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ARTICLE

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Priority effects in coral–macroalgae interactions can drive alternate community paths in the absence of top-down control

Thomas C. Adam[1] | **Sally J. Holbrook**[1,2] | **Deron E. Burkepile**[1,2] | **Kelly E. Speare**[2] | **Andrew J. Brooks**[1] | **Mark C. Ladd**[1,3] | **Andrew A. Shantz**[4] | **Rebecca Vega Thurber**[5] | **Russell J. Schmitt**[1,2]

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

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

[3]NOAA – National Marine Fisheries Service, Southeast Fisheries Science Center, Key Biscayne, Florida, USA

[4]Florida State University Coastal and Marine Laboratory, St. Teresa, Florida, USA

[5]Department of Microbiology, Oregon State University, Corvallis, Oregon, USA

Correspondence
Thomas C. Adam
Email: thomas.adam@lifesci.ucsb.edu

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Abstract

The outcomes of species interactions can vary greatly in time and space with the outcomes of some interactions determined by priority effects. On coral reefs, benthic algae rapidly colonize disturbed substrate. In the absence of top-down control from herbivorous fishes, these algae can inhibit the recruitment of reef-building corals, leading to a persistent phase shift to a macroalgae-dominated state. Yet, corals may also inhibit colonization by macroalgae, and therefore the effects of herbivores on algal communities may be strongest following disturbances that reduce coral cover. Here, we report the results from experiments conducted on the fore reef of Moorea, French Polynesia, where we: (1) tested the ability of macroalgae to invade coral-dominated and coral-depauperate communities under different levels of herbivory, (2) explored the ability of juvenile corals (*Pocillopora* spp.) to suppress macroalgae, and (3) quantified the direct and indirect effects of fish herbivores and corallivores on juvenile corals. We found that macroalgae proliferated when herbivory was low but only in recently disturbed communities where coral cover was also low. When coral cover was <10%, macroalgae increased 20-fold within 1 year under reduced herbivory conditions relative to high herbivory controls. Yet, when coral cover was high (50%), macroalgae were suppressed irrespective of the level of herbivory despite ample space for algal colonization. Once established in communities with low herbivory and low coral cover, macroalgae suppressed recruitment of coral larvae, reducing the capacity for coral replenishment. However, when we experimentally established small juvenile corals (2 cm diameter) following a disturbance, juvenile corals inhibited macroalgae from invading local neighborhoods, even in the absence of herbivores, indicating a strong priority effect in macroalgae–coral interactions. Surprisingly, fishes that initially facilitated coral recruitment by controlling algae had a net negative effect on juvenile corals via predation.

Corallivores reduced the growth rates of corals exposed to fishes by ~30% relative to fish exclosures, despite increased competition with macroalgae within the exclosures. These results highlight that different processes are important for structuring coral reef ecosystems at different successional stages and underscore the need to consider multiple ecological processes and historical contingencies to predict coral community dynamics.

KEYWORDS
alternate stable states, competition, corallivory, density dependence, herbivory, indirect effects, *Lobophora*, macroalgae, predation, recruitment, resilience, succession

INTRODUCTION

In many ecosystems, large consumers (predators and herbivores) have disproportionate impacts on community structure and dynamics (Estes et al., 2011). Loss of these consumers can result in irreversible shifts in ecosystem state, with far reaching consequences for ecosystem function and the provisioning of ecosystem goods and services (Burkepile & Vega Thurber, 2019; Folke et al., 2004). Yet, it can be difficult to predict how ecosystems will respond to species losses (Doak et al., 2008), in part because the strengths of species interactions can vary greatly in time and space (Chamberlain et al., 2014). Top-down impacts of consumers, in particular, can be highly dependent on ecological context such as disturbance history (Reed et al., 2011), climate (Rasher et al., 2020), and community diversity (Nell et al., 2018). Therefore, predicting how ecosystems will respond to the loss of consumers requires identifying conditions when their impacts have a strong structuring effect versus conditions when other processes predominate.

