CORAL RESTORATION: ROLES OF SHELTER FOR HERBIVORES AND REEF HEALTH IN EARLY RECRUITMENT SUCCESS

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Abstract

Survival and growth of new coral recruits is crucial for reef restoration, yet few details are known about coral demography during the first several years post-settlement. We experimentally tested how reef health and shelter availability for fishes and sea urchins affect juvenile coral demographic rates on coral-restoration platforms. On the island of Oʻahu, Hawaiʻi, we deployed cubic-meter concrete modules in both low- and high-shelter configurations at the relatively degraded reef off Waikīkī Beach and the relatively healthy reef at Hanauma Bay. Naturally settling corals, especially of the genera *Pocillopora*, *Montipora*, and *Porites*, were mapped and sized quarterly to track individual colony recruitment, survival, and growth for nearly the first four years post-deployment. We predicted that demographic metrics would be enhanced on high-shelter modules at both sites by providing refugia for herbivores (Shelter Hypothesis), and on all modules in the relatively healthy reefscape at Hanauma Bay (Reefscape Hypothesis). Across experimental modules, overgrowth of coral by benthic algae was negatively correlated with herbivore biomass, which was greater on high-shelter modules, and in turn, total coral cover often benefited from reduced algal abundance. However, the shelter effect was evident only for recruitment of the genus *Pocillopora*, as well as for survival of *Porites*. We hypothesize that this weak trend was due to very low recruitment of herbivores, except for a single pulse of sea urchins at Hanauma Bay. Significant patterns for *Montipora* and *Pocillopora* were more consistent with the benefits of a healthy reefscape. Compared to Waikīkī, corals at Hanauma Bay experienced higher recruitment (*Montipora* only), survival (*Pocillopora* only), and growth (*Montipora* only), with none of the predicted patterns occurring for *Porites*. We conclude that determinants of coral recruitment success in this Hawaiian system are idiosyncratic at small scales, due to fine-scale variation in larval settlement and environment, as well as differences in biology and life history among genera. Nonetheless, on average, herbivores benefitted corals by reducing competition with benthic algae, and the context of a healthy reefscape did enhance two common corals. We recommend that reef managers implement policies fostering herbivory, especially on coral restoration structures in degraded habitat and where patches of healthy reef occur nearby, to facilitate coral recruitment, survival, and growth.

Table of Contents

Acknowledgements ………………………………………………………………… ii

Abstract …………………………………………………………………………….. iii

Table of Contents …………………………………………………………………... v

List of tables ………………………………………………………………………... vi

List of figures ………………………………………………………………………. vii

Introduction ………………………………………………………………………… 1

Methods

Study sites ……………………………………………………….……………...….. 6

Experimental design ……………………………………………………………... 6

Coral surveys …………………………………………………………………….. 8

Herbivorous fish and urchin surveys …………………………………………….. 9

Benthic algal overgrowth estimates ……………………………………………… 9

Statistical analyses ……………………………………………………………….. 10

Results

Herbivore hypothesis …………………………………………………………….. 12

Shelter hypothesis ………………………………………………………………... 13

Reefscape hypothesis …………………………………………………………….. 14

Discussion

Shelter hypotheses ……………………………………………………………….…….. 16

Reefscape hypothesis …………………………………………………………….. 19

Implications for coral restoration ………………………………………………… 21

Literature Cited ……………………………………………………………………... 45

List of tables

Table 1: Summary of statistical models…………………………………………………. 24

Table 2: Summary of experimental results by coral genus ………………………………... 25

Table 3: *Pocillopora* transition matrices comparing low shelter vs. high shelter and Waikīkī vs. Hanauma Bay modules ………………………………………………………………. 26

Table 4: *Montipora* transition matrices comparing low shelter vs. high shelter and Waikīkī vs. Hanauma Bay modules ………………………………………………………………. 27

Table 5: *Porites* transition matrices comparing low shelter vs. high shelter and Waikīkī vs. Hanauma Bay modules ………………………………………………………………. 28

Table 6: *Pocillopora* transition matrices comparing Waikīkī -Low, Hanauma Bay-Low, Waikīkī -High, and Hanauma Bay-High ……………………………………………………… 29

Table 7: *Montipora* transition matrices comparing Waikīkī -Low, Hanauma Bay-Low, Waikīkī -High, and Hanauma Bay-High ………………………………………………………. 30

Table 8: *Porites* transition matrices comparing Waikīkī -Low, Hanauma Bay-Low, Waikīkī -High, and Hanauma Bay-High ………………………………………………………. 31

List of figures

Figure 1: Map of Oʻahu with study sites …………………………………………………….. 32

Figure 2: Regressions of algal overgrowth vs. urchin and herbivorous fish biomass …….. 33

Figure 3: Regressions of total coral cover vs. algal overgrowth ………………………….. 34

Figure 4: Bar plots of urchin biomass, herbivorous fish biomass, and algal overgrowth … 35

Figure 5: Bar plots of quarterly coral recruitment ………………………………………… 36

Figure 6: Bar plots of quarterly coral survival and growth for all four size classes ……… 37

Figure 7: Coral heat maps of quarterly transition probabilities for all size classes ……….. 38

Figure 8: CReME project experimental design …………………………………………… 39

Figure 9: CReME modules pre-deployment ………………………………………………. 40

Figure 10: CReME module representative side photos during the study …………………. 41

Figure 11: Urchin biomass, herbivorous fish biomass, and algal overgrowth time series ... 42

Figure 12: Coral recruitment time series ………………………………………………….. 43

Figure 13: End of study module coral colony densities for shelter and site ……………… 44

Introduction

Coral reefs are hotspots of marine biodiversity that provide a broad variety of ecosystem goods and services for society (Moberg and Folke 1999, Fisher et al. 2015). Unfortunately, reefs are declining worldwide due to climate disruption and other human disturbances that compromise resilience (Hoegh-Guldberg et al. 2007, Hughes et al. 2010). Resilient coral reefs resist and recover from natural and human-caused disturbances, such as coral bleaching, storms, and corallivore outbreaks (Rotjan and Lewis 2008, Hughes et al. 2017, Lam et al. 2020). Understanding the processes that foster coral resilience is therefore crucial for predicting how corals will fare in a changing climate and how reefs can be managed to ensure their persistence. Effective coral restoration efforts will rely on understanding the factors that enhance or inhibit newly settled juvenile corals that replenish reefs, knowledge which requires long-term field studies with high sampling frequency. Although valuable, prior studies of coral dynamics have sampled colonies either infrequently over long periods (Babcock 1991, Hughes 1996, Connell et al. 1997) or frequently over short periods (Oren and Benayahu 1997, Harrington et al. 2004, Martinez and Abelson 2013) rather than both.

Following larval settlement, the growth of corals is limited by factors affecting the rate of recruitment to detectable size, colony survival, and subsequent growth (Hughes and Connell 1987, Ritson-Williams et al. 2009, Arnold et al. 2010, Arnold and Steneck 2011). Besides physical disturbances, such as major storms and coral bleaching events, small-scale biotic interactions are important. Especially crucial is the early post-settlement phase, when tiny colonies are particularly susceptible to competition for space, predation, and incidental damage (amensalism). As juvenile corals grow, they become less susceptible to these local sources of mortality (Doropoulos et al. 2015), so focusing on early juvenile coral demography is key to effectively restoring and managing coral populations (Edmunds and Riegl 2020).

Benthic algae are effective space competitors that can impede corals (Rogers and Miller 2006, Arnold et al. 2010). Thick algal turfs and macroalgae can reduce coral settlement by preempting favorable microhabitats for the settlement of coral planula larvae (Doropoulos et al. 2016). Some algae also secrete harmful allelochemicals that can inhibit coral settlement (Kuffner et al. 2006, Evensen et al. 2019). Small juvenile corals are also susceptible to benthic algal overgrowth (Connell et al. 1997, Birrell et al. 2008, Arnold et al. 2010) and can be damaged by mechanical abrasion from algal thalli (Box and Mumby 2007), both of which can cause reduced growth (Venera-Ponton et al. 2011) or death (Arnold et al. 2010, Penin et al. 2011, Doropoulos et al. 2016). Additionally, algal turfs can harbor high concentrations of microbes that cause coral disease (Nugues et al. 2004, Smith et al. 2006).

Benthic algae benefit from elevated nutrient levels frequently associated with sewage discharge and agricultural runoff, thereby enhancing their ability to reduce coral recruitment (Tomascik 1991, Hunte and Wittenberg 1992) and survival (Wittenberg and Hunte 1992, Babcock and Smith 2002, Fabricius et al. 2003, Moeller et al. 2017), as well as to overgrow juvenile corals (Birkeland 1977, Lapointe et al. 2004, Smith et al. 2010, Vermeij et al. 2010). Areas with higher nutrient levels are also associated with more abundant colonial sponge and ascidian communities (Ward-Paige et al. 2005, Shenkar et al. 2008) that can prevent coral planulae from settling or overgrow small juvenile corals (Hill 1998, Brandt et al. 2019). Additionally, corallivorous fishes (Rotjan and Lewis 2008, Jayewardene et al. 2009, Mumby 2009, Penin et al. 2011) and invertebrates (Glynn and Krupp 1986, Colgan 1987) can substantially reduce survival rates of juvenile corals on exposed surfaces, yet this effect is reduced in microhabitats such as crevices that protect small recruits (Doropoulos et al. 2016, Gallagher and Doropoulos 2017).

The negative effects of benthic algae can be mitigated by the presence of an abundant and diverse assemblage of herbivorous fishes and invertebrates that remove algae, thereby reducing spatial competition with corals (McCook et al. 2001, Jompa and McCook 2002, Penin et al. 2011, Hixon 2015). Herbivory opens living space for settlement of coral larvae, thereby increasing coral recruitment (Mumby 2009, Arnold et al. 2010), survival (Birkeland 1977), and growth (Suchley and Alvarez-Filip 2017), although some larger parrotfishes, puffers, and other large fishes can be substantial corallivores (Rotjan and Lewis 2008, Hixon 2015). Sea urchin grazing also may increase juvenile coral recruitment (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006), survival (Idjadi et al. 2010), and growth (Davies and Vize 2008, Idjadi et al. 2010), and may also dislodge small sponges that would overgrow corals (Vance 1979). However, high densities of urchins can reduce juvenile coral survival via incidental damage or removal (Sammarco 1980, O'Leary et al. 2013). Herbivore abundance is enhanced by the availability of structural shelter, which serves as refugia from predation and extreme water motion (Lee 2006, Madin et al. 2019, Robinson et al. 2020). Additionally, healthy reefscapes are positively correlated with coral recruitment, particularly within marine reserves where herbivorous fishes are more abundant (Mumby et al. 2007, Steneck et al. 2018) and coral larvae are more available (Vermeij and Sandin 2008, Da-Anoy et al. 2017). Some species of crustose coralline algae (CCA), typical of highly grazed, protected reef areas, are known to enhance coral larval settlement via chemical cues (Ritson-Williams et al. 2009).

On highly degraded reefs, dead coral colonies eventually erode to low-relief rubble (Alvarez-Filip et al. 2009). The resulting lack of physical shelter reduces the abundance of herbivores, such that collapsed reefs become dominated by algal turfs and macroalgae (Mumby and Steneck 2008). Artificial structures have great potential as a coral restoration tool given that they immediately increase habitat complexity, which in turn can replenish herbivore populations, thereby reducing algae and enhancing coral colonization. It is well documented that concrete structures with many holes can support high concentrations of coral reef fishes (Molles 1978 in Mexico, Talbot et al. 1978 in Australia, Hixon and Beets 1993 in Caribbean, Carr and Hixon 1997 in Bahamas), reflecting patterns on natural reefs (Madin et al. 2019, Santano et al. 2021). Concrete has also been used as an effective coral settlement substrate in various regions (Clark and Edwards 1999, Al-Horani and Khalaf 2013, Chamberland et al. 2017, Leonard et al. 2022), including Hawaiʻi (Fitzhardinge and Bailey-Brock 1989). Artificial structures have also been constructed to provide platforms for coral outplanting (Ortiz-Prosper et al. 2001, Cummings et al. 2015) and to grow coral fragments for later outplanting (Forsman et al. 2018). However, empirical studies are lacking on the mechanisms by which concrete structures, especially those providing shelter for fishes and macroinvertebrates, may directly or indirectly enhance juvenile coral recruitment, survival, and growth.

We conducted the Coral Resilience Module Experiment (CReME) to assess the factors affecting the demography of juvenile corals recruiting to concrete modules on the south shore of Oʻahu, Hawaiʻi. We compared patterns at a degraded reefscape offshore of densely populated Waikīkī with patterns at the legally protected and relatively healthy reefscape of the Hanauma Bay Marine Life Conservation District, established in 1967. We used standardized roughly cubic-meter concrete settlement modules providing either low or high shelter availability for herbivores. These modules allowed us to identify and track naturally settling corals for nearly the first four years post-deployment, thereby conducting the longest detailed juvenile coral demographic monitoring effort on artificial structures of which we are aware.

Our factorial experimental design tested hypotheses regarding the mechanisms enhancing or inhibiting coral colonization under different environmental conditions. Foundational to more detailed mechanistic hypotheses that were the main focus of this study was the Herbivore Hypothesis: increasing herbivore abundance benefits juvenile corals at local spatial scales (in our study, experimental modules). This general hypothesis predicted that algal overgrowth of corals will vary inversely with herbivore biomass, and that coral cover will vary inversely with algal overgrowth (e.g., Hixon 2015). If the Herbivore Hypothesis was corroborated in this system, then the Shelter Hypothesis could be tested, i.e., that higher shelter availability for herbivores indirectly benefits juvenile corals independent of the local reef environment (e.g., Mumby and Steneck 2008). This hypothesis predicts that greater shelter increases herbivore biomass locally, therefore decreasing algal overgrowth and thereby increasing coral recruitment, survival, and growth. Also tested (and not mutually exclusive) was the Reefscape Hypothesis that, independent of shelter availability, relatively healthy reef environments (described below) benefit juvenile corals (e.g., Vermeij and Sandin 2008, Da-Anoy et al. 2017). This hypothesis predicts that, compared to modules near degraded Waikīkī reefs, modules near relatively healthy reefs at Hanauma Bay would experience greater herbivore biomass, lower algal overgrowth, and greater coral recruitment, survival, and growth. The results of this field experiment marginally corroborated the Herbivore Hypothesis, and partly corroborated both the Shelter and Reefscape Hypotheses, providing detailed insight on the complexity and idiosyncrasies of interacting mechanisms that affect coral recruitment and resilience.

