided regions of the tiles with sediment, sponges, and red filamentous algae while preferring areas with green filamentous algae. Selection for and against individual taxa was strongest for the smallest neighborhoods (1-2mm radii) and was dominated by selecting against rather than for taxa. Ultimately, our results show that coral larvae make complex choices among multiple taxa simultaneously when selecting habitat to settle and that these choices occur at multiple spatial scales, with the spatial scale often determining which benthic taxa drive settlement choice.

4.1. Scale-dependent habitat selection

Coral larvae range in size from several hundred microns to one millimeter when they recruit, but after settlement corals grow several orders of magnitude in size throughout their lives, some species reaching the size of large cars. For settling coral larvae, tiles that are ~3 × 3 cm, or 9 cm^2, are landscapes. To put this into context, this area to a coral larva is analogous to 5.1 hectares of land to an adult moose (assuming an adult moose is 3 m long), or approximately the area of five soccer fields. Coral larvae are extremely small at the time of settlement, however, the scales at which we describe habitat selection (millimeters to centimeters) are large relative to the size of coral larvae, and are ecologically relevant to interactions that these corals will have with other taxa as they grow in size in the weeks to months following settlement.

The abundance of benthic space holders on our settlement tiles influenced coral settlement at several spatial scales. At the scale of whole settlement tiles, larvae preferred tiles with high abundance of bare substrate, but low abundance of CCA, red thick filamentous algae, and red fine filamentous algae. At finer scales within tiles (neighborhoods of 1-6 mm radii around a settler), settling coral larvae preferentially settled near green fine filamentous algae, but avoided red thick filamentous algae, red fine filamentous algae, sediment, and sponges. When animals decide when and where to spend time, they must balance accessing resources and avoiding risks, and they sometimes accomplish this by selecting for habitat characteristics at different scales (Senft et al., 1987). This multi-scaled habitat selection commonly results in trade-offs among habitat characteristics (Dussault et al., 2005; Hebblewhite & Merrill, 2009). For example, Dussault et al. (2005) showed that at broad spatial scales moose spatially segregate themselves from predators by avoiding habitats with low snowfall. Although this choice enables moose to avoid predators, food is less available in snowier habitats, and therefore to overcome this limitation, moose make finer scale decisions based on food availability (Dussault et al., 2005).

Although coral larvae select settlement habitats at spatial scales that are orders of magnitude smaller than the landscapes that moose navigate, our work shows that coral larvae also select for different habitat characteristics at different spatial scales. Settlement choices by *O. favolata* larvae in our experiments resulted in tradeoffs between spatial scales. At the tile scale, larvae strongly preferred tiles with bare space, but larvae did not show significant selection for bare space at the finer neighborhood scales. Instead, at smaller spatial scales larvae avoided space holders that may compete with coral recruits or otherwise threaten recruit survival. Avoidance of these space holders at fine spatial scales, but not at broader spatial scales, may reflect the relative importance of these threats throughout different stages of coral ontogeny. *O. faveolata* is a habitat-forming species of coral that can live for hundreds of years and reach adult size as large as cars. At settlement, however, *O. faveolata* larvae are approximately 400µm in diameter, three orders of magnitude smaller than their adult size. Small sponges, sediment, and turf algae may be significant sources of mortality for small newly settled recruits (R Babcock & Smith, 2000; Brandt, Olinger, Chaves-

Fonnegra, Olson, & Gochfeld, 2019) but likely pose little threat to these corals as they grow into successively larger size classes. At the broader scale of tiles, larvae strongly preferred tiles with bare space, but had no preference for or against sediment or sponges. As these corals grow, the relative threats or benefits that certain space holders pose to recruit survival likely change as corals grow out of size classes that are vulnerable to competition (Arnold & Steneck, 2011).

Within tiles, there was scale dependence in habitat selection by coral larvae In the largest neighborhoods (5-6 mm) there was also significant positive selection for macroalgae, and this somewhat paradoxical positive selection most likely reflects trade-offs rather than real preference for macroalgae. Past studies have shown that larvae avoid many species of macroalgae and that macroalgae can increase post-settlement mortality of coral recruits (Diaz-Pulido, Harii, McCook, & Hoegh-Guldberg, 2010; Kuffner et al., 2006; Paul et al., 2011). We intentionally selected tiles with minimal amounts of macroalgae because of the well-established negative effects of macroalgae on coral settlement. The most likely explanation for the positive selection that we observed is that larvae prioritized avoiding settling near certain space holders (sponges, sediment, red filamentous algae) resulting in a trade-offs of settling intermediate distance from macroalgae. As larvae balance avoiding the least preferred functional groups and selecting for the most preferred functional groups their choices may result in selecting locations near some groups of intermediate preference. Balancing these preferences creates the potential for animals to make trade-offs when selecting habitats. For example, elk avoid predators to minimalize predation risk while maximizing forage quality, resulting in a trade-off of spending time near roads (Anderson et al., 2005). There are many examples of large mobile animals making these types of trade-offs, but to the best of our knowledge our work is the first example of a sessile animal making similar trade-offs when selecting habitats.