On coral reefs, herbivorous fishes can exert strong pressure on benthic community structure by suppressing algae that can outcompete reef-building corals for space (Burkepile & Hay, 2006). When herbivores are lost to overfishing, coral reefs can undergo a phase shift from a coral- to a macroalgae-dominated state with reduced capacity to build reefs and provide habitat for other organisms (Hughes et al., 2010). These algal phase shifts often occur following large, coral-killing disturbances that liberate space for algae to colonize (Cheal et al., 2010; Graham et al., 2015; Hughes, 1994; Roff et al., 2015). Once macroalgae become abundant, several reinforcing feedbacks can operate to prevent coral recovery (Mumby & Steneck, 2008). For example, macroalgae can inhibit coral recruitment by suppressing the settlement of coral larvae and by killing newly settled coral recruits (Johns et al., 2018; Kuffner et al., 2006; Vermeij et al., 2009). Yet, when abundant, corals can also limit macroalgae, and consequently corals may not be easily displaced by algae in the absence of a disturbance (Aronson & Precht, 2006; McCook et al., 2001; Nugues & Bak, 2006). In addition to preempting space, established corals can inhibit the growth and expansion of macroalgae (De Ruyter van Steveninck et al., 1988) and can increase mortality rates of algae by concentrating grazing activity of herbivorous fishes (Mumby et al., 2007; Williams et al., 2001). Therefore, when abundant, both macroalgae and corals make it more difficult for their competitors to proliferate. Similar priority effects occur in a wide variety of marine and terrestrial ecosystems and can result in alternate community trajectories that depend on the initial colonization sequence following a disturbance (Chase, 2003; Connell & Slatyer, 1977; Fukami, 2015).

In addition to exerting strong top-down control on algal assemblages, many herbivorous fishes prey directly on corals or damage corals incidentally while feeding on algae (Bonaldo et al., 2014; Rotjan & Lewis, 2008). In fact, predation on corals by nominally herbivorous and corallivorous fishes can be strong enough to exclude corals from particular reef habitats (Littler et al., 1989; Miller & Hay, 1998; Neudecker, 1979), or restrict corals to refuges inaccessible to fishes (Lenihan et al., 2015; White & O'Donnell, 2010). Corals may be especially sensitive to predation during early life stages, when a single predation event can result in whole colony mortality (Penin et al., 2010). In addition, predation intensity on corals may increase with declining coral abundance, as coral predators concentrate their feeding on fewer coral colonies (Burkepile, 2012; Knowlton, 1992; Kopecky et al., 2021). Therefore, predation intensity on corals by herbivorous and corallivorous fishes could be especially important for determining the trajectory of benthic communities during the initial recovery period following a disturbance when the abundance of corals is low.

Here we describe the results of a field experiment to better understand how overfishing of herbivorous fishes influences the ability of macroalgae to invade coral-dominated and coral-depauperate communities. Additional field experiments tested whether juvenile corals can limit colonization by macroalgae and also quantified the net effects of herbivorous and corallivorous fishes on juvenile corals during a period of coral recovery. We hypothesized that, due to the presence of strong priority effects between corals and algae, macroalgae would only become abundant under conditions of low herbivory and low coral cover, and that the proliferation of algae under such conditions would prevent coral recruitment. In the absence of adult corals, we hypothesized that juvenile corals would be unable to suppress macroalgae and would benefit from herbivory. Therefore, the net effect of fishes on juvenile corals would be positive despite their negative consumptive effects on corals. Most of our predictions were upheld; however, we found that juvenile corals actually suppressed macroalgae and, as a result, the negative effect of fish predation outweighed the benefits of algal removal.