Methods

Study sites

Our study was conducted on the south shore of Oʻahu, Hawaiʻi, at two sites: approximately 800m offshore of Waikīkī Beach (21°16’10”N, 157°50’15”W), and at the Hanauma Bay Marine Life Conservation District (21°16’5”N, 157°41’33”W; Fig. 1). Reefs at Waikīkī are typically characterized as spur-and-groove, with grooves dominated by sand or rubble, and are known for relatively high nutrient levels (548.7 kg/year) from sewage (Lecky 2016), low coral cover of between 8% (Franklin et al. 2013) and 16% (N.T. Altman-Kurosaki, personal communication), and abundant invertebrate coral predators (mostly the cushion sea star, *Culcita novaeguineae*, but also occasional crown-of-thorns sea star, *Acanthaster planci*, as well as drupellid snails). Waikīkī reefs also supported both fewer and smaller fish, this site being just offshore of a major urban center and subject to intensive fishing (Friedlander et al. 2019). Hanauma Bay, a fully protected marine reserve since 1967, consists of continuous reef surrounding large sand patches. The site has substantially lower nutrient levels (39.2 kg/year) compared to Waikīkī (Lecky 2016), relatively high live coral cover of between 30% (Franklin et al. 2013) and 33% (N.T. Altman-Kurosaki, personal communication), few invertebrate corallivores (personal observation), and supports more abundant and larger fish, especially parrotfishes and other herbivores (Friedlander et al. 2014, 2018).

Experimental design

The CReME modules were designed to cross-factor shelter availability for herbivores (low vs. high) and reefscape context (relatively degraded Waikīkī vs. relatively healthy Hanauma Bay, Fig. 8). All modules were deployed during the summer of 2016 on large sand flats adjacent to reefs at both sites, ranging from 12 to 18 m in depth. At each site, we constructed three low-shelter and three high-shelter modules in the same alternating sequence from shallower to deeper water (i.e., high-low-high-low-high-low), separated from each other and the nearest reef by at least 33 meters. (The placement of the modules on sand and the limited number of module replicates were mandated by the State of Hawai‘i permitting process.) Each 0.71 m^3 module was made of 48 standard concrete blocks (40 x 19 x 19 cm) that had been soaked in freshwater for 2 weeks and bound together with 316-grade 2-cm stainless-steel banding (duplicating a prior successful design by Hixon and Beets 1993 in the Virgin Islands and Carr and Hixon 1997 in the Bahamas). Shelter holes of a range of sizes are known to be important for supporting local abundances of reef fishes of various body sizes (Hixon and Beets 1993). We therefore compared the effects of shelter availability by constructing modules either with all holes covered with concrete fiberboard (low-shelter treatment) or with 16 tiny (1 × 0.5 cm each), 8 small (9 × 2 cm each), and 24 large holes (15 × 14 cm each) running horizontally through the entire structure (high-shelter treatment, Fig. 9). Low-shelter modules served as a control for any “fish aggregating device” (FAD) effect of fish and mobile invertebrates being attracted to structure regardless of shelter availability. All modules were aligned north and south, with holes running parallel to shore. Benthic succession was monitored only on the holeless north sides (facing onshore) and south sides (facing offshore) of each module (Fig. 10) to keep the surface area studied consistent between shelter treatments. The exposed edges of the blocks were concave, providing 2-cm deep ledges and overhangs on these settlement surfaces (Fig. 9). Thus, each module essentially provided two large, vertical, scalloped concrete settling plates, each about 0.75 m^2 in area. Corals were also monitored on the tops of the modules, yet there was little settlement there, likely due to high amounts of sedimentation on these horizontal surfaces, so those data are not reported here.

Coral surveys

Juvenile coral demography was quantified by tracking all individual coral colonies that settled on the north and south sides of the modules (ca.1.5 m^2 combined). Corals were censused quarterly from May 2017 (about one year after deployment of the modules) to March 2020. Divers used Sola Nightsea UV dive lights (Light & Motion) and yellow visors over their face masks to visualize coral fluorescence, which facilitated finding tiny new settlers as small as a single polyp (Martinez and Abelson 2013, Leonard et al. 2022). Recruitment was quantified by counting all colonies ≤ 5 mm in diameter and dividing by the total available settlement area (i.e., newly observed colonies per m^2). Survival was calculated as the percentage of colonies that were alive at the end compared to the beginning of each quarter. Colony growth was calculated based on colony maximum diameter (D_m) measurements to the nearest millimeter. Maximum orthogonal diameter (D_o) was also measured for a subset of colonies (*Pocillopora*: n = 234; *Montipora*: n = 51; *Porites*: n = 21). For all other colonies, an estimated D_o was modelled as a function of D_m based on these representative measurements (*Pocillopora*: $r^2 = 0.290$, *Montipora*: $r^2 = 0.833$, *Porites*: $r^2 = 0.782$). D_o was modelled to account for differences in growth patterns between the three focal genera. *Pocillopora* fit for D_o was lower than *Montipora* and *Porites* because pocilloporid corals tend to grow variably upward, even at small sizes, increasing the variance in D_m and therefore D_o estimation. *Montipora* and *Porites* are relatively two-dimensional as new recruits. Individual colony planar area was estimated based on an ellipse including the D_m and D_o values for each colony. Growth was calculated as the change in planar area for each colony at the end compared to the beginning of each quarter (cm^2/quarter). Colonies that eventually fragmented, fused, or had shrunk in the previous quarter were excluded from all analyses to differentiate recovery from growth. However, all measurements that preceded these cases were analyzed. Genus specific coral cover for each module was calculated by summing the total estimated area of all colonies combined.

Herbivorous fish and urchin surveys

During each coral survey, all herbivorous fish and urchins within 1 meter of each module (as well as all other fish species and larger mobile invertebrates) were counted and sized by species to assess relative herbivory between low and high shelter modules and between reefscape types. Urchin test diameters and herbivorous fish total lengths were estimated visually to the nearest centimeter and converted to biomass estimates based on published length-weight relationships (Levitan 1988, Letourneur et al. 1998, Kamikawa et al. 2015, Nadon et al. 2015, Lewis et al. 2018). Where species-specific parameters were not available, those of closely related species were used.

Benthic algal overgrowth estimates

Algal overgrowth provides an index for coral-algal competition at the colony scale. Starting in the third quarterly coral census (November 2017), algal overgrowth was assessed for each colony by visually estimating the percentage of each coral colony covered by benthic algae, categorized into quartiles (1: 0-25%, 2: 26-50%, 3: 51-75%, 4: 76-100% of colony covered by algae). When surge was present, the observer would categorize overgrowth as the average seen in each wave cycle to also account for possible abrasion by adjacent algae.

Statistical analyses

To test the Herbivore Hypothesis, two separate sets of models were used to determine whether correlations were present (1) between herbivore biomass and algal overgrowth and (2) between algal overgrowth and coral cover for each coral genus. Herbivore biomass was the total mass of urchins or herbivorous fish during each survey period. Algal overgrowth was determined by calculating mean algal overgrowth of coral colonies at the module scale whereas coral cover (for all colonies 1-20 mm in diameter) was totaled at the module scale for each survey period (both north and south sides combined). The first models were a series of linear mixed effects models using the *lmer* function in the R package 'lme4' (Bates et al. 2015) with algal overgrowth and coral cover as response variables, herbivore biomass and algal overgrowth as fixed effects, and random effects for module number and season nested within year to account for repeated measures. We ran mixed effects models on module-scale measurements of herbivore biomass, mean algal overgrowth, and total coral cover through time. Second, we ran a series of simple linear models using the *lm* function (R Core Team 2020) to test the same response variables and predictors as in the mixed effects models, but on grand means for both model predictors and response variables (Table 1). Grand means were calculated for the herbivore biomass, mean algal overgrowth, and total coral cover of all colonies for each module (n=11) across survey time steps. This was done to condense the amount of variation at the module scale in response variables over the course of the study to test for broad average trends.

To test the Shelter Hypothesis and Reefscape Hypothesis regarding how coral demographic rates differ between shelter treatments and study sites, respectively, coral colonies were binned in four size classes: 1: 1-5 mm, 2: 6-10 mm, 3: 11-15 mm, and 4: 16-20 mm maximum diameter. Although other studies have used 10 mm size class bins (Doropoulos et al. 2015), the unprecedented frequency of quarterly sampling and the growth of corals to 1-2 cm in diameter during the first year post-settlement provided justification for using 5 mm size classes. A series of linear mixed effects models were created with shelter treatment, reefscape, and their interaction as fixed effects, and with module number as a random effect in addition to year and quarter as nested random effects to account for repeated measures (Table 1). Model means for urchin biomass, herbivorous fish biomass, coral recruitment, and coral survival were calculated at the module scale whereas model means for benthic algal overgrowth and coral growth were calculated at the colony scale. Because algal overgrowth and coral growth can be measured for a single colony during multiple surveys, coral colony identity was also used as a random effect to account for repeated measures at the colony scale. All mixed effects models were run with the *lmer* function in the 'lme4' package in R (Bates et al. 2015) with coral demographic models run for each coral genus and size class combination. For analyses where significant interactions were detected, pairwise multiple comparisons using the `emmeans` package were used to calculate comparison p-values using the Kenward-Rogers method. Response variables were transformed when necessary to meet assumptions of normality and homoscedasticity. Coral recruitment and urchin biomass were $\log(x + 1)$ transformed whereas herbivorous fish biomass was $x^{1/4}$ transformed to account for zero-inflated, continuous data.

To illustrate patterns of survival and growth more explicitly, demographic transition matrices were constructed to determine probabilities of growth, stasis, shrinkage, or death within each size class for each coral genus. Mean transition matrices were calculated according to Doropoulos et al. (2015) and represent mean probabilities of size class transitions per quarter throughout the study.

Results

Settling corals were primarily of three genera – *Pocillopora*, *Montipora*, and *Porites* – so these were the corals we analyzed. Species could not be identified with any certainty at the small colony sizes occurring during this study, yet larger colonies at both sites were clearly dominated by *Pocillopora meandrina*, *Montipora capitata, M. patula*, and *Porites lobata*. Additional relatively rare corals settling on the modules included *Porites hawaiiensis, P. compressa, Cyphastrea ocellina*, and the genus *Leptastrea*. Note that the shallowest module at Hanauma Bay was subjected to repeated severe sand scour during large swells, and so supported little benthos for the duration of the experiment. Therefore, this high-shelter module was deleted from all analyses.

Herbivore hypothesis

The hypothesis that herbivores reduce benthic algal overgrowth of corals, thus creating space for coral recruitment and growth, was foundational for the more mechanistic hypotheses that were the primary focus of this study. Urchin biomass, herbivorous fish biomass, and algal overgrowth all varied greatly through time (Fig. 11a-c). Although algal overgrowth was only marginally negatively correlated with herbivore biomass for both urchins ($p = 0.086$, $r^2 = 0.022$) and herbivorous fishes ($p = 0.102$, $r^2 = 0.027$) for the mixed effects models (*lmer* in R), both urchins ($p = 0.027$, $r^2 = 0.44$; Fig. 2a) and herbivorous fish ($p = 0.05$, $r^2 = 0.36$; Fig. 2b) were significantly negatively correlated with algal overgrowth in the simple linear model (*lm* in R). Also as predicted, total coral cover was negatively correlated with benthic algal overgrowth for *Montipora* ($p < 0.01$, $r^2 = 0.064$; Fig. 3a) and *Porites* ($p = 0.023$, $r^2 = 0.056$; Fig. 3b), both of which grew as crusts at small sizes (1-20 mm in diameter; size classes 1-4). In contrast, total cover of relatively vertically growing *Pocillopora* was not significantly correlated with algal overgrowth.

Surgeonfishes (Family Acanthuridae) were by far the dominant herbivorous fishes, especially *Acanthurus nigrofuscus*, *A. olivaceus*, and *A. dussumieri*. Parrotfishes (Family Labridae) were rare, being severely overfished around Oʻahu (Friedlander and DeMartini 2002, Nadon 2017, Friedlander et al. 2018) except in the few marine reserves such as Hanauma Bay. Yet even in Hanauma Bay, parrotfish were seldom observed on the modules. Very few new recruits of any herbivorous fishes were observed throughout the experiment, so colonization was almost exclusively via immigration. The dominant sea urchins colonizing the modules at both sites were *Echinothrix calamaris*, *Tripneustes gratilla*, and *Echinometra mathaei*. Both the fishes and the urchins colonizing the modules were representative of the surrounding natural reefs (unpublished data). An early assessment of macroalgae (algal height > 2 cm) colonizing the modules revealed the genera *Lobophora*, *Dictyota*, *Padina*, and *Peyssonnelia* (Guiry 2013).

Shelter hypothesis

The hypothesis that higher shelter availability for herbivores indirectly benefits juvenile corals independent of the local reef environment predicted that the presence of structural shelter would increase herbivore biomass locally, therefore decreasing benthic algal overgrowth and thereby enhancing demographic metrics for corals. Results mostly confirmed the predictions regarding shelter and herbivores, yet seldom translated to reducing algae and benefitting corals.

Urchin biomass was significantly greater on high-shelter modules at Hanauma Bay ($p = 0.037$, $r^2 = 0.27$; Fig. 4a). The same pattern appeared to occur on average at Waikīkī, yet almost no urchins colonized modules there, so the pattern was nonsignificant. Herbivorous fish biomass was greater on high-shelter modules at both sites ($p < 0.001$, $r^2 = 0.31$; Fig. 4b). However, benthic algal overgrowth was not significantly different between low and high-shelter modules (Fig. 4c).

Given the above patterns, shelter was a significant predictor of coral recruitment only for *Pocillopora*, with greater recruitment occurring on high-shelter modules, yet only at Hanauma Bay ($p = 0.01$, $r^2 = 0.037$; Figs. 5a and 12a). Recruitment was not significantly different between shelter treatments for *Montipora* or *Porites*, though was nonetheless greater on average on high-shelter modules in most cases (Figs. 5b and c, respectively).

As predicted, *Porites* survival was greater on high-shelter modules for size class 1 (but only at Hanauma Bay, $p < 0.002$, $r^2 = 0.18$; Fig. 6c), where it suffered far greater mortality on low-shelter modules (Fig. 7c, Table 8). *Porites* survival was also greater in general on high-shelter modules for size class 2 ($p = 0.027$, $r^2 = 0.073$) and size class 3 ($p < 0.01$, $r^2 = 0.12$; Figs. 6c and 7c, Table 5). In contrast, survival of neither *Pocillopora* nor *Montipora* was significantly different between shelter treatments (Fig. 6a and b, respectively).