4.2. Habitat selection by marine larvae

Our work shows how coral larvae select for settlement locations among communities of benthic space holders, and that larvae can discriminate among habitat characteristics at the scale of millimeters to centimeters. The settlement of corals and the larvae of other sessile marine invertebrates has been studied extensively, and most of this work focused on whether individual taxa (i.e. species of fleshy macroalgae, CCA, other conspecifics) either promote or inhibit settlement (Pawlik, 1992; Raphael Ritson-Williams et al., 2009; Rodriguez, Ojeda, & Inestrosa, 1993). This body of work is an important foundation for understanding how individual space holders can promote or inhibit settlement. However, experiments with individual taxa in isolation underestimate the complexity of the natural environment that larvae navigate during settlement. This is analogous to asking, 'Will an elk walk into a coniferous forest?' when a more relevant question would be 'Where do elk spend time when they can choose among coniferous forests, wetlands, and open areas, which each have different levels of risks and rewards?' Our work is an important step toward understanding how larvae make decisions in complex communities. Moving forward, we need to integrate multiple taxa of space holders into settlement experiments and work across spatial scales to understand how larvae choose settlement locations within communities of organisms, where some taxa are attractive and some repulsive to larvae.

Our work is a first step towards understanding how coral larvae discriminate among communities of organisms that positively and negatively influence the settlement of larvae.

Our results show that coral larvae avoid some taxa and simultaneously are attracted to others. At the tile scale, there was a negative relationship between the abundance of CCA and the number of coral larvae that settled on a tile, and a positive relationship between the abundance of green fine filamentous algae and the number of larvae that settled on a tile (Fig. 1A). The abundance of CCA and green fine filamentous algae were inversely correlated in our ordination, therefore it is not possible to discern whether larvae were avoiding CCA, or attracted to green fine filamentous algae, or both. A large body of work has shown that some species of CCA facilitate coral settlement and increase post-settlement survival (Harrington et al., 2004; Price, 2010; R. Ritson-Williams, Paul, Arnold, & Steneck, 2010; Raphael Ritson-Williams, Arnold, & Paul, 2016), but not all CCA promote coral settlement and some species can repel coral larvae and compete with newly settled recruits (Russ Babcock & Mundy, 1996; Harrington, Fabricius, Eaglesham, & Negri, 2005). It was not possible to identify the species of CCA in our experiments, because the small, immature patches of CCA on our tiles lack the reproductive structures that are critical for identification. However, our results suggest that the CCA in our experiment were not species that facilitate coral settlement. It is possible that these CCA were species that utilize allelopathic anti-fouling defenses to deter settling organisms including coral larvae (Masaki et al.1981, Suzuki et al. 1998, Degnan and Johnson 1999). Or coral larvae may respond to other cues associated with CCA traits that pose risks to coral recruits such as spatial competitiveness or the ability of some CCA to slough their outer tissue layers.

Coral larvae avoided red thick filamentous algae at the scale of tiles and at the neighborhood scale, but they only avoided red fine filamentous algae at the neighborhood scale. In a previous study on coral settlement in this system we showed that algal turfs did not impede coral settlement (Speare, Duran, Miller, & Burkepile, 2019), but in our past work we did not differentiate different types of algal turfs (i.e. greens vs. reds or fine vs. thick thalli filaments) or different scales (i.e. the tile scale vs. the neighborhood scale) as we have done in this study. Taken together, our past work and the present study suggest that coral larvae avoid some, but not all, types of turf algae. Larvae avoided red thick filamentous algae (with thallus diameter >200 microns) at both spatial scales. These thick filaments of algae may have posed a physical barrier to settling coral larvae (Birrell, McCook, & Willis, 2005) or they may have been species of algae that exude allelopathic chemical defenses that deter settling corals. It is also important to note that the abundance of red thick filamentous turfs and CCA were positively correlated at the tile scale, so the negative relationship that we observe between coral settlement and red thick filamentous turfs could be driven by larvae avoiding CCA, red thick filamentous algae, or both. In contrast, the abundance of red fine filamentous algae (<150 microns in diameter) was not related to coral settlement at the tile scale, but at finer scales larvae avoided settling in neighborhoods with red fine filamentous algae. These algal turfs with thinner thalli may not pose a barrier to coral larvae, or they may be composed of species that are less repulsive to coral larvae. Our results show that the effects of algal turfs on coral settlement are context dependent on the types of turfs and are consistent with past literature showing that qualitatively different algal turfs may have different effects on coral settlement (Arnold, Steneck, & Mumby, 2010; Birrell et al., 2005; O’Brien & Scheibling, 2018). Further, our work suggests that the effects of algal turfs on coral settlement may be dependent on the scale examined.