METHODS

Site description and recent history

All experiments were conducted on the oligotrophic fore reef on the north shore of Moorea, French Polynesia (17°28.39′ S, 149°49.06′ W; Appendix S1: Figure S1). Moorea, in the central south Pacific, is a volcanic high island with a ~60 km perimeter and an offshore barrier reef that encloses a shallow lagoon. The fore reef of Moorea has experienced multiple cycles of disturbance and recovery over the past 40 years, with reefs consistently recovering to a coral-dominated state following a disturbance (Adjeroud et al., 2009; Holbrook et al., 2018; Kayal et al., 2018; Lamy et al., 2016; Moritz et al., 2021). During 2007–2009, the reefs experienced an outbreak of the coral-eating crown-of-thorns sea star (*Acanthaster planci*; hereafter "COTS") followed by a strong cyclone in 2010, that together reduced coral cover from ~40% to ~1% on the north shore fore reef by 2011 (Adam et al., 2011, 2014). In the decade that followed, these north shore reefs recovered rapidly, with coral cover continuing to increase after reaching predisturbance levels in 2015 (Holbrook et al., 2018; Moritz et al., 2021). The rapid recovery was driven by high recruitment of the branching coral *Pocillopora* spp. (Holbrook et al., 2018). We initiated the field experiments described here between 2011 and 2018, during this dynamic period of recovery. Throughout the study, herbivorous fishes were abundant, nutrients were low, and reefs had little macroalgae (Appendix S1: Figures S2 and S3).

Experiment I: Effect of coral cover and herbivory on proliferation of macroalgae following a disturbance

Experimental setup

We quantified the abundance of macroalgae across a gradient of coral cover and herbivory on 64, 1.25 m^2 plots at 12 m depth on the north shore fore reef. Plots were initially characterized in July 2018 when corals were abundant (mean cover = 57%; range = 47%–68%) and macroalgae were rare (mean cover = 1%; range = 0%–8%). Plots were then manipulated to test the effects of herbivores, nutrients, and disturbance on coral and algal communities (see Appendix S2 for full details of experimental design), and the abundance of macroalgae was assessed one-year postmanipulation.

Herbivore pressure was manipulated using exclosures with different size openings to create a gradient in herbivory that mimics the effects of different levels of fishing pressure (Holbrook et al., 2016; Schmitt et al., 2019). Using plastic coated, galvanized wire mesh we created the following treatments: (1) No Herbivory (2.5 cm × 2.5 cm openings); (2) Low Herbivory (5 cm × 5 cm openings); (3) Medium Herbivory (7.5 cm × 7.5 cm openings); and (4) High Herbivory (4 sides of 2.5 cm × 2.5 cm openings but no top). Exclosure dimensions were ~112 cm × 112 cm × 50 cm (L × W × H). Fish biomass at our site was dominated by herbivores (Appendix S1: Figure S4 and Table S1), but our exclosures also reduced access by other fishes including coral predators. Therefore, our herbivory treatments represent a gradient in overall consumer pressure.

In addition to herbivory, we also manipulated nutrients. Half of the plots were assigned to a nutrient enrichment treatment. Plots were enriched with 175 g of Osmocote (19-6-12, N-P-K) slow-release fertilizer placed in 15 cm diameter polyvinyl chloride (PVC) tubes with 10, 1.5 cm holes drilled into them ($N = 5$ enrichment tubes per exclosure). Fertilizer tubes were replaced every ~12 weeks. Nutrient enrichment resulted in ~2–4-fold increases in water column concentrations of ammonium, nitrate plus nitrite, and phosphate (Becker et al., 2021). In addition, tissue from the brown macroalga, *Lobophora* spp., was significantly elevated in nitrogen in the enriched plots relative to control plots, demonstrating that our enrichment treatment was effective in increasing nutrient availability for benthic organisms (Becker et al., 2021).