Opposite our predictions, *Porites* grew faster on low-shelter compared to high-shelter modules for size class 1 ($p = 0.032$, $r^2 = 0.13$; Figs. 6f and 7c) and on low-shelter modules at Waikīkī for size class 2 ($p = 0.028$, $r^2 = 0.078$; Fig. 6f, Table 8). *Pocillopora* and *Montipora* growth was not significantly different between shelter treatments.

Reefscape hypothesis

The hypothesis that, independent of shelter availability, relatively healthy reef environments benefit juvenile corals predicted that, compared to modules near degraded Waikīkī reefs, modules near relatively healthy reefs at Hanauma Bay would experience greater herbivore biomass, lower algal overgrowth, and enhanced coral demographic metrics. Urchin biomass was indeed greater on modules at Hanauma Bay ($p = 0.037$, $r^2 = 0.27$; Fig. 4a), particularly on high-shelter modules. However, herbivorous fish biomass was not significantly different between the two study sites, though on high-shelter modules was on average greater at Hanauma Bay (Fig. 4b). Also as predicted, benthic algal overgrowth was lower on modules at Hanauma Bay compared to Waikīkī ($p = 0.033$, $r^2 = 0.023$; Fig. 4c).

As expected, *Montipora* recruitment was greater at Hanauma Bay, yet only on high-shelter modules ($p < 0.01$, $r^2 = 0.16$; Fig. 5b; Table 7). Yet, contrary to our predictions, recruitment of *Pocillopora* and *Porites* was not significantly different between the two study sites (Fig. 5a and c, respectively).

As predicted, survival of *Pocillopora* was greater at Hanauma Bay for size class 4 ($p = 0.05$, $r^2 = 0.097$; Figs. 6a and 7a, Table 3). However, survival of both *Montipora* and *Porites* was not significantly different between sites (Fig. 6b and c, respectively).

Opposite our predictions, growth of *Pocillopora* was greater at Waikīkī on low-shelter modules for size class 1 ($p < 0.01$, $r^2 = 0.032$; Fig. 6d, Table 6). Nonetheless, as predicted, growth of *Montipora* was greater at Hanauma Bay for size class 2 ($p < 0.01$, $r^2 = 0.05$; Fig 6e, Table 4). Growth of *Porites* was not significantly different between the two study sites (Fig. 6f).

Discussion

The results of this multiyear field experiment revealed complex environmental effects on new coral recruits at both the relatively micro scale of shelter availability for herbivores and the relatively macro scale of surrounding reef state. Comparisons across modules largely confirmed the Herbivore Hypothesis in that mean benthic algal overgrowth varied inversely with mean herbivore biomass and mean coral cover of two of three coral genera. This foundational pattern provided the basis for testing the relative benefits of shelter for herbivores and healthy reefscape for early post-settlement demographic rates of corals.

Shelter hypotheses

As summarized in Table 2, multiple demographic predictions of the Shelter Hypothesis that spatial refugia for herbivores indirectly benefit corals (regardless of reefscape) were mostly rejected. This outcome occurred despite patterns that (1) herbivores were more abundant on high-shelter modules, albeit at low densities, (2) algal overgrowth varied inversely with herbivore biomass in a simple linear model, and (3) coral cover varied inversely with algal overgrowth for two of the three most common genera (*Montipora* and *Porites*). We believe that the Shelter Hypothesis was largely rejected because the abundance of herbivores in our system was generally very low compared to other regions where fishing intensity is much less (Edwards et al. 2014). Indeed, herbivorous fishes, such as parrotfishes and surgeonfishes, are severely overfished on the main Hawaiian Islands (Friedlander and DeMartini 2002, Nadon 2017, Friedlander et al. 2018). In addition to problems associated with overfishing, reef fish populations in Hawaiʻi may be additionally suppressed due to recruitment limitation (Walsh 1987). Recruitment of sea urchins is also patchy in time and space, often occurring in infrequent, large pulses (Bak 1985), which happened once at the beginning of this study and only at Hanauma Bay. The local distribution and abundance of urchins can change drastically over time as mobile groups move over large tracts of sand (Coppard and Campbell 2005). During this study, we only occasionally observed large *E. calamaris* and *T. gratilla* moving over sand between modules and the natural reef at Waikīkī and Hanauma Bay (personal observation). With few herbivores in general, the direct and indirect effects of structural shelter were likely obscured relative to general patterns found elsewhere in the world (e.g., Mumby and Steneck 2008, Hixon 2015).

While most predictions of the Shelter Hypothesis were rejected, a couple were confirmed. First, *Pocillopora* recruitment was greater on high-shelter modules, yet this pattern occurred only at Hanauma Bay. Unlike the other common coral genera, the cover of *Pocillopora* was not negatively correlated with benthic algal overgrowth, indicating that early recruits of this genus are potentially tolerant of competition with algae. Indeed, *Pocillopora* was unique among the common corals in this study in that it grew vertically at a much smaller size than other genera, which exhibited encrusting growth forms. However, growth form does not explain initial patterns of recruitment, which occurred before any colonies grew vertically. As a known rapid colonizer compared to other genera (Pearson 1981, Bianchi et al. 2006), pocilloporid larvae preferentially settle on bare substrate with low sediment (Hodgson 1990, Price 2010), low abundance of cyanobacteria (Kuffner and Paul 2004), and low algal abundance (Lee et al. 2012), which likely explains why recruitment was greater on the relatively bare high-shelter modules at Hanauma Bay. However, Waikīkī low- and high-shelter modules had considerable recruitment despite lacking preferred settlement habitat. This pattern may be due to a potentially greater abundance of *Pocillopora* larvae at Waikīkī (Tsounis and Edmunds 2016), where adult *Pocillopora* were far more abundant on the surrounding natural reefs than at Hanauma Bay (unpublished data). Perhaps as a result, *Pocillopora* colony density was the same across Waikīkī modules at the end of this study regardless of shelter (Fig. 13a). We therefore hypothesize that *Pocillopora* benefitted from the exceptionally clean surfaces of high-shelter modules at

Hanauma Bay, despite not being a dominant coral genus found on the continuous reef at that site, yet at the same time, relatively high larval supply at Waikīkī may have compensated for the poorer settlement habitat at that site.

The second confirmed prediction was that high-shelter modules at Hanauma Bay also exhibited greater *Porites* survivorship, particularly for the smallest size class (Table 2). Herbivory may have fostered this pattern in that *Porites* cover was negatively correlated with algal overgrowth, which was on average lower on Hanauma Bay high-shelter modules, and herbivorous fish biomass, although relatively low across the study, was marginally greater on high-shelter modules regardless of site. However, greater survival of *Porites* also occurred on high-shelter modules for size classes 2 and 3 regardless of site, despite greater algal overgrowth on Waikīkī modules. Sediment retention by thick algal turfs (Nugues and Roberts 2003) and the presence of algal metabolites and allelochemicals that can harm corals and create hypoxic conditions (Brown et al. 2020) may be important factors in early survivorship of *Porites* in particular. Water motion that perturbs thick turfs can decrease sediment retention, prevent hypoxic conditions, and reduce the concentration of pathogens and harmful metabolites (Jorissen et al. 2016). Indeed, *Porites* in contact with algal turf has been found to incur greater tissue damage in habitats with conditions of low water flow and high sedimentation (Gowan et al. 2014). Therefore, we hypothesize that the many holes in high-shelter modules created conditions of more variable water flow that reduced sediment loads and the negative effects of thick turfs, thereby enhancing the survival of juvenile *Porites* colonies. Reduced survival on low-shelter modules may also be attributed to greater *Porites* growth rates in response to intense competition with algal turfs. Contrary to our predictions, *Porites* growth was greater for the smallest colonies on low-shelter modules, particularly at Waikīkī. We hypothesize that faster growth that escapes unfavorable microhabitats within thick algal turfs may represent a tradeoff that inhibits coral recovery (Denis et al. 2013) as well as resistance to pathogens and harmful metabolites. Rapid early growth combined with the negative effects of thick algal turfs may therefore contribute to greater colony mortality over time, as seen in lower survivorship of *Porites* on low shelter modules for size classes 2 and 3 (Table 5).

Reefscape hypothesis

Compared to the Shelter Hypothesis, more predictions were confirmed for the Reefscape Hypothesis that a relatively healthy reef will benefit the demographic rates of juvenile corals (regardless of shelter). In particular, recruitment and growth of the genus *Montipora* and survival of the genus *Pocillopora* were greater on experimental modules near relatively healthy Hanauma Bay reefs than those near relatively degraded Waikīkī Reefs. Nonetheless, this hypothesis was not fully corroborated for either genus, and was fully rejected for *Porites* for unknown reasons.

What explains these discrepancies? Regarding recruitment, *Montipora* showed significantly higher values on high-shelter modules at Hanauma Bay. Vermeij et al. (2009) demonstrated that *Montipora* larvae undergo reduced settlement success in the presence of harmful microbes associated with algal turfs. At Waikīkī, where algal turfs dominated all module surfaces, recruitment was significantly lower for *Montipora* compared to the other genera. Additionally, Lager et al. (2020) demonstrated that *M. capitata* planulae have significantly lower survival in treatments with moderate to high suspended sediments. Algal turfs on modules at Waikīkī were often sediment laden during this study compared to Hanauma Bay (unpublished data). Considering the proximity to runoff from the Ala Wai Canal and urban

Honolulu, sediment may be an important factor in suppressing *Montipora* settlement at Waikīkī. Sponges were also more abundant on modules at Waikīkī (unpublished data), possibly due to greater eutrophication, and are known to reduce coral recruitment (Brandt et al. 2019) which could have affected *Montipora* in particular. In Palau, *Montipora* has been documented to recruit to habitats with abundant crustose coralline algae (CCA; Gouezo et al. 2020), which has been shown to produce chemical cues that enhance larval settlement (Ritson-Williams et al. 2009). During this study, CCA were rarely seen at Waikīkī compared to high-shelter modules at Hanauma Bay (unpublished data) where *Montipora* recruitment was greater. The lack of suitable settlement habitat and cues at Waikīkī may therefore act as a recruitment and survival bottleneck, resulting in very few *Montipora* recruits over this study. Assuming *Montipora* is particularly susceptible to deleterious microbes, suspended sediments, and sponges compared to other corals, and given that the cleanest settlement surfaces with higher CCA cover were on high-shelter modules at Hanauma Bay, it follows that recruitment of this genus was greater at this site.

Regarding survival, mortality of *Pocillopora* was greater at Waikīkī than Hanauma Bay, as evidenced by significantly lower survival to the largest size class at Waikīkī. Relative to the other coral genera, *Pocillopora* may have been at a disadvantage because cushion stars and crown-of-thorns sea star were more abundant on modules at Waikīkī than at Hanauma Bay, where they were never observed (unpublished data). These corallivores have been shown to prefer pocilloporid corals over other genera in Hawaiʻi (Glynn and Krupp 1986) and therefore likely reduced the survival of larger *Pocillopora* juveniles at Waikīkī in this study.

Our last confirmed prediction was greater *Montipora* growth for size class 2 at Hanauma Bay, regardless of shelter. Why only size class 2? Relative to Hanauma Bay, Waikīkī had very few *Montipora* colonies throughout this study leading to highly unbalanced sample sizes between the sites. The relative lack of *Montipora* at Waikīkī may reflect a recruitment bottleneck at this site which possibly obscured underlying differences in growth rates between sites. Therefore, *Montipora* growth could have been greater at Hanauma Bay in general, despite our inability to detect significant patterns in other size classes.

Implications for coral restoration

The Coral Resilience Module Experiment (CReME) was designed to test whether artificial high-shelter structures can be an effective tool for coral restoration on highly degraded reefs by increasing local herbivory, and indirectly, coral abundance. Our factorial experimental design allowed us to test the relative and combined effects of shelter availability (i.e., low vs. high shelter modules) and reefscape (i.e., relatively degraded Waikīkī vs. relatively healthy Hanauma Bay). There were both genus-specific and context-dependent patterns in the demographic rates of the juvenile coral colonies that naturally recruited. We conclude that extreme patchiness in time and space of both biotic and abiotic environmental factors affect coral recruitment in ways that defy broad generalizations in our Hawaiian study system.

Although resulting patterns over four years post-deployment were variable, we nonetheless found that herbivores, although generally uncommon in our system, were a key component to fostering juvenile corals by creating space for larvae to settle, reducing coral-algal competition for space, and potentially reducing harmful microbial communities that thrive in algal turfs. Thus, as emphasized in previous studies, it is vital to properly manage herbivores to reduce algae to levels where corals can successfully settle and grow (Chung et al. 2019). In Hawai‘i, where herbivorous fishes are severely overfished (Friedlander and DeMartini 2002, Nadon 2017, Friedlander et al. 2018), the Division of Aquatic Resources has successfully used hatchery-reared collector urchins (*Tripneustes gratilla*) to control invasive algal populations in Kāneʻohe Bay on Oʻahu (Neilson et al. 2018). Additionally, an herbivore replenishment reserve on Maui has demonstrated that herbivore populations can recover and start shifting reefs covered by macroalgae on a trajectory back toward coral dominance (Williams et al. 2016).

For herbivore management to be effective in enhancing juvenile corals, a number of key conditions must be met. First, assuming larval supply is sufficient, which may not be true in Hawaiʻi (Walsh 1987), shelter is necessary to attract and recruit resident herbivores. The concrete modules we studied provide physical relief and shelters of varying sizes, which were attractive to herbivorous fishes and urchins in prior studies in the Virgin Islands (Hixon and Beets 1993) and the Bahamas (Carr and Hixon 1997). Such structures thus have the potential to be viable platforms for coral restoration efforts on collapsed reefs that have lost rugose habitats. In addition to providing shelter for herbivores, such modules may also serve as platforms for outplanting corals from nurseries or attaching dislodged "corals of opportunity" (Hixon et al., unpublished data). Outplanting and reattaching colonies increases the local abundance of corals, which are known to emit chemical cues that can attract coral planulae to settle naturally (Vermeij and Sandin 2008, Da-Anoy et al. 2017). Enhanced coral settlement and survival would increase the capacity of coral populations to recover from disturbances such as storms and coral bleaching.

Ultimately, this field experiment demonstrated that the proximity of relatively healthy coral reefs often enhances coral recruitment, survival, and growth on coral-restoration modules. Additionally, the study showed that cubic-meter concrete modules provide substantial settlement surfaces for studying patterns colonization and early post-settlement demography of corals. We followed hundreds of individual colonies on these modules quarterly for three and a half years, uniquely demonstrating the feasibility of long-term and frequent monitoring of juvenile coral demographic rates *in situ*. Understanding the mechanisms underlying patterns of coral recruitment, survival, and growth will be crucial for reef restoration efforts in a rapidly warming ocean, where ever worsening bleaching events will certainly test the ability of corals to resist and recover from climate disruption (Hooidonk et al. 2016).