4.3. Future directions

Here we show that coral larvae make complex, scale-dependent decisions about where to settle in relation to communities of other benthic taxa. The coral larvae in our study made choices at extremely small spatial scales from millimeters to centimeters. However, the tiles that we used in our settlement experiments were relatively small (2-3 x 2-3 cm LxW) and therefore we only had the ability to evaluate habitat selection at small spatial scales. Future work should investigate habitat selection by coral larvae at broader spatial scales such as at the meter scale or kilometer scale. Further, our study investigated how coral larvae selected their habitats, and not how these individual settlement choices impact long-term success such as growth and survival. Linking habitat selection to survival will be a key next step forward to understanding the consequences of habitat selection by coral larvae and other sessile marine invertebrates. Several studies have linked settlement choices to survival of coral recruits, but these studies investigated the effects of single taxa on coral recruit success (Harrington et al., 2004; Price, 2010). Understanding how communities of organisms, and the relative importance of certain taxa compared to others, influence post-settlement survivorship will be an important step forward.

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References

Aebischer, N. J., Robertson, P. A., & Kenward, R. E. (1993). Compositional Analysis of Habitat Use From Animal Radio-Tracking Data. *Ecology*, *74*(5), 1313–1325.

Álvarez-Noriega, M., Burgess, S. C., Byers, J. E., Pringle, J. M., Wares, J. P., & Marshall, D. J. (2020). Global biogeography of marine dispersal potential. *Nature Ecology and Evolution*, *4*(9), 1196–1203. https://doi.org/10.1038/s41559-020-1238-y

Anderson, D. P., Turne, M. G., Forester, J. D., Zhu Jun, Boyce, M. S., Beyer, H., & Stowell, L. (2005). Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management*, *69*(1), 298–310. https://doi.org/10.2193/0022-541X(2005)069<0298:SSRSBR>2.0.CO;2

Arnold, S. N., & Steneck, R. S. (2011). Settling into an Increasingly Hostile World: The Rapidly Closing "Recruitment Window" for Corals. *PLoS ONE*, *6*(12), e28681. https://doi.org/10.1371/journal.pone.0028681

Arnold, S. N., Steneck, R. S., & Mumby, P. J. (2010). Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series*, *414*, 91–105. https://doi.org/10.3354/meps08724

Babcock, R, & Smith, L. (2000). Effects of sedimentation on coral settlement and survivorship. In *Marine Biology* (Vol. I, pp. 1–4). Proceedings 9th International Coral Reef Symposium, Bali, Indonesia 23-27 October 2000. Retrieved from http://www.coremap.or.id/downloads/ICRS9th-BabcockEffectsofsedimentationcameraready-corrected.pdf

Babcock, Russ, & Mundy, C. (1996). Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. *Journal of Experimental Marine Biology and Ecology*, *206*(1), 179–201. Retrieved from http://www.sciencedirect.com/science/article/pii/S0022098196026226

Baird, A. H., Babcock, R. C., & Mundy, C. P. (2003). Habitat selection by larvae influences the depth distribution of six common coral species. *Marine Ecology Progress Series*, *252*, 289–293. Retrieved from http://eprints.jcu.edu.au/1522

Beijbom, O., Edmunds, P. J., Roelfsema, C., Smith, J., Kline, D. I., Neal, B. P., … Kriegman, D. (2015). Towards Automated Annotation of Benthic Survey Images : Variability of Human Experts and Operational Modes of Automation, 1–22. https://doi.org/10.1371/journal.pone.0130312

Birrell, C. L., McCook, L. J., & Willis, B. L. (2005). Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin*, *51*(1–4), 408–414. https://doi.org/10.1016/j.marpolbul.2004.10.022

Birrell, C. L., Mccook, L. J., Willis, B. L., & Harrington, L. (2008). Chemical effects of macroalgae on larval settlement of the broadcast spawning coral Acropora millepora. *Marine Ecology Progress Series*, *362*, 129–137. https://doi.org/10.3354/meps07524

Brandt, M. E., Olinger, L. K., Chaves-Fonnegra, A., Olson, J. B., & Gochfeld, D. J. (2019). Coral recruitment is impacted by the presence of a sponge community. *Marine Biology*, *166*(4), 1–13. https://doi.org/10.1007/s00227-019-3493-5

Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3–4), 516–519.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*(1), 117–143.

https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology*, *93*(1–2), 11–45. https://doi.org/10.1016/0022-0981(85)90146-7

Connolly, S. R., & Baird, A. H. (2010). Estimating dispersal potential for marine larvae : dynamic models applied to scleractinian corals. *Ecology*, *91*(12), 3572–3583.

Deegan, L. A. (1990). Effects of estuarine environmental conditions on population dynamics of young-of-the-year gulf menhaden. *Marine Ecology Progress Series*, *68*(1–2), 195–205. https://doi.org/10.3354/meps068195

Diaz-Pulido, G., Harii, S., McCook, L. J., & Hoegh-Guldberg, O. (2010). The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs*, *29*(1), 203–208. https://doi.org/10.1007/s00338-009-0573-x

Dussault, C., Ouellet, J., Courtois, R., Huot, J., Breton, L., & Jolicoeur, H. (2005). Linking Moose Habitat Selection to Limiting Factors. *Ecography*, *28*(5), 619–628.