Coral cover was manipulated by assigning half of the 64 plots to an experimental disturbance treatment in which all branching corals (mostly *Acropora* and *Pocillopora* spp.) were removed and encrusting (mostly *Montipora* spp.) and mounding corals (mostly *Porites* spp.) were scrubbed with wire brushes to mimic the scouring impacts of a cyclone (Adam et al., 2014). Coral cover was also impacted by an unanticipated bleaching event resulting from a prolonged marine heat wave that began in December 2018 and peaked in May 2019, causing extensive coral mortality by July 2019 (Burgess et al., 2021; Speare et al., 2022). As a result of the bleaching event, 31 of 32 experimentally undisturbed plots experienced a decline in coral cover (mean decline = 16%; SD = 8.8) by July 2019. The decline in coral cover was independent of the level of herbivory (ANOVA, $F_{3,18} = 0.59$, $p = 0.63$) but was significantly related to nutrient enrichment, with coral cover declining ~40% less in the experimentally enriched plots compared with the unenriched plots (ANOVA, $F_{1,6} = 9.29$, $p = 0.02$; Appendix S2: Figure S2) for all levels of herbivory (Herbivory × Nutrient interaction: ANOVA, $F_{3,18} = 0.77$, $p = 0.52$). Ultimately, the bleaching event resulted in a wide range in coral cover in the plots that were not experimentally disturbed, with coral cover ranging from 26% to 57% after the event. By contrast, coral cover changed little in the experimentally disturbed plots, with a slight increase from 7% to 9% and no effect of herbivory (ANOVA, $F_{3,18} = 2.16$, $p = 0.13$) or nutrient enrichment (ANOVA, $F_{1,6} = 1.83$, $p = 0.22$) and no interaction between these two factors (ANOVA, $F_{3,18} = 0.20$, $p = 0.89$). Together, our experimental manipulation and the bleaching event resulted in a large range in coral cover among the plots after 1 year (range = 2%–57%). This allowed us to test whether coral cover and herbivory interacted to influence the proliferation of macroalgae.

The abundances of macroalgae and corals were assessed at the beginning of the experiment and after 1 year via photographic analysis. In each exclosure 64 photographs of the benthos were taken with a TG 5 Olympus Tough camera and then used to create high resolution photomosaics (Agisoft Metashape Professional Version 1.7.0). Photomosaics were uploaded to CoralNet (Beijbom et al., 2015) where we analyzed percent cover of benthic space holders using 225 evenly spaced point contacts per photomosaic, with all points identified by a trained observer. Corals and macroalgae were identified to genus or species level. In addition, for macroalgae in the genus *Lobophora*, we distinguished encrusting or prostrate forms from the three-dimensional foliose form that develops under low grazing pressure (see Figure S3 in Appendix S2 for example photographs of the two forms).

Data analysis

We hypothesized that macroalgae would only become abundant under conditions of low herbivory and low coral cover. To test this, we fitted linear mixed-effects models using the *lme4* package in R (Bates et al., 2015). We accounted for the nested and blocked study design by including "plot" nested in "block" as a random effect. In addition to the main effects of herbivory, coral cover, and nutrients, we also tested for interactions between these factors on the abundance (% cover) of macroalgae. Cover of macroalgae was log-transformed to homogenize variances. Models were fitted with restricted maximum likelihood (REML) with *p*-values calculated using type II Wald F-tests and degrees of freedom estimated via the Kenward–Roger's method (Kenward & Roger, 1997).

Experiment II: Effect of macroalgae on coral recruitment

Experimental setup

To understand the effect of macroalgae on coral recruitment, we quantified coral recruitment to two haphazardly placed 10 cm × 10 cm limestone tiles secured to the reef within each of the 64 1.25 m^2 herbivore exclosures described in *Experiment I*. During June and July 2019 (~1 year postdeployment), each tile was removed and brought back to the laboratory. Tiles were kept in running sea water for up to 24 h and all coral recruits (living and dead) were counted on each tile surface (bottom, side, and top) under a dissecting light microscope at ×15–20 magnification. In this experiment we were interested in the effects of macroalgae, but not predation, on coral recruitment, so we focused on the bottom tile surface where corals are protected from predation (Brandl & Bellwood, 2016; Doropoulos et al., 2016; Edmunds et al., 2014; Price, 2010). In addition to quantifying recruitment on tiles, we also counted and sized all juvenile corals (1–5 cm diameter) on natural substrate in each of the 64 1.25 m^2 exclosures after 1 year. Unlike the recruits identified on the bottom of settlement tiles, once corals are visible on the reef they have grown out of their cryptic settlement locations and therefore are susceptible to predation by fishes.