Table 1 Summary table of R model functions used and equations for each hypothesis. The Herbivore Hypothesis predicts that greater herbivore biomass (urchins and fish separately) will result in less algal overgrowth and consequently greater coral cover. "Reefscape" contrasts study sites (Waikīkī vs. Hanauma Bay) and "Shelter" contrasts the availability of shelter for herbivores (low vs. high shelter modules). Equations for simple linear models (lm) contain a single response variable and predictor while linear mixed effects models (lmer) incorporate fixed effects for Reefscape and Shelter as well as random effects for module replicate (1|mod), quarter nested in year (1|time), and coral colony identity (1|ident) to account for repeated measures.

Hypothesis	Model	Response Variable	Equation (Response ~ Predictors)
Herbivore (urchin)	lm (base R)	Algal overgrowth (AO)	AO ~ UB
Herbivore (fish)	lm (base R)	Algal overgrowth (AO)	AO ~ HFB
Herbivore	lm (base R)	Coral cover (CC)	CC ~ AO
Reefscape/Shelter (R/S)	lmer (lme4)	Urchin biomass (UB)	UB ~ R + S + (R × S) + (1|mod) + (1|time)
Reefscape/Shelter (R/S)	lmer (lme4)	Herbivorous fish biomass (HFB)	HB ~ R + S + (R × S) + (1|mod) + (1|time)
Reefscape/Shelter (R/S)	lmer (lme4)	Algal overgrowth (AO)	AO ~ R + S + (R × S) + (1|ident) + (1|mod) + (1|time)
Reefscape/Shelter (R/S)	lmer (lme4)	Coral recruitment (CR)	CR ~ R + S + (R × S) + (1|mod) + (1|time)
Reefscape/Shelter (R/S)	lmer (lme4)	Coral survival (CS)	CS ~ R + S + (R × S) + (1|mod) + (1|time)
Reefscape/Shelter (R/S)	lmer (lme4)	Coral growth (CG)	CG ~ R + S + (R × S) + (1|ident) + (1|mod) + (1|time)

Table 2: Summary of experimental results by coral genus. The foundational Herbivore Hypothesis predicted negative correlations between benthic algal overgrowth and herbivores (confirmed, Fig. 2), and between corals and macroalgae for simple linear models (*lm* in R). The Shelter Hypothesis predicted that all demographic metrics would be greater on high-shelter (HIGH) modules than on low-shelter (LOW) modules. The Reefscape Hypothesis predicted that all metrics would be greater at relatively healthy Hanauma Bay (HAN) than at relatively degraded Waikīkī (WAI). For the Shelter and Reefscape Hypotheses, *lmer* model results are also presented (columns labeled "both"). Superscripts represent size classes in which correlations were significant for coral survival and growth. Symbols: ✓ = prediction significantly confirmed; 0 = no significant difference; < = results significantly opposite predicted. See Results for details.

	Coral Genus								
	Pocillopora			*Montipora*			*Porites*		
Herbivore Hypothesis predicts negative correlations									
Coral vs. Algae:	0			✓			✓		
Shelter Hypothesis predicts HIGH > LOW shelter									
Site:	WAI	HAN	both	WAI	HAN	both	WAI	HAN	both
Recruitment:	0	✓	0	0	0	0	0	0	0
Survival:	0	0	0	0	0	0	0	✓^{1,3}	✓^{2,3}
Growth:	0	0	0	0	0	0	<^{2}	0	<^{1}
Reefscape Hypothesis predicts HAN > WAI site									
Shelter:	LOW	HIGH	both	LOW	HIGH	both	LOW	HIGH	both
Recruitment:	0	0	0	0	✓	✓	0	0	0
Survival:	0	0	✓^{4}	0	0	0	0	0	0
Growth:	<^{1}	0	<^{1}	✓^{2}	0	✓^{2}	0	0	0

Table 3 *Pocillopora* transition matrices comparing low shelter vs. high shelter and Waikīkī vs. Hanauma Bay modules throughout the experiment. Columns represent the 5 mm diameter size class at the beginning of a quarter while rows represent the size class at the end of the quarter. Cells contain mean probabilities of either growth (below the diagonal line), stasis (along the diagonal), or shrinkage (above the diagonal) for each possible size class transition with associated standard error. The third to last row shows cases where corals grew to greater than 20 mm in diameter. The second to last row (*M*) shows percent mortality during each transition, such that the sum of values in each column equals 1.0. The last row (*n*) represents the total number of observations for each given size class.

End Quarter Size Class	Initial Size Class			
Low Shelter	*1*	*2*	*3*	*4*
1	0.22 ± 0.041	0.009 ± 0.005	0.007 ± 0.004	0
2	0.252 ± 0.038	0.229 ± 0.034	0.038 ± 0.011	0.02 ± 0.01
3	0.101 ± 0.028	0.355 ± 0.037	0.176 ± 0.03	0.032 ± 0.012
4	0.045 ± 0.017	0.184 ± 0.036	0.447 ± 0.046	0.288 ± 0.046
≥5	0	0.05 ± 0.021	0.165 ± 0.034	0.571 ± 0.047
M	0.381 ± 0.044	0.173 ± 0.031	0.169 ± 0.034	0.089 ± 0.021
n	296	288	263	225

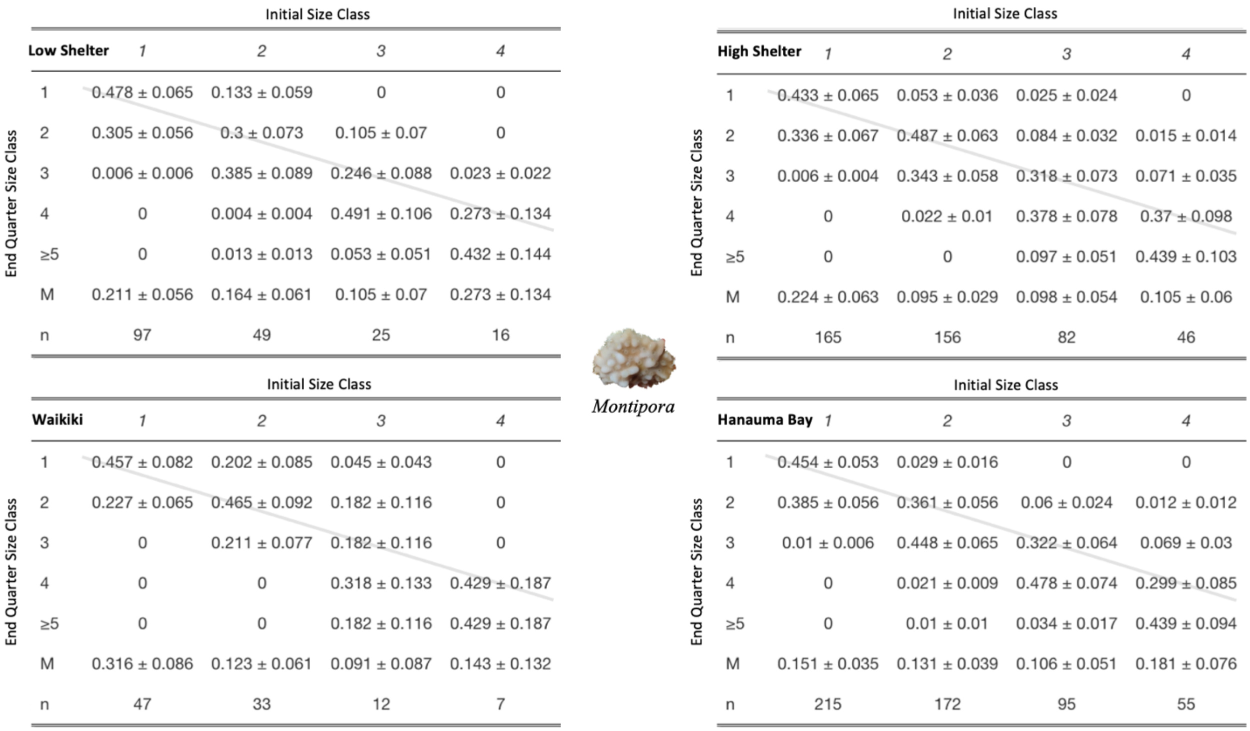
End Quarter Size Class	Initial Size Class			
High Shelter	*1*	*2*	*3*	*4*
1	0.237 ± 0.029	0.034 ± 0.011	0.009 ± 0.007	0
2	0.32 ± 0.038	0.251 ± 0.035	0.066 ± 0.018	0.039 ± 0.02
3	0.152 ± 0.042	0.338 ± 0.034	0.227 ± 0.037	0.063 ± 0.023
4	0.012 ± 0.008	0.193 ± 0.041	0.372 ± 0.037	0.222 ± 0.035
≥5	0	0.049 ± 0.024	0.207 ± 0.038	0.563 ± 0.045
M	0.279 ± 0.036	0.136 ± 0.031	0.119 ± 0.031	0.113 ± 0.03
n	339	303	244	208

Pocillopora

End Quarter Size Class	Initial Size Class			
Waikiki	*1*	*2*	*3*	*4*
1	0.212 ± 0.028	0.025 ± 0.008	0.011 ± 0.006	0
2	0.3 ± 0.03	0.191 ± 0.027	0.068 ± 0.015	0.023 ± 0.009
3	0.148 ± 0.036	0.33 ± 0.031	0.194 ± 0.025	0.054 ± 0.014
4	0.044 ± 0.015	0.196 ± 0.037	0.366 ± 0.031	0.268 ± 0.034
≥5	0	0.075 ± 0.026	0.186 ± 0.031	0.502 ± 0.035
M	0.297 ± 0.033	0.183 ± 0.03	0.175 ± 0.028	0.152 ± 0.025
n	384	409	373	326

End Quarter Size Class	Initial Size Class			
Hanauma Bay	*1*	*2*	*3*	*4*
1	0.251 ± 0.045	0.013 ± 0.008	0.003 ± 0.003	0
2	0.268 ± 0.049	0.303 ± 0.042	0.027 ± 0.014	0.036 ± 0.023
3	0.099 ± 0.036	0.37 ± 0.042	0.21 ± 0.044	0.036 ± 0.023
4	0.008 ± 0.008	0.177 ± 0.039	0.472 ± 0.057	0.239 ± 0.052
≥5	0	0.015 ± 0.009	0.183 ± 0.043	0.66 ± 0.059
M	0.374 ± 0.05	0.121 ± 0.032	0.104 ± 0.038	0.028 ± 0.022
n	251	182	134	107

Table 4 *Montipora* transition matrices comparing low shelter vs. high shelter and Waikīkī vs. Hanauma Bay modules throughout the experiment. Columns represent the 5 mm diameter size class at the beginning of a quarter while rows represent the size class at the end of the quarter. Cells contain mean probabilities of either growth (below the diagonal line), stasis (along the diagonal), or shrinkage (above the diagonal) for each possible size class transition with associated standard error. The third to last row shows cases where corals grew to greater than 20 mm in diameter. The second to last row (*M*) shows percent mortality during each transition, such that the sum of values in each column equals 1.0. The last row (*n*) represents the total number of observations for each given size class.



Initial Size Class

End Quarter Size Class

Low Shelter	*1*	*2*	*3*	*4*
1	0.478 ± 0.065	0.133 ± 0.059	0	0
2	0.305 ± 0.056	0.3 ± 0.073	0.105 ± 0.07	0
3	0.006 ± 0.006	0.385 ± 0.089	0.246 ± 0.088	0.023 ± 0.022
4	0	0.004 ± 0.004	0.491 ± 0.106	0.273 ± 0.134
≥5	0	0.013 ± 0.013	0.053 ± 0.051	0.432 ± 0.144
M	0.211 ± 0.056	0.164 ± 0.061	0.105 ± 0.07	0.273 ± 0.134
n	97	49	25	16

Initial Size Class

End Quarter Size Class

High Shelter	*1*	*2*	*3*	*4*
1	0.433 ± 0.065	0.053 ± 0.036	0.025 ± 0.024	0
2	0.336 ± 0.067	0.487 ± 0.063	0.084 ± 0.032	0.015 ± 0.014
3	0.006 ± 0.004	0.343 ± 0.058	0.318 ± 0.073	0.071 ± 0.035
4	0	0.022 ± 0.01	0.378 ± 0.078	0.37 ± 0.098
≥5	0	0	0.097 ± 0.051	0.439 ± 0.103
M	0.224 ± 0.063	0.095 ± 0.029	0.098 ± 0.054	0.105 ± 0.06
n	165	156	82	46

Montipora

Initial Size Class

End Quarter Size Class

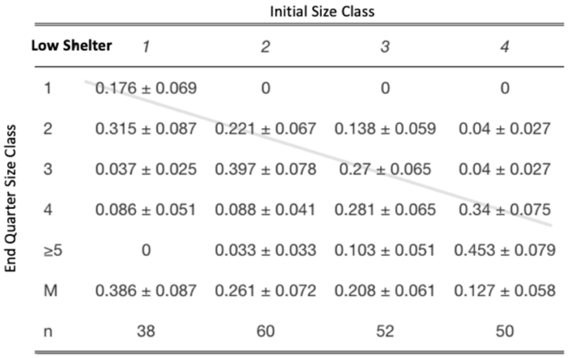
Waikiki	*1*	*2*	*3*	*4*
1	0.457 ± 0.082	0.202 ± 0.085	0.045 ± 0.043	0
2	0.227 ± 0.065	0.465 ± 0.092	0.182 ± 0.116	0
3	0	0.211 ± 0.077	0.182 ± 0.116	0
4	0	0	0.318 ± 0.133	0.429 ± 0.187
≥5	0	0	0.182 ± 0.116	0.429 ± 0.187
M	0.316 ± 0.086	0.123 ± 0.061	0.091 ± 0.087	0.143 ± 0.132
n	47	33	12	7

Initial Size Class

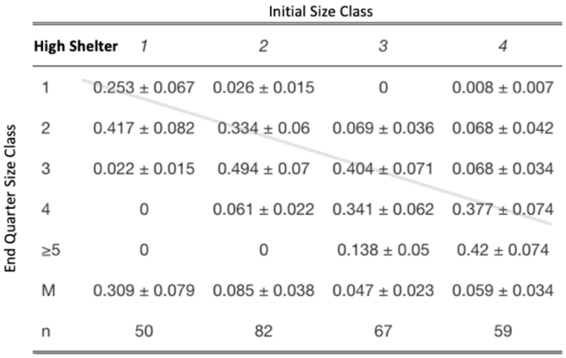
End Quarter Size Class

Hanauma Bay	*1*	*2*	*3*	*4*
1	0.454 ± 0.053	0.029 ± 0.016	0	0
2	0.385 ± 0.056	0.361 ± 0.056	0.06 ± 0.024	0.012 ± 0.012
3	0.01 ± 0.006	0.448 ± 0.065	0.322 ± 0.064	0.069 ± 0.03
4	0	0.021 ± 0.009	0.478 ± 0.074	0.299 ± 0.085
≥5	0	0.01 ± 0.01	0.034 ± 0.017	0.439 ± 0.094
M	0.151 ± 0.035	0.131 ± 0.039	0.106 ± 0.051	0.181 ± 0.076
n	215	172	95	55

Table 5 *Porites* transition matrices comparing low shelter vs. high shelter and Waikīkī vs. Hanauma Bay modules throughout the experiment. Columns represent the 5 mm diameter size class at the beginning of a quarter while rows represent the size class at the end of the quarter. Cells contain mean probabilities of either growth (below the diagonal line), stasis (along the diagonal), or shrinkage (above the diagonal) for each possible size class transition with associated standard error. The third to last row shows cases where corals grew to greater than 20 mm in diameter. The second to last row (*M*) shows percent mortality during each transition, such that the sum of values in each column equals 1.0. The last row (*n*) represents the total number of observations for each given size class.