Elmer, F., Bell, J. J., & Gardner, J. P. A. (2018). Coral larvae change their settlement preference for crustose coralline algae dependent on availability of bare space. *Coral Reefs*, *37*(2), 397–407. https://doi.org/10.1007/s00338-018-1665-2

Fisher, J. T., Anholt, B., & Volpe, J. P. (2011). Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecology and Evolution*, *1*(4), 517–528. https://doi.org/10.1002/ece3.45

Harrington, L., Fabricius, K., De'Ath, G., & Negri, A. (2004). Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology*, *85*(12), 3428–3437. Retrieved from http://www.esajournals.org/doi/abs/10.1890/04-0298

Harrington, L., Fabricius, K., Eaglesham, G., & Negri, A. (2005). Synergistic effects of diuron and sedimentation on photosynthesis and survival of crustose coralline algae. *Marine Pollution Bulletin*, *51*(1–4), 415–427. https://doi.org/10.1016/j.marpolbul.2004.10.042

Hebblewhite, M., & Merrill, E. H. (2009). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, *90*(12), 3445–3454.

Holland, J. D., Bert, D. G., & Fahrig, L. (2004). Determining the Spatial Scale of Species' Response to Habitat. *BioScience*, *54*(3), 227–233. https://doi.org/10.1641/0006-3568(2004)054[0227:DTSSOS]2.0.CO;2

Holland, J. D., & Yang, S. (2016). Multi-scale Studies and the Ecological Neighborhood. *Current Landscape Ecology Reports*, *1*(4), 135–145. https://doi.org/10.1007/s40823-016-0015-8

Jackson, H. B., & Fahrig, L. (2012). What size is a biologically relevant landscape? *Landscape Ecology*, *27*(7), 929–941. https://doi.org/10.1007/s10980-012-9757-9

Jenkins, S. R. (2005). Larval habitat selection , not larval supply , determines settlement patterns and adult distribution in two chthamalid barnacles. *Journal of Animal Ecology*, *74*, 893–904. https://doi.org/10.1111/j.1365-2656.2005.00985.x

Johnson, C. J., Parker, K. L., Heard, D. C., Michael, P., & Gillinghamt, M. P. (2002). Movement Parameters of Ungulates and Scale-Specific Responses to the Environment. *Journal of Animal Ecology*, *71*(2), 225–235.

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference Stable URL : http://www.jstor.org/stable/1937156 REFERENCES Linked references are available on JSTOR for this article : You may need to log in to JSTOR to access the. *Ecology*, *61*(1), 65–71.

Johnson, L. E., & Strathmann, R. R. (1989). Settling barnacle larvae avoid substrata previously occupied by a mobile predator. *Journal of Experimental Marine Biology and Ecology*, *128*(1), 87–103. https://doi.org/10.1016/0022-0981(89)90094-4

Jorissen, H., & Nugues, M. M. (2021). Coral larvae avoid substratum exploration and settlement in low-oxygen environments. *Coral Reefs*, *40*(1), 31–39. https://doi.org/10.1007/s00338-020-02013-6

Kuffner, I. B., Walters, L. J., Becerro, M. A., Paul, V. J., Ritson-Williams, R., & Beach, K. S. (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series*, *323*, 107–117. Retrieved from http://parkinson.cos.ucf.edu/Courses/seminar/papers/Kuffner et al. 2006.pdf

Larsson, A. I., & Jonsson, P. R. (2006). Barnacle larvae actively select flow environments supporting post-settlement growth and survival. *Ecology*, *87*(8), 1960–1966. https://doi.org/10.1890/0012-9658(2006)87[1960:BLASFE]2.0.CO;2

Lecchini, D., Osenberg, C. W., Shima, J. S., St Mary, C. M., & Galzin, R. (2007). Ontogenetic changes in habitat selection during settlement in a coral reef fish: Ecological determinants and sensory mechanisms. *Coral Reefs*, *26*(2), 423–432. https://doi.org/10.1007/s00338-007-0212-3

Miller, M. W. (2014). Post-settlement survivorship in two Caribbean broadcasting corals. *Coral Reefs*, *33*(4), 1041–1046. https://doi.org/10.1007/s00338-014-1177-7

Mundy, C. N., & Babcock, R. C. (1998). Role of light intensity and spectral quality in coral settlement: Implications for depth-dependent settlement? *Journal of Experimental Marine Biology and Ecology*, *223*(2), 235–255. https://doi.org/10.1016/S0022-0981(97)00167-6

O'Brien, J. M., & Scheibling, R. E. (2018). Turf wars: Competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. *Marine Ecology Progress Series*, *590*, 1–17. https://doi.org/10.3354/meps12530

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., … Wagner, H. (2013). Package "vegan." Community Ecol. Package Version 2.