Data analysis

Because most tiles had either zero or one coral recruit we treated recruitment as binary and used logistic regression to test whether the probability of successful recruitment (i.e., a tile had at least one living coral recruit) was related to the abundance of macroalgae. Because macroalgae were patchily distributed within and among the 1.25 m^2 exclosures, we quantified the percentage cover of macroalgae in a 50-cm radius from the center of each settlement tile. Our analyses focused on the foliose form of the brown macroalga *Lobophora* spp. (hereafter "*Lobophora*"), which was the dominant genus of macroalgae in the exclosures after 1 year (see *Results*). In addition to testing for an association between *Lobophora* and coral recruitment to settlement tiles, we used linear mixed-effects models to test whether the abundance of juvenile corals (*Pocillopora* spp., hereafter "*Pocillopora*") on natural substrate was related to the abundance (% cover) of *Lobophora* in an exclosure. For this analysis, we focused on the 32 plots where coral had been experimentally removed at the beginning of the experiment to ensure that the juvenile corals reflected recruitment during the experimental period. However, the relatively large size of these corals (mean diameter = 2.6 cm; SD = 0.95 cm) suggests that most juvenile corals had probably settled to cryptic surfaces (cracks, crevices, etc.) in our plots prior to our manipulation and only became visible to us as they grew out of these locations (see Doropoulos et al., 2022; Mumby et al., 2016). Finally, to test whether fish consumers had an overall impact on the size structure of juvenile corals we used a linear mixed-effects model to test whether the mean size of these juvenile corals varied among the four herbivory treatments. Because half of our plots was experimentally enriched with nutrients, we also tested for an effect of nutrients in all analyses. Predicted means and SEs from linear mixed-effects models were calculated using the *emmeans* package in R (Lenth, 2020).

Experiment III: Effect of juvenile corals on colonization of macroalgae

Experimental setup

To test whether juvenile *Pocillopora* corals could suppress macroalgae and whether this was density dependent, we experimentally transplanted different densities of juvenile *Pocillopora* corals to the fore reef in full herbivore exclosures and quantified the amount of macroalgae that colonized after 2 years, beginning in July 2014. We established four density treatments, with 0, 1, 2, or 4 juvenile *Pocillopora* corals transplanted to initially bare 15 cm × 15 cm terra cotta tiles. These densities span the range of densities observed during the initial stages of coral recovery following the large coral-killing disturbances that reduced coral cover from ~40% to ~1% on the north shore fore reef from 2007 to 2010, and are well within the maximum numbers of Pocilloporid settlers to terra cotta tiles of the same size deployed during this period of coral recovery (Edmunds, 2018). For tiles with <4 corals, a 2.2 cm diameter glass marble was affixed in place of each "missing coral" as a physical control. Juvenile corals between 2 and 3 cm in diameter were chipped from the reef with a rock hammer and chisel and brought back to the laboratory where they were kept in running seawater before being affixed to tiles with underwater epoxy (Z-Spar A-788 Splash Zone Epoxy). Before deployment in the field each tile was enclosed in a 20 cm × 20 cm × 13 cm cage with 2.5 cm mesh size or placed within a cage control with a cage bottom and two cage sides but no top that allowed access by herbivorous fishes. Corals were kept in the laboratory for <24 h, with no apparent handling mortality. Each treatment was replicated 10 times in a randomized block design.

Data analysis

Upon termination of the experiment two perpendicular measurements of diameter were taken for all previously transplanted juvenile corals. In addition, all macroalgae that had colonized the tiles were identified and weighed. For each replicate, areal coverage of coral was calculated by summing the planar area of all corals on a tile, estimated as the area of an ellipse. Quantile regression as implemented in the *quantreg* package in R (Koenker, 2020) tested whether the amount of algae (by weight) in a replicate was related to the areal coverage of coral at the end of the experiment. Quantile regression allowed us to test whether the upper quantiles of algal abundance were related to coral cover in addition to the median, a useful test for our wedge-shaped data in which the cover of macroalgae was consistently low when coral cover was high, but highly variable when coral cover was low (Cade & Noon, 2003).