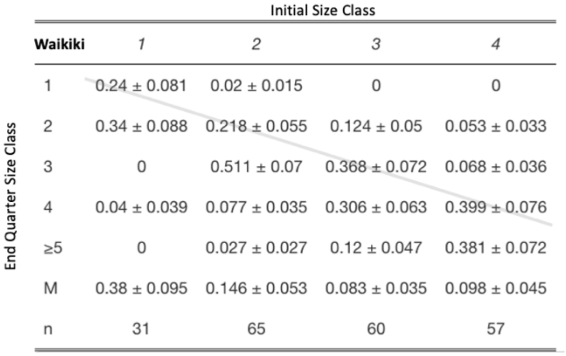


	Initial Size Class			
Low Shelter	*1*	*2*	*3*	*4*
1	0.176 ± 0.069	0	0	0
2	0.315 ± 0.087	0.221 ± 0.067	0.138 ± 0.059	0.04 ± 0.027
3	0.037 ± 0.025	0.397 ± 0.078	0.27 ± 0.065	0.04 ± 0.027
4	0.086 ± 0.051	0.088 ± 0.041	0.281 ± 0.065	0.34 ± 0.075
≥5	0	0.033 ± 0.033	0.103 ± 0.051	0.453 ± 0.079
M	0.386 ± 0.087	0.261 ± 0.072	0.208 ± 0.061	0.127 ± 0.058
n	38	60	52	50

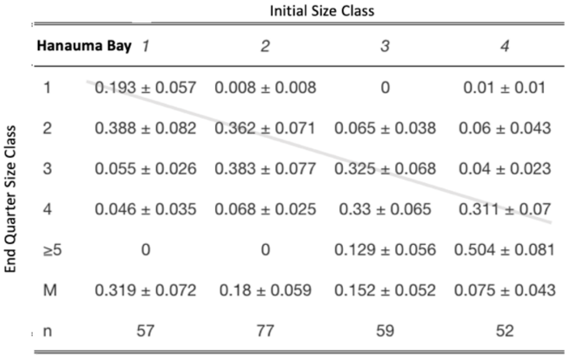


	Initial Size Class			
High Shelter	*1*	*2*	*3*	*4*
1	0.253 ± 0.067	0.026 ± 0.015	0	0.008 ± 0.007
2	0.417 ± 0.082	0.334 ± 0.06	0.069 ± 0.036	0.068 ± 0.042
3	0.022 ± 0.015	0.494 ± 0.07	0.404 ± 0.071	0.068 ± 0.034
4	0	0.061 ± 0.022	0.341 ± 0.062	0.377 ± 0.074
≥5	0	0	0.138 ± 0.05	0.42 ± 0.074
M	0.309 ± 0.079	0.085 ± 0.038	0.047 ± 0.023	0.059 ± 0.034
n	50	82	67	59

Porites



	Initial Size Class			
Waikiki	*1*	*2*	*3*	*4*
1	0.24 ± 0.081	0.02 ± 0.015	0	0
2	0.34 ± 0.088	0.218 ± 0.055	0.124 ± 0.05	0.053 ± 0.033
3	0	0.511 ± 0.07	0.368 ± 0.072	0.068 ± 0.036
4	0.04 ± 0.039	0.077 ± 0.035	0.306 ± 0.063	0.399 ± 0.076
≥5	0	0.027 ± 0.027	0.12 ± 0.047	0.381 ± 0.072
M	0.38 ± 0.095	0.146 ± 0.053	0.083 ± 0.035	0.098 ± 0.045
n	31	65	60	57



	Initial Size Class			
Hanauma Bay	*1*	*2*	*3*	*4*
1	0.193 ± 0.057	0.008 ± 0.008	0	0.01 ± 0.01
2	0.388 ± 0.082	0.362 ± 0.071	0.065 ± 0.038	0.06 ± 0.043
3	0.055 ± 0.026	0.383 ± 0.077	0.325 ± 0.068	0.04 ± 0.023
4	0.046 ± 0.035	0.068 ± 0.025	0.33 ± 0.065	0.311 ± 0.07
≥5	0	0	0.129 ± 0.056	0.504 ± 0.081
M	0.319 ± 0.072	0.18 ± 0.059	0.152 ± 0.052	0.075 ± 0.043
n	57	77	59	52

Table 6 Mean *Pocillopora* transition matrices for Waikīkī-Low, Hanauma Bay-Low, Waikīkī-High, and Hanauma Bay-High modules with standard error. Matrices show the initial size class vs the end quarter size class, mortality (*M*), and total number of observations in a given initial size class (*n*). Gray diagonal lines are the lines of stasis where shrinkage occurs above the line and growth occurs below the line.

End Quarter Size Class	Initial Size Class			
WAI-Low	*1*	*2*	*3*	*4*
1	0.201 ± 0.045	0.011 ± 0.007	0.012 ± 0.007	0
2	0.265 ± 0.045	0.158 ± 0.032	0.058 ± 0.017	0.027 ± 0.016
3	0.143 ± 0.043	0.35 ± 0.047	0.213 ± 0.036	0.057 ± 0.02
4	0.079 ± 0.028	0.194 ± 0.047	0.336 ± 0.04	0.28 ± 0.051
≥5	0	0.083 ± 0.037	0.202 ± 0.041	0.486 ± 0.05
M	0.312 ± 0.051	0.203 ± 0.048	0.18 ± 0.03	0.15 ± 0.032
n	205	207	215	176

End Quarter Size Class	Initial Size Class			
HAN-Low	*1*	*2*	*3*	*4*
1	0.246 ± 0.074	0.007 ± 0.007	0	0
2	0.236 ± 0.065	0.311 ± 0.059	0.013 ± 0.013	0.01 ± 0.009
3	0.046 ± 0.027	0.36 ± 0.058	0.131 ± 0.049	0
4	0	0.173 ± 0.054	0.583 ± 0.083	0.298 ± 0.08
≥5	0	0.012 ± 0.012	0.119 ± 0.055	0.679 ± 0.082
M	0.473 ± 0.072	0.138 ± 0.038	0.154 ± 0.065	0.013 ± 0.013
n	91	81	48	49

Pocillopora

End Quarter Size Class	Initial Size Class			
WAI-High	*1*	*2*	*3*	*4*
1	0.222 ± 0.033	0.041 ± 0.014	0.01 ± 0.01	0
2	0.334 ± 0.038	0.225 ± 0.043	0.079 ± 0.025	0.019 ± 0.01
3	0.153 ± 0.056	0.308 ± 0.038	0.175 ± 0.035	0.051 ± 0.02
4	0.01 ± 0.007	0.198 ± 0.057	0.396 ± 0.046	0.257 ± 0.045
≥5	0	0.067 ± 0.037	0.171 ± 0.045	0.517 ± 0.048
M	0.281 ± 0.043	0.161 ± 0.036	0.169 ± 0.047	0.155 ± 0.038
n	179	202	158	150

End Quarter Size Class	Initial Size Class			
HAN-High	*1*	*2*	*3*	*4*
1	0.257 ± 0.051	0.022 ± 0.017	0.007 ± 0.007	0
2	0.3 ± 0.074	0.292 ± 0.059	0.046 ± 0.025	0.069 ± 0.048
3	0.152 ± 0.064	0.385 ± 0.061	0.306 ± 0.073	0.081 ± 0.049
4	0.016 ± 0.015	0.184 ± 0.054	0.335 ± 0.062	0.167 ± 0.056
≥5	0	0.021 ± 0.014	0.264 ± 0.065	0.635 ± 0.084
M	0.275 ± 0.064	0.096 ± 0.055	0.043 ± 0.018	0.048 ± 0.046
n	160	101	86	58

Table 7 Mean *Montipora* transition matrices for Waikīkī -Low, Hanauma Bay-Low, Waikīkī -High, and Hanauma Bay-High modules with standard error. Matrices show the initial size class vs the end quarter size class, mortality (*M*), and total number of observations in a given initial size class (*n*). Gray diagonal lines are the lines of stasis where shrinkage occurs above the line and growth occurs below the line.

		Initial Size Class			
	WAI-Low	*1*	*2*	*3*	*4*
End Quarter Size Class	1	0.497 ± 0.099	0.315 ± 0.135	0	0
	2	0.246 ± 0.069	0.296 ± 0.119	0.286 ± 0.171	0
	3	0	0.222 ± 0.114	0.143 ± 0.132	0
	4	0	0	0.286 ± 0.171	0.333 ± 0.272
	≥5	0	0	0.143 ± 0.132	0.333 ± 0.272
	M	0.257 ± 0.106	0.167 ± 0.111	0.143 ± 0.132	0.333 ± 0.272
	n	31	15	7	3

		Initial Size Class			
	HAN-Low	*1*	*2*	*3*	*4*
End Quarter Size Class	1	0.465 ± 0.085	0.031 ± 0.03	0	0
	2	0.347 ± 0.08	0.301 ± 0.092	0	0
	3	0.01 ± 0.01	0.476 ± 0.118	0.306 ± 0.113	0.031 ± 0.029
	4	0	0.007 ± 0.007	0.611 ± 0.122	0.25 ± 0.153
	≥5	0	0.021 ± 0.02	0	0.469 ± 0.168
	M	0.179 ± 0.058	0.163 ± 0.072	0.083 ± 0.08	0.25 ± 0.153
	n	66	34	18	13

Montipora

		Initial Size Class			
	WAI-High	*1*	*2*	*3*	*4*
End Quarter Size Class	1	0.417 ± 0.13	0.1 ± 0.095	0.125 ± 0.108	0
	2	0.208 ± 0.11	0.617 ± 0.118	0	0
	3	0	0.2 ± 0.105	0.25 ± 0.217	0
	4	0	0	0.375 ± 0.207	0.5 ± 0.25
	≥5	0	0	0.25 ± 0.217	0.5 ± 0.25
	M	0.375 ± 0.133	0.083 ± 0.054	0	0
	n	16	18	5	4

		Initial Size Class			
	HAN-High	*1*	*2*	*3*	*4*
End Quarter Size Class	1	0.445 ± 0.065	0.027 ± 0.014	0	0
	2	0.422 ± 0.078	0.415 ± 0.066	0.105 ± 0.038	0.019 ± 0.018
	3	0.01 ± 0.007	0.422 ± 0.062	0.335 ± 0.073	0.093 ± 0.044
	4	0	0.034 ± 0.014	0.378 ± 0.083	0.329 ± 0.1
	≥5	0	0	0.059 ± 0.027	0.421 ± 0.11
	M	0.124 ± 0.04	0.102 ± 0.034	0.123 ± 0.065	0.138 ± 0.077
	n	149	138	77	42

Table 8 Mean *Porites* transition matrices for Waikīkī -Low, Hanauma Bay-Low, Waikīkī -High, and Hanauma Bay-High modules with standard error. Matrices show the initial size class vs the end quarter size class, mortality (*M*), and total number of observations in a given initial size class (n). Gray diagonal lines are the lines of stasis where shrinkage occurs above the line and growth occurs below the line.