Pardieck, R. A., Orth, R. J., Diaz, R. J., & Lipcius, R. N. (1999). Ontogenetic changes in habitat use by postlarvae and young juveniles of the blue crab. *Marine Ecology Progress Series*, *186*, 227–238. https://doi.org/10.3354/meps186227

Paul, V., Kuffner, I., Walters, L., Ritson-Williams, R., Beach, K., & Becerro, M. (2011). Chemically mediated interactions between macroalgae Dictyota spp. and multiple life-history stages of the coral Porites astreoides. *Marine Ecology Progress Series*, *426*, 161–170. https://doi.org/10.3354/meps09032

Pawlik, J. R. Chemical ecology of the settlement of benthic marine invertebrates, 30 Oceanography and marine biology: an annual review. Vol. 30 § (1992).

Price, N. (2010). Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. *Oecologia*, *163*(3), 747–758. https://doi.org/10.1007/s00442-010-1578-4

R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/.

Raimondi, P. T., & Morse, A. N. C. (2000). The Consequences of Complex Larval Behavior in a Coral. *Ecology*, *81*(11), 3193–3211. https://doi.org/https://doi.org/10.1890/0012-

9658(2000)081[3193:TCOCLB]2.0.CO;2

Rettie, W. J., & Messier, F. F. (2000). Hierarchical Habitat Selection by Woodland Caribou : Its Relationship to Limiting Factors, *23*(4), 466–478.

Richards, R. A. (1992). Habitat selection and predator avoidance: ontogenetic shifts in habitat use by the Jonah crab Cancer borealis (Stimpson). *Journal of Experimental Marine Biology and Ecology*, *156*(2), 187–197.

Ritson-Williams, R., Arnold, S. N., Paul, V. J., & Steneck, R. S. (2014). Larval settlement preferences of Acropora palmata and Montastraea faveolata in response to diverse red algae. *Coral Reefs*, *33*(1), 59–66. https://doi.org/10.1007/s00338-013-1113-2

Ritson-Williams, R., Paul, V. J., Arnold, S. N., & Steneck, R. S. (2010). Larval settlement preferences and post-settlement survival of the threatened Caribbean corals Acropora palmata and A. cervicornis. *Coral Reefs*, *29*(1), 71–81. https://doi.org/10.1007/s00338-009-0555-z

Ritson-Williams, Raphael, Arnold, S., Fogarty, N., Steneck, R. S., Vermeij, M., & Paul, V. J. (2009). New perspectives on ecological mechanisms affecting coral recruitment on reefs. *Smithsonian Contributions to the Marine Sciences*, (38), 437–457. https://doi.org/10.5479/si.01960768.38.437

Ritson-Williams, Raphael, Arnold, S. N., & Paul, V. J. (2016). Patterns of larval settlement preferences and post-settlement survival for seven Caribbean corals. *Marine Ecology Progress Series*, *548*, 127–138. https://doi.org/10.3354/meps11688

Ritson-Williams, Raphael, Arnold, S. N., & Paul, V. J. (2020). The impact of macroalgae and cyanobacteria on larval survival and settlement of the scleractinian corals Acropora palmata, A. cervicornis and Pseudodiploria strigosa. *Marine Biology*, *167*(3), 1–12. https://doi.org/10.1007/s00227-019-3639-5

Rodriguez, S. R., Ojeda, F. P., & Inestrosa, N. C. (1993). Settlement of benthic marine invertebrates. *Marine Ecology Progress Series*, *97*(2), 193–207. https://doi.org/10.3354/meps097193

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., & Swift, D. M. (1987). Large Herbivore Foraging and Ecological Hierarchies. *BioScience*, *37*(11), 789–799. https://doi.org/10.2307/1310545

Speare, K. E., Duran, A., Miller, M. W., & Burkepile, D. E. (2019). Sediment associated with algal turfs inhibits the settlement of two endangered coral species. *Marine Pollution Bulletin*, *144*(April), 189–195. https://doi.org/10.1016/j.marpolbul.2019.04.066

Sponaugle, S., & Cowen, R. (1996). Nearshore patterns of coral reef fish larval supply to Barbados, West Indies. *Marine Ecology Progress Series*, *133*, 13–28. https://doi.org/10.3354/meps133013

Stuber, E. F., F. Gruber, L., & Fontaine, J. J. (2018). Predicting species-habitat relationships: does body size matter? *Landscape Ecology*, *33*(7), 1049–1060. https://doi.org/10.1007/s10980-018-0648-6

Stuber, E. F., & Fontaine, J. J. (2019). How characteristic is the species characteristic selection scale? *Global Ecology and Biogeography*, *28*(12), 1839–1854. https://doi.org/10.1111/geb.12998

Tebben, J., Motti, C. A., Siboni, N., Tapiolas, D. M., Negri, A. P., Schupp, P. J., … Harder, T. (2015). Chemical mediation of coral larval settlement by crustose coralline algae. *Scientific Reports*, *5*, 1–11. https://doi.org/10.1038/srep10803

Vermeij, M. J. A., Marhaver, K. L., Huijbers, C. M., Nagelkerken, I., & Stephen, D. (2010).