Experiment IV: Effects of fish consumers on juvenile corals

Experimental setup

To test the effects of herbivorous and corallivorous fishes on juvenile corals, we quantified growth and survivorship of juvenile *Pocillopora* corals transplanted to the fore reef. Cages with the same size openings as in Experiment I were used to create the same gradient in herbivory, mimicking the effects of overfishing (Holbrook et al., 2016; Schmitt et al., 2019). We used a randomized block design with each block having three 37 cm × 37 cm × 12 cm cages with different size openings (No Herbivory: 2.5 cm × 2.5 cm; Low Herbivory: 5 cm × 5 cm; Medium Herbivory: 7.5 cm × 7.5 cm), an open treatment (High Herbivory) consisting of a cage bottom but no sides, and a cage control, which had a cage bottom and two cage sides but no top. Each cage (as well as replicates of the cage control and open treatment) contained four 15 cm × 15 cm terra cotta tiles with four juvenile *Pocillopora* corals affixed to each tile.

Juvenile corals between 1 and 3 cm in diameter were collected from the fore reef and affixed to tiles using the methods described for Experiment III. Corals were measured and photographed before being deployed in the field in August 2011. None of the 800 corals died within the first several days of the experiment and only 1% died within the first 4 months; therefore handling mortality was assumed negligible. A small number of corals (3.4%; 27 out of 800) was dislodged from the tiles during the experiment and they were excluded from further analyses. The experiment was sampled at 4-month intervals until its conclusion in July 2013. At each sampling interval, we photographed each coral with a ruler and assessed whether it was alive or dead. In addition, we recorded all competitive interactions with algae (defined as overgrowth or contact between upright algae and coral) and counted in situ the total number of conspicuous bite scars from excavating corallivores. At the conclusion of the experiment we measured the diameters of each coral using calipers, and we identified and weighed all macroalgae that had colonized any of the experimental tiles. To obtain a time series of coral growth, we used ImageJ 1.53 software (Schneider et al., 2012) to measure the diameters of each coral at 8 months and 16 months; growth was assessed as change in planar area.

Data analysis

For each replicate, we calculated the mean proportion of corals competing with algae, the mean number of bite scars observed per coral, and the mean growth and mortality rates. Comparison of coral growth and mortality between the open treatment and the cage control indicated no caging artifacts (Appendix S3: Figure S1), and cage controls were removed from further analyses. Differences among treatments were tested with linear mixed-effects models with block included as a random effect. Data on bite scars were log-transformed to homogenize variances.

RESULTS

Experiment I: Effect of coral cover and herbivory on proliferation of macroalgae following a disturbance

In the absence of herbivory, there was a strong, negative effect of coral cover on the abundance of macroalgae, a relationship that disappeared with increasing levels of herbivory (Figure 1; Herbivory × Coral Cover interaction, ANOVA, $F_{3,37.2} = 11.6$, $p < 0.0001$). Macroalgae were uniformly low under Medium and High Herbivory, with mean cover ~1% (Figure 1). By contrast, under No and Low Herbivory, macroalgae became abundant in plots with low coral cover, reaching ~25% cover when coral cover was <5%, but did not become abundant in exclosures with the highest coral cover (Figure 1). The dominant macroalgae in the No and Low Herbivory treatments were the foliose brown alga, *Lobophora*, which accounted for 73% of all macroalgae, followed by the calcified green algae, *Halimeda* spp. (21%). Other species of macroalgae, including *Caulerpa* spp., *Padina*