		Initial Size Class			
	WAI-Low	*1*	*2*	*3*	*4*
End Quarter Size Class	1	0.269 ± 0.117	0	0	0
	2	0.423 ± 0.132	0.146 ± 0.083	0.133 ± 0.088	0.036 ± 0.034
	3	0	0.438 ± 0.108	0.322 ± 0.101	0.036 ± 0.034
	4	0.077 ± 0.074	0.125 ± 0.07	0.289 ± 0.097	0.369 ± 0.103
	≥5	0	0.062 ± 0.061	0.1 ± 0.07	0.452 ± 0.102
	M	0.231 ± 0.117	0.229 ± 0.098	0.156 ± 0.074	0.107 ± 0.075
	n	14	25	22	27

		Initial Size Class			
	HAN-Low	*1*	*2*	*3*	*4*
End Quarter Size Class	1	0.089 ± 0.07	0	0	0
	2	0.214 ± 0.11	0.306 ± 0.103	0.143 ± 0.079	0.045 ± 0.043
	3	0.071 ± 0.047	0.35 ± 0.11	0.213 ± 0.078	0.045 ± 0.043
	4	0.095 ± 0.071	0.046 ± 0.035	0.273 ± 0.084	0.303 ± 0.107
	≥5	0	0	0.107 ± 0.075	0.455 ± 0.125
	M	0.53 ± 0.115	0.298 ± 0.107	0.264 ± 0.096	0.152 ± 0.092
	n	24	35	30	23

Porites

		Initial Size Class			
	WAI-High	*1*	*2*	*3*	*4*
End Quarter Size Class	1	0.208 ± 0.11	0.036 ± 0.025	0	0
	2	0.25 ± 0.11	0.274 ± 0.072	0.118 ± 0.059	0.066 ± 0.052
	3	0	0.567 ± 0.089	0.396 ± 0.098	0.092 ± 0.056
	4	0	0.04 ± 0.027	0.316 ± 0.082	0.421 ± 0.107
	≥5	0	0	0.132 ± 0.063	0.329 ± 0.099
	M	0.542 ± 0.138	0.083 ± 0.051	0.038 ± 0.029	0.092 ± 0.056
	n	17	40	38	30

		Initial Size Class			
	HAN-High	*1*	*2*	*3*	*4*
End Quarter Size Class	1	0.289 ± 0.081	0.014 ± 0.013	0	0.018 ± 0.017
	2	0.55 ± 0.106	0.405 ± 0.096	0	0.071 ± 0.069
	3	0.039 ± 0.026	0.408 ± 0.106	0.417 ± 0.101	0.036 ± 0.023
	4	0	0.085 ± 0.035	0.377 ± 0.095	0.318 ± 0.093
	≥5	0	0	0.147 ± 0.081	0.543 ± 0.104
	M	0.122 ± 0.053	0.088 ± 0.057	0.059 ± 0.039	0.014 ± 0.014
	n	33	42	29	29

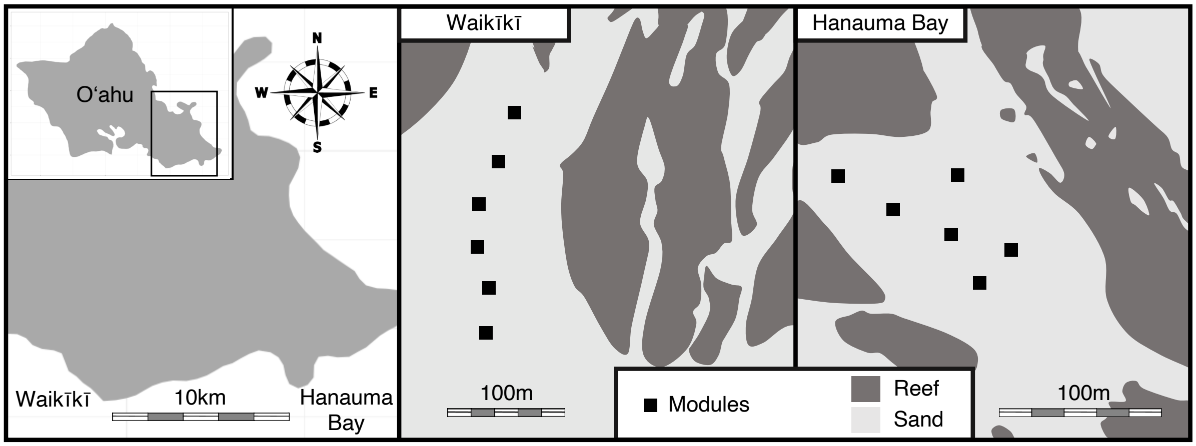


Fig. 1 Maps of Waikīkī and Hanauma Bay study sites on the south shore of O‘ahu, Hawai‘i.

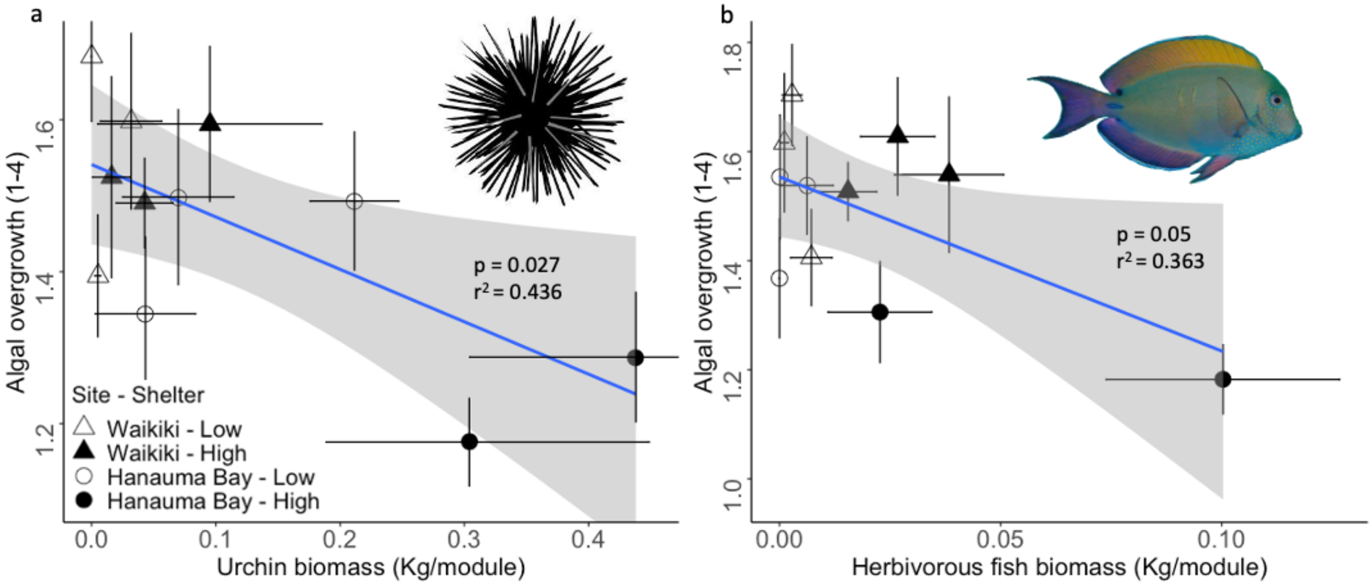


Fig. 2 Regressions of urchin biomass (a) and herbivorous fish biomass (b) as predictors of benthic algal overgrowth (defined in text). Individual points represent the grand mean of all surveys for each individual module throughout the study, identified by site and shelter treatment. Error bars are standard errors, and shaded areas represent 95% confidence intervals across 10 surveys per module.

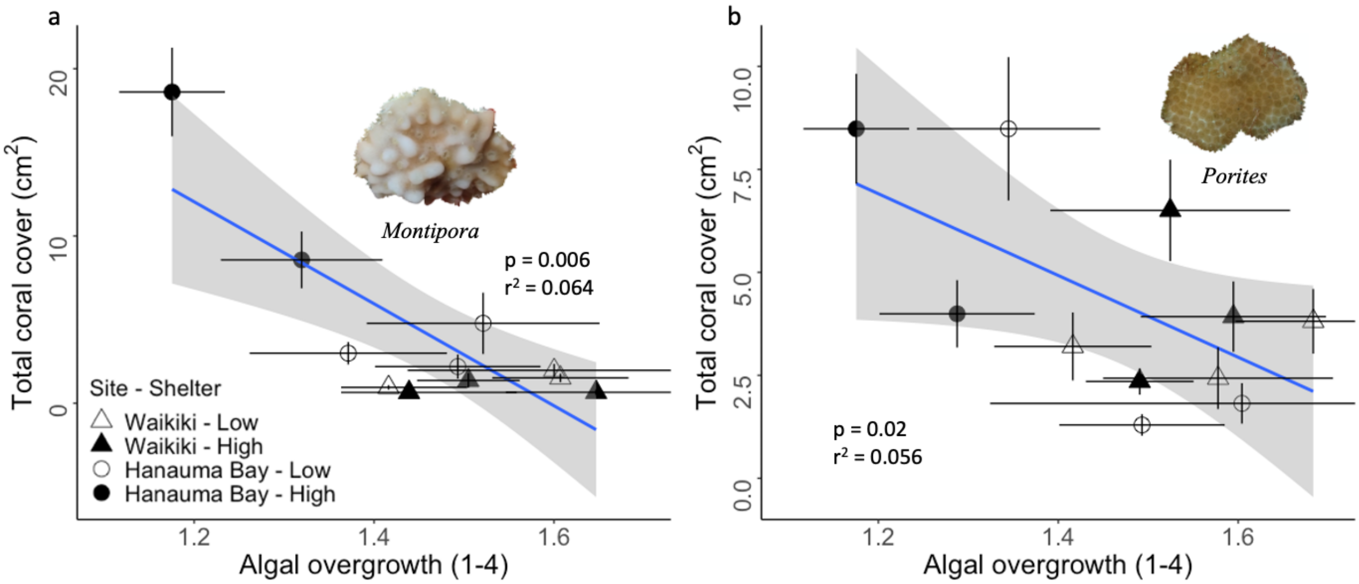


Fig. 3 Regressions of benthic algal overgrowth (defined in text) as a predictor of total cover of *Montipora* (a) and *Porites* (b) for all colonies 1-20 mm in diameter. Individual points represent the grand mean of all surveys for each individual module throughout the experiment, identified by site and shelter treatment. Error bars are standard errors, and shaded areas represent 95% confidence intervals across 10 surveys per module.

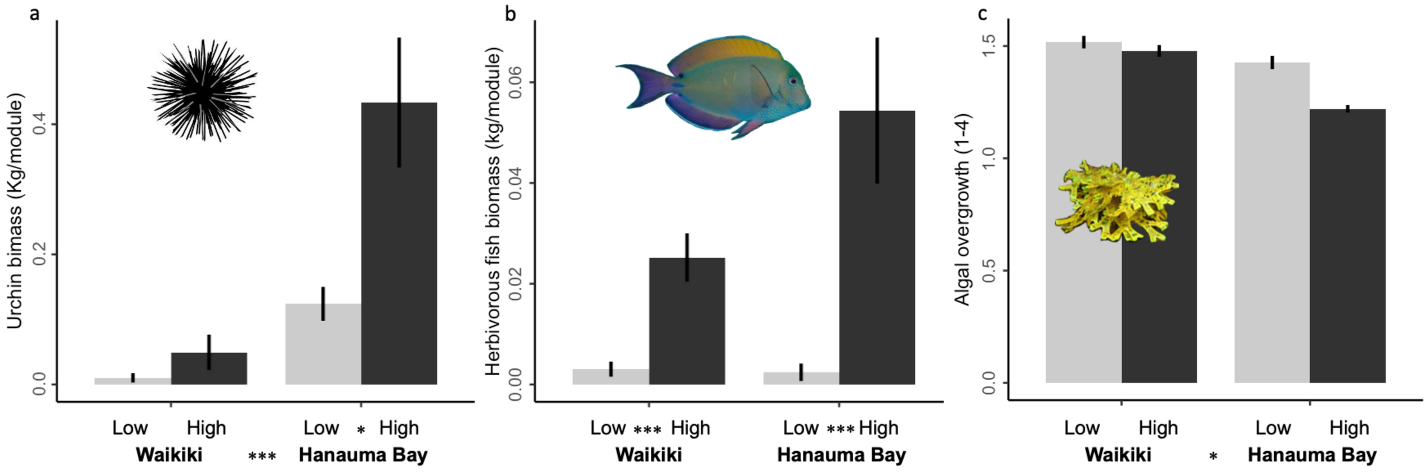


Fig. 4 Urchin biomass (a), herbivorous fish biomass (b), and benthic algal overgrowth (c) among the four experimental treatments averaged throughout the study (grand means with standard error bars, n = 3 modules each, except for one high-shelter module excluded from Hanauma Bay). Asterisks between shelter comparisons (low and high) and site comparisons (Waikīkī and Hanauma Bay) indicate significant differences (* $p<0.05$, *** $p<0.001$, see text for model results). Algal overgrowth is defined in the text.

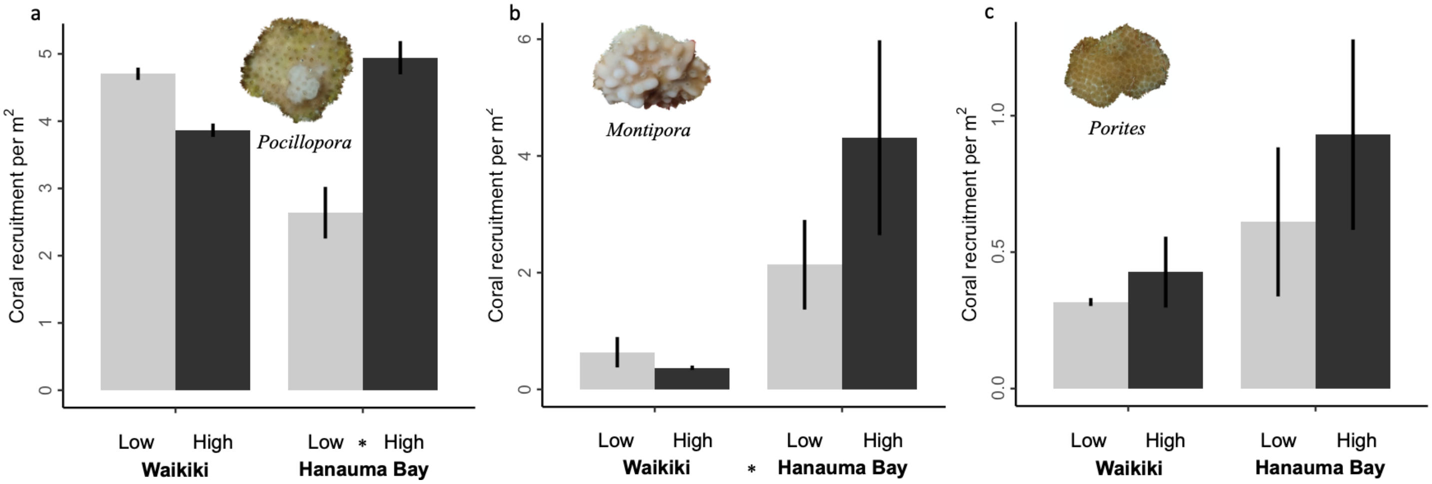


Fig. 5 Recruitment (number of new colonies per square meter) of *Pocillopora* (a), *Montipora* (b), and *Porites* (c) among the four experimental treatments averaged throughout the study (grand means with standard error bars, n = 3 modules each, except for one high-shelter module excluded from Hanauma Bay). Asterisks between specific shelter comparisons (low and high) and site comparisons (Waikīkī and Hanauma Bay) indicate significant differences (* $p<0.05$, see text for model results).