Coral Larvae Move toward Reef Sounds, *5*(5), 3–6. https://doi.org/10.1371/journal.pone.0010660

Walters, L. J. (1992). Post-settlement success of the arborescent bryozoan Bugula neritina (L.): the importance of structural complexity. *Journal of Experimental Marine Biology and Ecology*, *164*(1), 55–71. https://doi.org/10.1016/0022-0981(92)90136-X

Wiens, J. A. (1976). Population Responses to Patchy Environments. *Annual Review of Ecology and Systematics*, *7*(1), 81–120. https://doi.org/10.1146/annurev.es.07.110176.000501

Figures

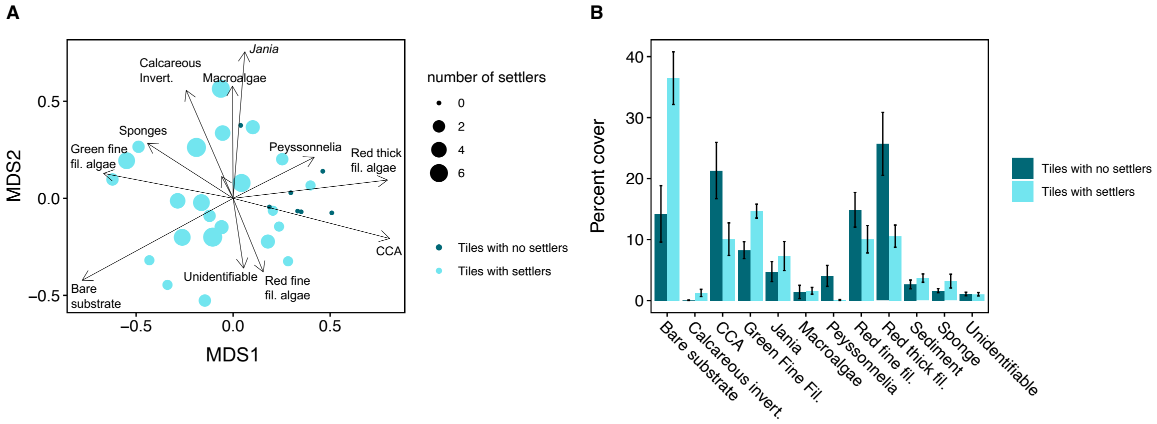

Figure 1. a) Two-dimensional nonmetric multidimensional scaling plot of settlement tile community composition. Points represent individual tile communities and are scaled to the number of coral larvae that settled on each tile. Points are colored to indicate whether there was at least one coral settler (light blue) or no coral settlers (dark teal) on each tile. Size of points scales with the number of settlers on each tile. Vectors correspond to the direction of increasing abundance of each benthic group. b) Comparison of the mean (± SE) percent cover of each group on tiles with no settlers (dark teal) and tiles with settlers (light blue).

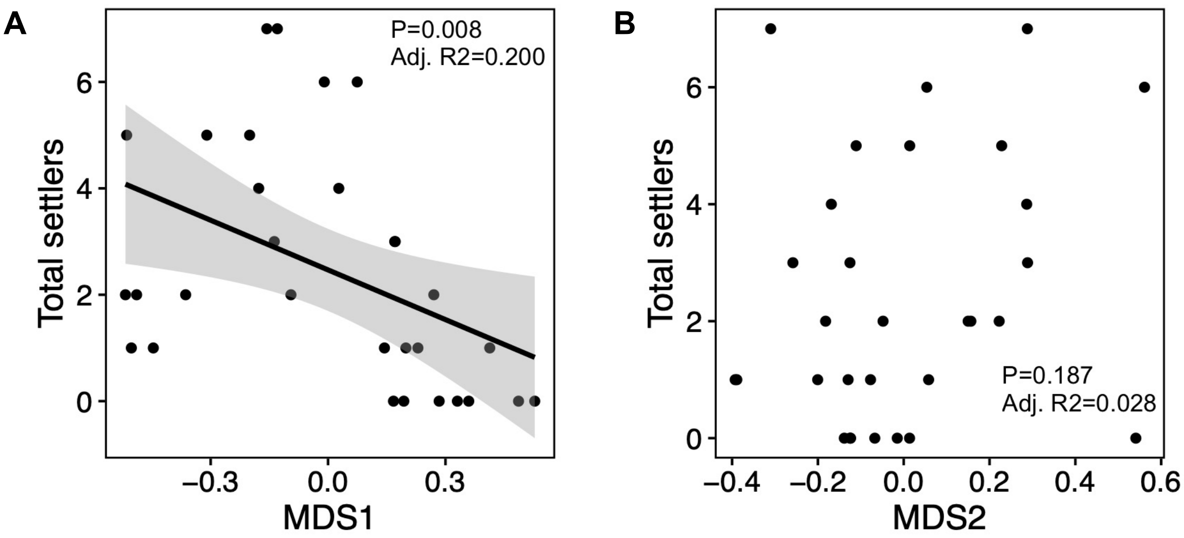

Figure 2. a) Scatter plot showing the negative relationship between the number of settlers on each tile and the tile's position along MDS1. b) Scatter plot showing no relationship between the number of settlers on each tile and the tile's position along MDS2. Statistics are from linear regression.