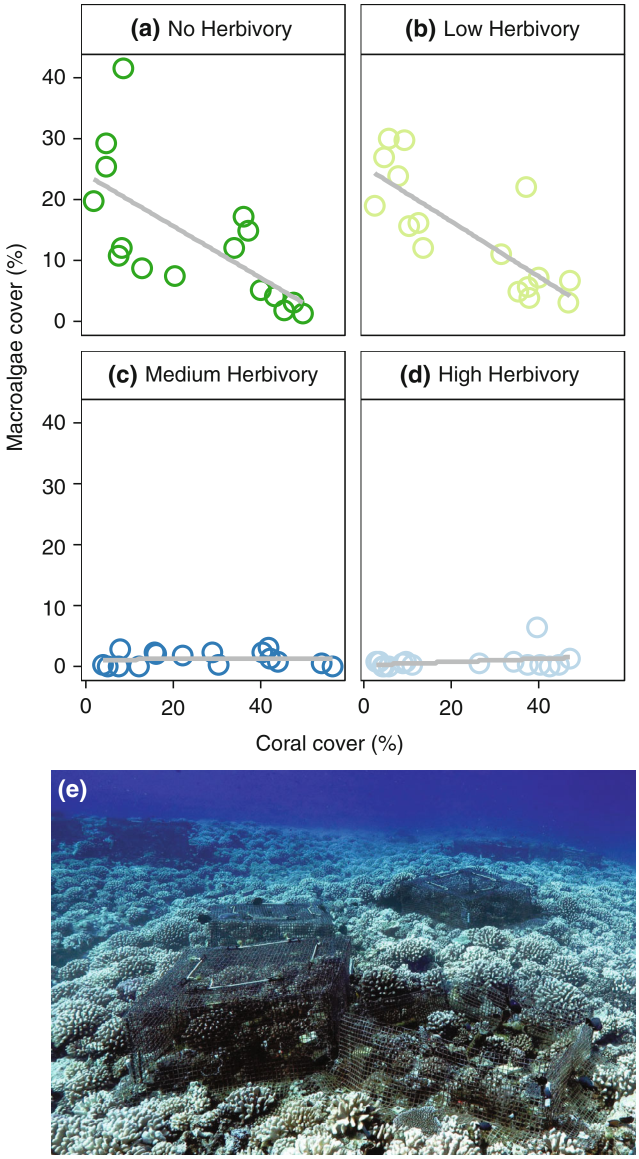

FIGURE 1 Cover of macroalgae after 1 year plotted against coral cover in Experiment I for the (a) No Herbivory, (b) Low Herbivory, (c) Medium Herbivory, and (d) High Herbivory treatments showing the significant interaction between herbivory and coral cover on the abundance of macroalgae ($N = 16$ exclosures for each herbivory treatment). Colors in all plots correspond to the four herbivory treatments. (e) Image of one of the experimental plots with four exclosures corresponding to the four different herbivory treatments (each exclosure is ~1.12 m × 1.12 m). Image credit: Andrew Thurber.

boryana, *Turbinaria ornata*, and *Sargassum pacificum* were often present in exclosures, but their cover in any replicate never exceeded 3%. There was an unexpected negative effect of nutrients on the abundance of macroalgae, with macroalgae being ~28% less abundant in experimentally enriched plots compared with unenriched plots (ANOVA, $F_{1,11.9} = 6.1$, $p = 0.03$). There were no significant interactions between nutrient enrichment and herbivory level or nutrient enrichment and coral cover on the abundance of macroalgae ($p > 0.1$ for all interactions involving nutrients; Appendix S2: Figure S4, Table S1).