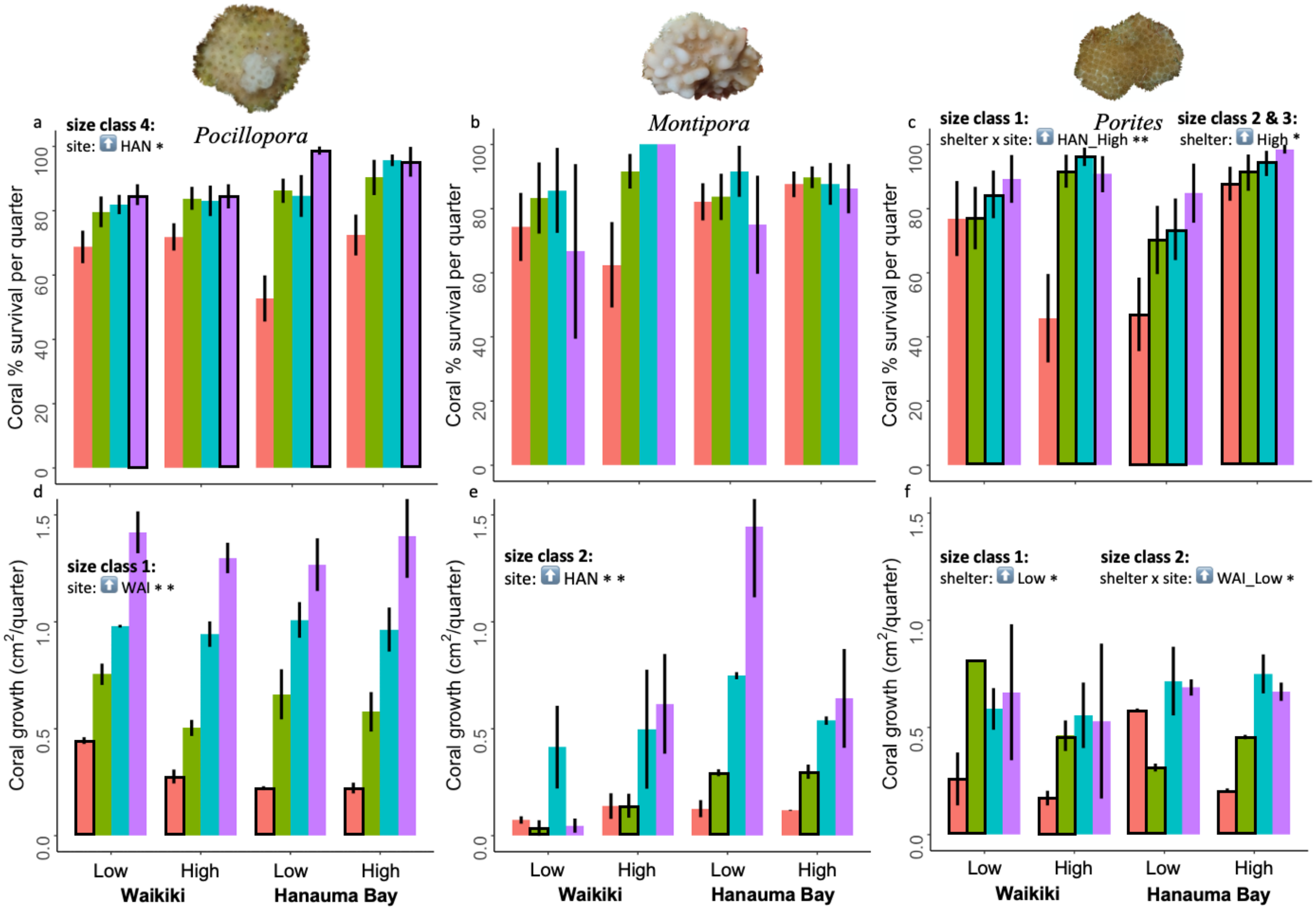


Fig. 6 Quarterly survival of *Pocillopora* (a), *Montipora* (b), and *Porites* (c), as well as quarterly growth of *Pocillopora* (d), *Montipora* (e), and *Porites* (f), among the four experimental treatments averaged throughout the study (grand means with standard error bars, n = 3 modules each, except for one high-shelter module excluded from Hanauma Bay). Survival and growth were calculated separately for each size class (1: 1-5 mm: red, 2: 6-10 mm: green, 3: 11-15 mm: blue, 4: 16-20 mm: purple). Bars outlined in black indicate size classes where significant differences were detected. Size-class specific significant differences between shelter (low vs. high) and site (WAI = Waikīkī, HAN = Hanauma Bay) treatments, including interactions, are also indicated: upward arrow indicates that treatment was significantly greater (*$p<0.05$, **$p<0.01$, see text for statistical test results).

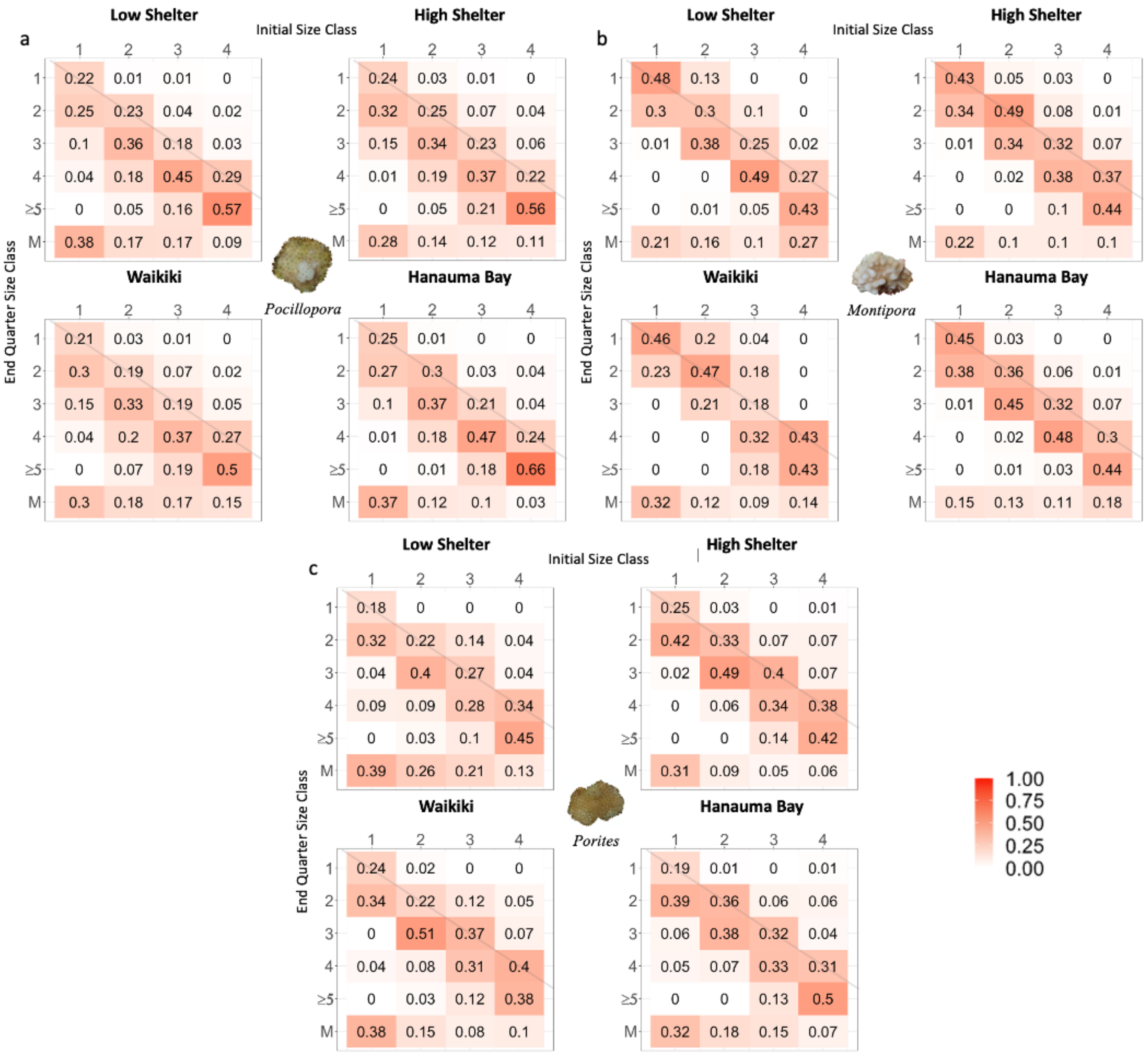


Fig. 7 Heat maps reflecting demographic transition matrices for *Pocillopora* (a), *Montipora* (b), and *Porites* (c) comparing low shelter vs. high shelter and Waikīkī vs. Hanauma Bay throughout the experiment. Columns represent the 5 mm diameter size class at the beginning of a quarter while rows represent the size class at the end of the quarter. Cells contain mean probabilities of either growth (below the diagonal line), stasis (along the diagonal), or shrinkage (above the diagonal) for each possible size-class transition. The second to last row shows cases where corals grew to greater than 20 mm in diameter. The last row (*M*) shows percent mortality during each transition, such that the sum of values in each column equals 1.0.

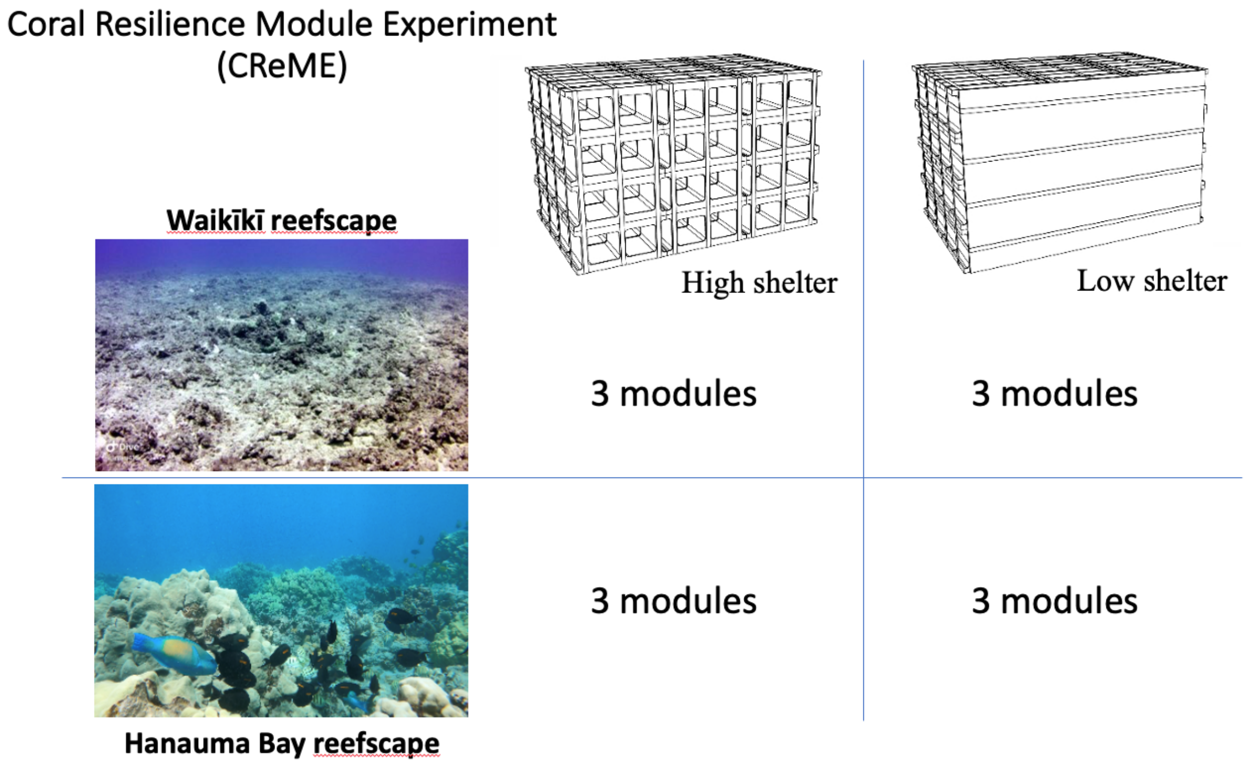
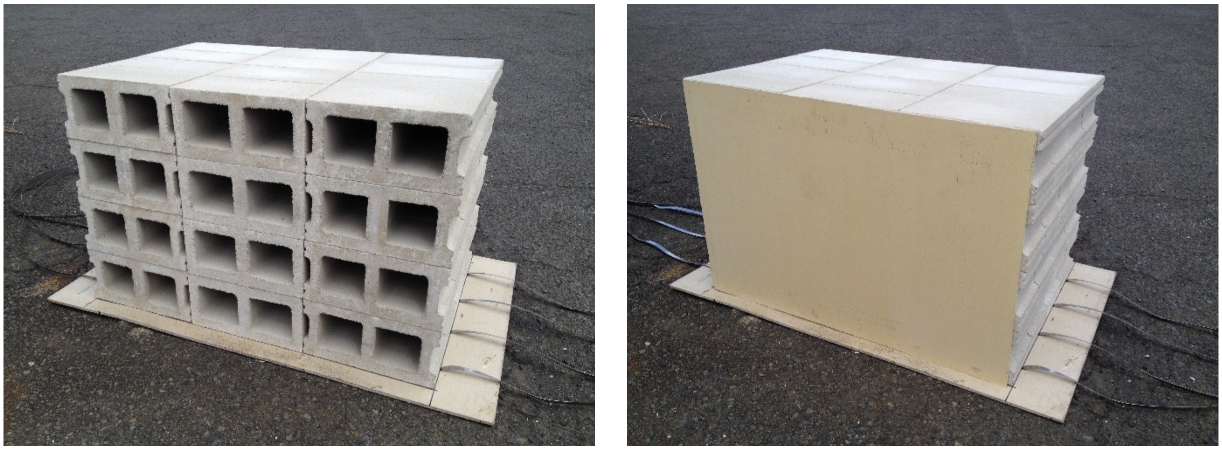


Fig. 8 Graphic illustrating the factorial experimental design of the CReME project, with high and low shelter modules at both Waikīkī (relatively degraded reef) and Hanauma Bay (relatively healthy reef).



high-shelter module:

Low-shelter module:

Fig. 9. Modules onshore before banding and deployment. Note the 16 tiny (1 × 0.5 cm each), 8 small (9 × 2 cm each), and 24 large holes (15 × 14 cm each) holes on the high-shelter module, that concrete fiberboard was used to cover the holes in the low-shelter module, and that the holeless sides of modules where corals were monitored are scalloped.