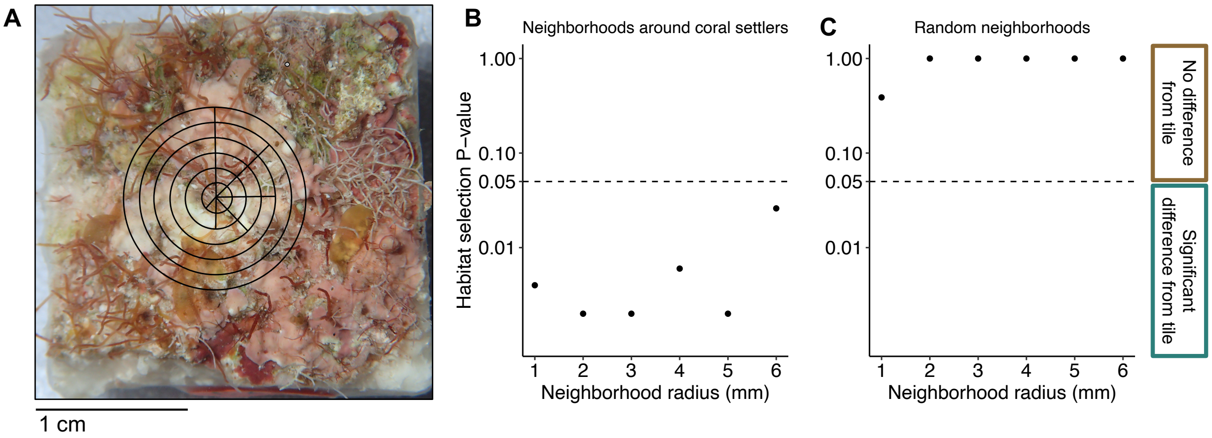

Figure 3. a) A photograph of one of the settlement tiles with overlaid concentric circles used to determine community composition of neighborhoods around each coral settler. b) Results of the compositional analysis of habitat use for neighborhoods around coral settlers. c) Results of the compositional analysis of habitat use for neighborhoods in randomly selected locations on the tiles. For plots b and c, p-values represent results of testing difference between the community within each neighborhood radius as compared to the community on the tile as a whole. P-values <0.05 suggest that neighborhoods within that radius differed from the community on the whole tile.

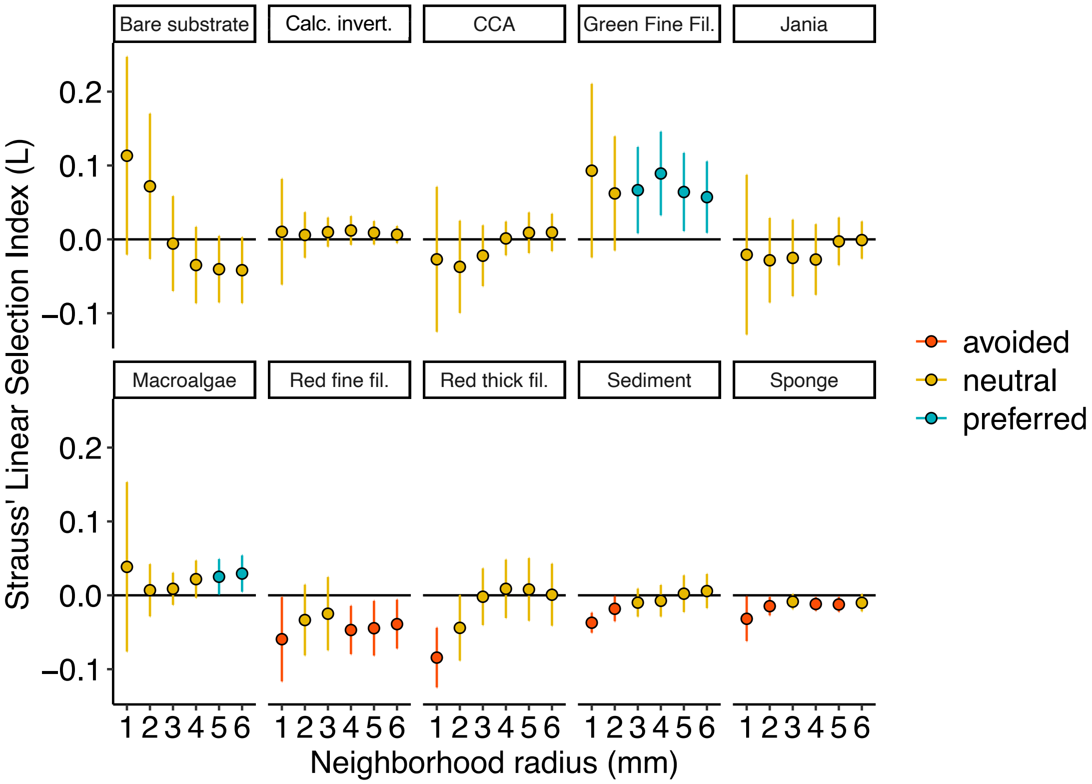

Figure 4. Mean values of L, Strauss' Linear Selection Index, ±95% CI showing preference or avoidance of taxa across neighborhoods of different radii. Green dots indicate taxa that were present in coral settler neighborhoods in significantly higher abundance than on the tile as a whole, suggesting preference for these taxa. Purple dots indicate taxa that were present in coral settler neighborhoods in significantly lower abundance than on the tile as a whole, suggesting avoidance of these taxa. Yellow dots indicate taxa that were in present in coral settler neighborhoods in abundance that was proportional to the tile as a whole, suggesting no selection for or against these taxa.

Table 1. Results of SIMPER analysis testing how benthic taxa contributed to the community dissimilarity between tiles with settlers (SET) and tiles with no settlers (NO SET).

	Contribution to average dissimilarity	**Standard deviation of contribution**	**Dissimilarity /SD Ratio**	**Abund. on tiles with settlers**	**Abund. on tiles without settlers**	**Cumulative % contribution to dissimilarity**
Bare substrate	13.05	9.42	1.39	36.47	14.22	25.55
Red thick fil.	9.06	5.78	1.57	10.56	25.69	43.24
CCA	8.55	5.47	1.56	10.07	21.32	59.95
Red fine fil.	5.51	3.93	1.40	10.06	14.87	70.74
Jania	4.05	4.54	0.89	7.31	4.75	78.65
Green fine fil.	3.75	2.51	1.50	14.67	8.27	85.97
Peyssonnelia	2.02	2.08	0.97	0.10	4.05	89.92
Sediment	1.41	1.26	1.12	3.68	2.65	92.69
Sponge	1.41	2.42	0.58	3.19	1.63	95.45
Macroalgae	1.17	1.46	0.81	1.60	1.42	97.74
Calcareous invert.	0.62	1.39	0.45	1.25	0.05	98.95
Unidentifiable	0.54	0.53	1.01	1.04	1.07	100.00

Appendix

Table 1. Description of tile community members

Group	**Description**	**Examples of taxa (if known) included in the group**
Bare substrate	No visible living organisms, colorless, bare tile substrate	
Calcareous invertebrates	Calcareous tube worms	feather duster tubes (*Bispira* spp.)
Cyanobacteria	Very fine filamentous, green-brown filamentous cyanobacteria	
Green fine filamentous algae	Species of Chlorophyta (green algae) with cylindrical thallus, usually smaller than 150 micron in diameter.	*Cladophora* spp. *Enteromorpha* spp., *Derbesia* spp.
Jania	Red, upright, calcareous algae in the genus *Jania*	*Jania adhaerens* *Jania capillacea*

Macroalgae	Upright macroalgae species with different morphologies (e.g., spherical, flat-corticated, parasol-shape)	*Acetabularia* spp., *Valonia* spp., *Dictyota* spp.
Peyssonnelia	Red, crustose non-calcareous macroalgae, in the genus *Peyssonnelia*	*Peyssonnelia* spp.
Red fine filamentous algae	Species of Rhodophyta (red algae) with cylindrical thallus, usually smaller than 150 micron in diameter.	*Polysiphonia* spp., *Herposiphonia* spp., *Lobosiphonia* spp., *Ceramiun* spp., *Centroceras* spp., *Digenea simplex*
Red thick filamentous algae	Species of Rhodophyta (red algae) with cylindrical thallus, usually greater than 200 micron in diameter.	*Laurencia* spp., *Champia* spp., *Chondria* spp., *Hypnea* spp.,
CCA	Red crustose calcareous macroalgae	*Mesophyllum* spp. *Porolithon* spp.

Sediment	Fine sediment accumulated on the tile’s surface	
Sponges	Small (less than 1 cm diameter) sponge colonies	

Table 2. Compositional analysis of habitat use at different spatial scales

Neighborhood Radius (mm)	**Number of point IDs**	**Number of settlers included in analysis**	***P*-value for neighborhoods around settlers**	***P*-value for randomly selected neighborhoods**
1	3	19	0.004	0.344
2	13	30	0.002	~1
3	28	29	0.002	~1
4	50	24	0.006	~1
5	79	19	0.002	~1
6	113	17	0.026	~1