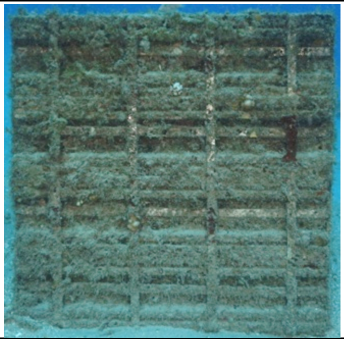
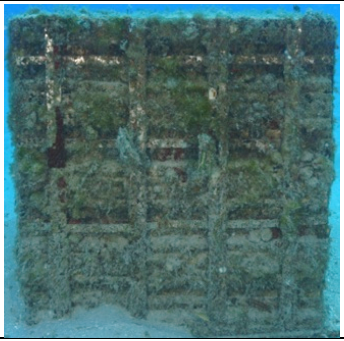
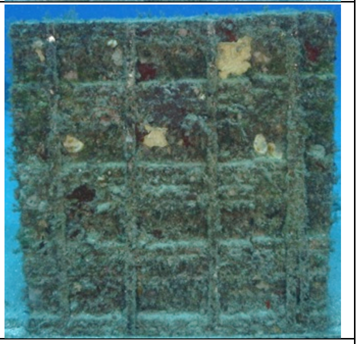
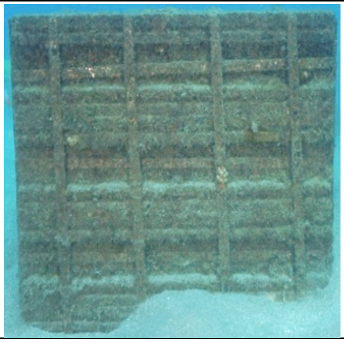
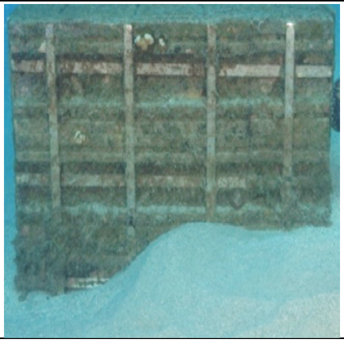
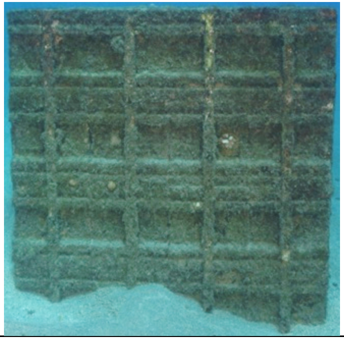
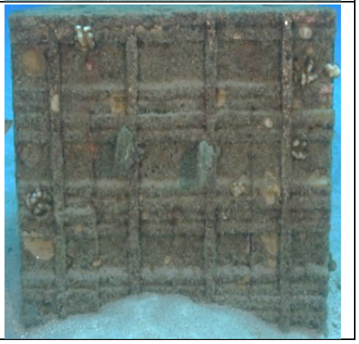
Waikīkī:	shallowest	mid-depth	deepest
low shelter			
high shelter			
Hanauma Bay:			
low shelter			
high shelter	excluded from analysis because of sand scour		

Fig. 10 Photos near the end of the experiment of experimental modules at the relatively degraded reef of Waikīkī (9/26/2019) and the relatively healthy reef of Hanauma Bay (9/24/2019). Turf, macroalgae, and encrusting sessile benthos (e.g., sponges, ascidians, and bryozoans), all of which displace corals, were much more prevalent at Waikīkī, whereas larger coral colonies were more prevalent at Hanauma Bay.

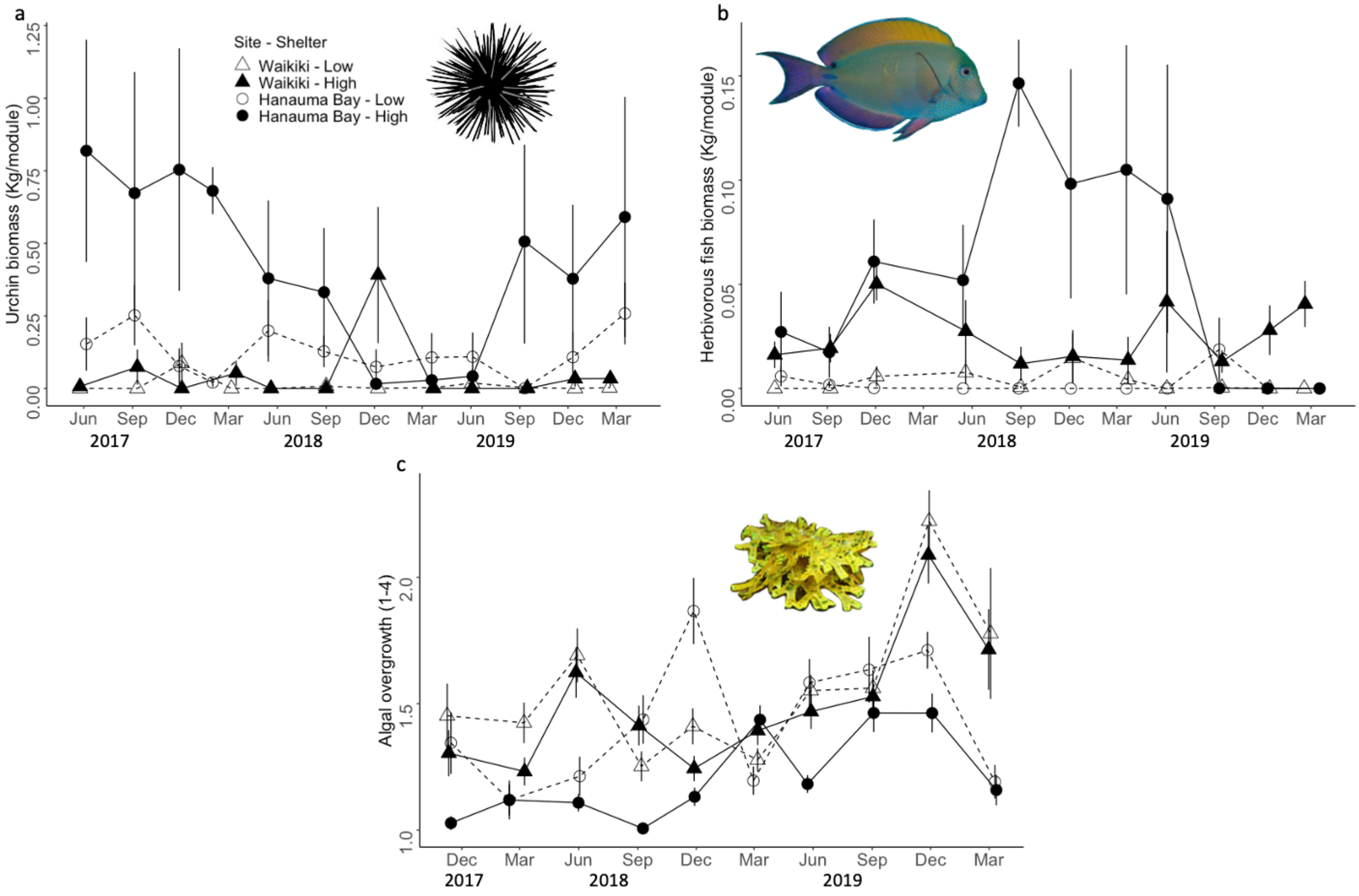


Fig. 11 Time series plots for mean urchin biomass (a), mean herbivorous fish biomass (b), and mean algal overgrowth (c). Triangle points represent module means for Waikīkī and circle points represent module means for Hanauma Bay. White points represent module means for low shelter modules whereas black points represent module means for high shelter modules. Note that all modules were deployed in the summer of 2016, and that algal overgrowth measurements started at the third sampling interval of this study.

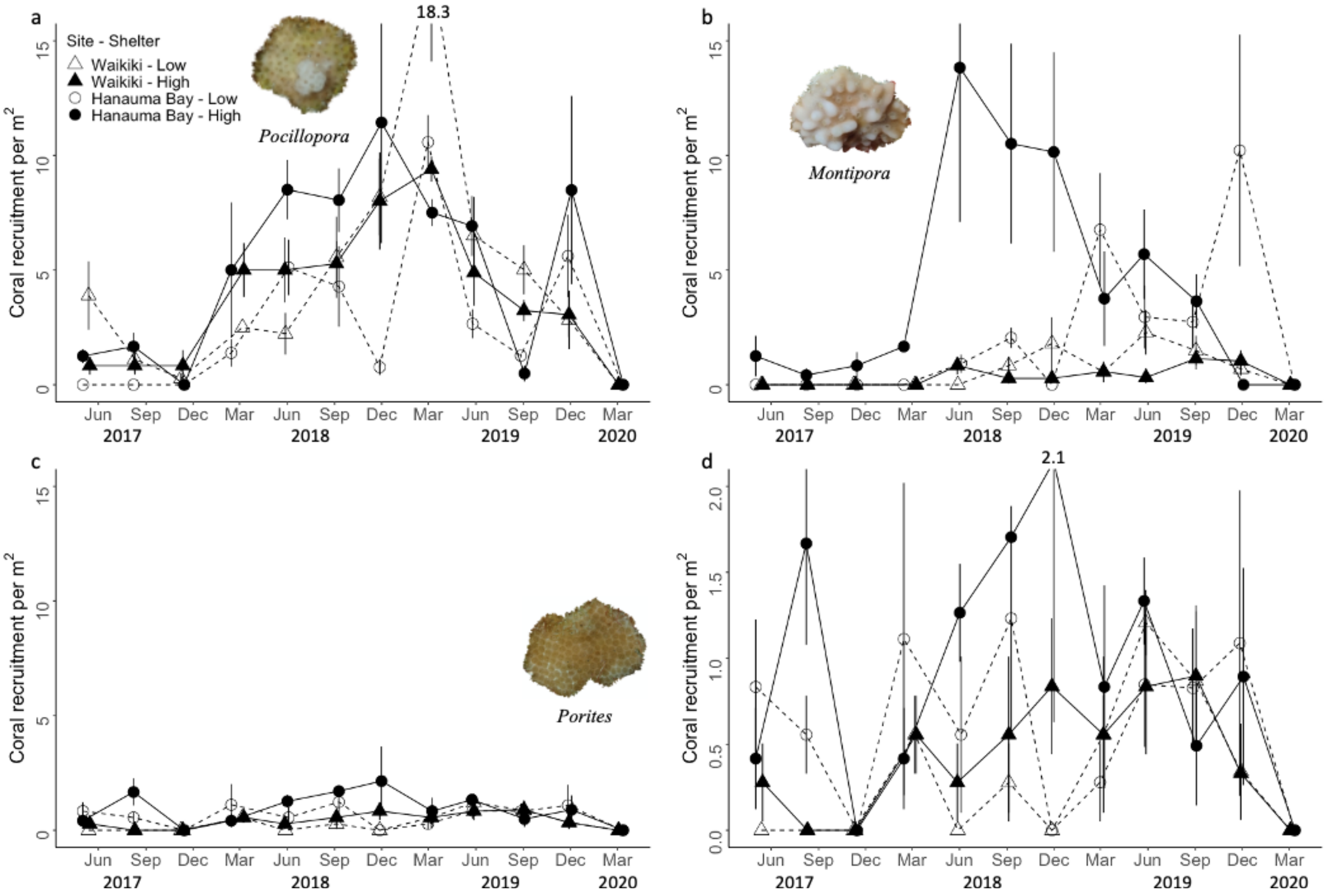


Fig. 12 Time series plots for recruitment (mean ± standard error, n = 3 modules each except for high-shelter modules at Hanauma Bay) of *Pocillopora* (a), *Montipora* (b), *Porites* (c), and *Porites* re-scaled for easier interpretation (d). Triangles represent Waikīkī, circles represent Hanauma Bay, white symbols represent low shelter modules, and black symbols represent high shelter modules.

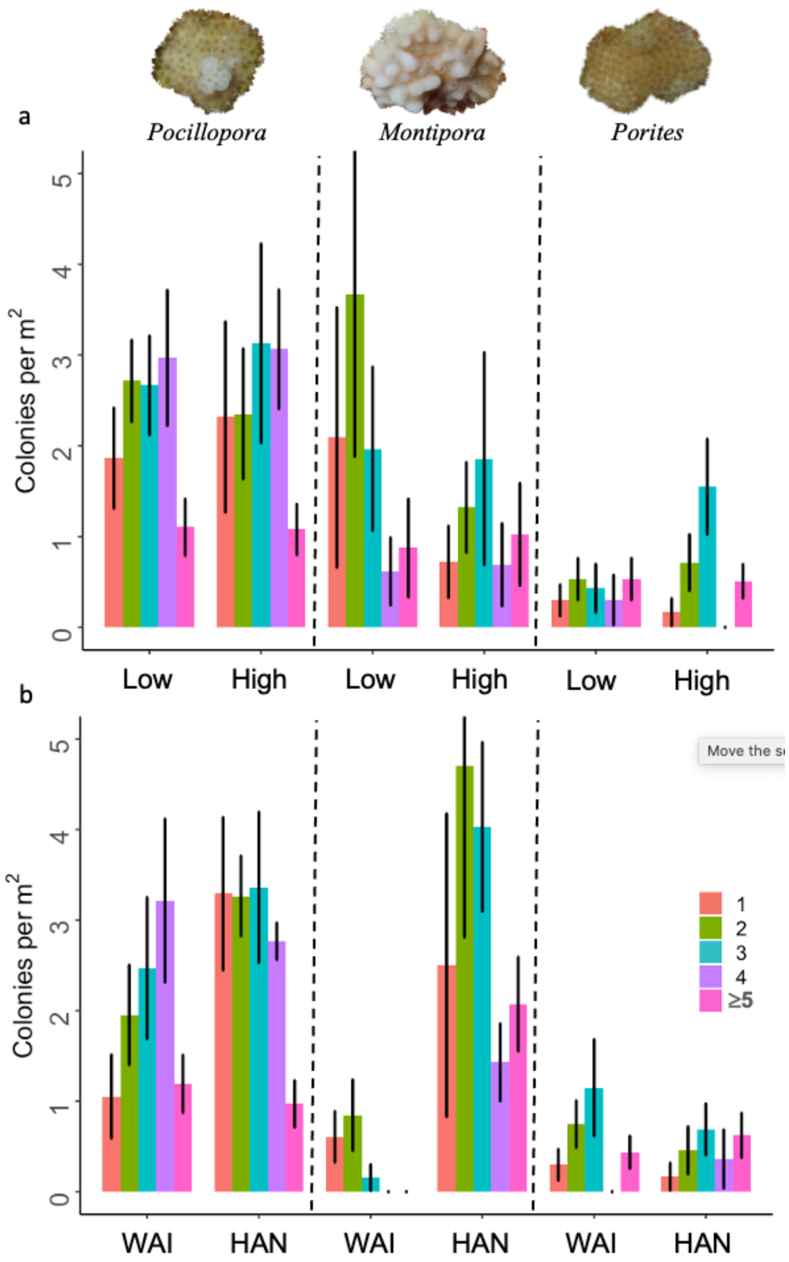


Fig. 13 Coral colony abundance per meter squared of substrate at the last coral census during the study period. *Pocillopora*, *Montipora*, and *Porites* abundance are illustrated by (a) low or high shelter and by (b) study sites at Waikīkī (WAI) and Hanauma Bay (HAN).

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