Experiment II: Effect of macroalgae on coral recruitment

We observed a total of 41 coral recruits on 127 settlement tiles after 1 year of experimental treatment. Although we were unable to consistently identify coral recruits to genus, extensive prior work at a nearby site suggests that the majority of recruits were *Pocillopora* (Edmunds, 2018). *Lobophora* was abundant on many of the tiles and was frequently observed in close proximity to coral recruits (Figure 2a). The probability of recruitment was negatively related to the abundance of *Lobophora* within a 50-cm radius of a tile, although this result was only marginally significant (logistic regression, $p = 0.056$; Figure 2b). For recruitment to reef surfaces, 71% of juvenile corals observed on the benthos in the experimentally disturbed plots after 1 year were *Pocillopora*, with a total of 317 juvenile *Pocillopora* corals observed (mean = 9.9 corals per exclosure; SD = 5.4). *Lobophora* was sometimes observed overgrowing juvenile *Pocillopora* (Figure 2c), and the abundance of juvenile *Pocillopora* was negatively related to the abundance of *Lobophora* within an exclosure (ANOVA, $F_{1,23.4} = 5.5$, $p = 0.028$) (Figure 2d). Juvenile *Pocillopora* in the Medium and High Herbivory treatments frequently exhibited evidence of corallivory by fishes (Figure 2e), and there was a decline in the mean size of juvenile *Pocillopora* as the level of consumer pressure increased (ANOVA, $F_{3,13.9} = 4.0$, $p = 0.029$) (Figure 2f). Recruitment to tiles, recruitment to reef surfaces, and the size structure of juvenile corals were all unrelated to nutrient enrichment ($p > 0.2$ for all comparisons).

Experiment III: Effect of juvenile corals on colonization of macroalgae

Our manipulation of the density of juvenile *Pocillopora* colonies on otherwise bare substrate resulted in a wide range in coral cover after 2 years, with cover of *Pocillopora* ranging from 0% to 99% (median = 26%) (Figure 3). Macroalgae did not colonize any of the cage controls, demonstrating that herbivores completely prevented the establishment of macroalgae irrespective of coral density. By contrast, many of the replicates in the herbivore exclosures were colonized by a significant amount of macroalgae (Figure 3). The two most common taxa of macroalgae were *Amansia rhodantha*, and *Lobophora*, with *Turbinaria ornata*, *Sargassum pacificum*, *Hypnea* sp., and *Halimeda* spp. also observed in some cages. The total biomass of macroalgae was highly variable among replicates but was significantly negatively associated with the areal coverage of *Pocillopora* (Figure 3). Specifically, there was a negative relationship between the cover of *Pocillopora* and the median biomass of macroalgae (Figure 3), although this was only marginally significant (quantile regression, bootstrap $p = 0.09$). This negative relationship was much stronger when considering the upper (85th) quantile of macroalgae (Figure 3; quantile regression, bootstrap $p = 0.001$), indicating that the highest levels of macroalgae were only observed on substrate with low coral cover.

Experiment IV: Effects of fish consumers on juvenile corals

When access to juvenile corals by herbivorous fishes was reduced, juvenile corals experienced increased encounters with macroalgae. Approximately 83% of these encounters involved *Lobophora*, with juvenile corals ~nine times more likely to encounter *Lobophora* under reduced herbivory conditions compared with the High Herbivory treatment (ANOVA, $F_{3,27} = 8.8$, $p = 0.0003$, Figure 4a). Indeed, less than 3% of corals fully exposed to herbivores encountered *Lobophora*, yet 21% of corals in the reduced herbivory treatments were in contact with, or overgrown by *Lobophora* at some point during the 2-year experiment (Figure 4a). Encounters with *Lobophora* were associated with a 20% reduction in growth (ANOVA, $F_{1,517.6} = 9.70$, $p = 0.002$) and this was independent of the level of herbivory (Herbivory × *Lobophora* interaction, ANOVA, $F_{3,534.9} = 0.25$, $p = 0.86$) (Figure 4b). Encounters with *Lobophora* were also associated with more than a two-fold increase in mortality (Fisher's exact test, $p = 0.002$) (Figure 4c).

Fish frequently preyed on the experimental corals, resulting in conspicuous bite scars on the coral colonies. The mean number of bite scars on a coral colony during the first year of the experiment varied significantly among treatments (ANOVA, $F_{3,27} = 143.4$, $p < 0.0001$) with corals in the High Herbivory treatment having

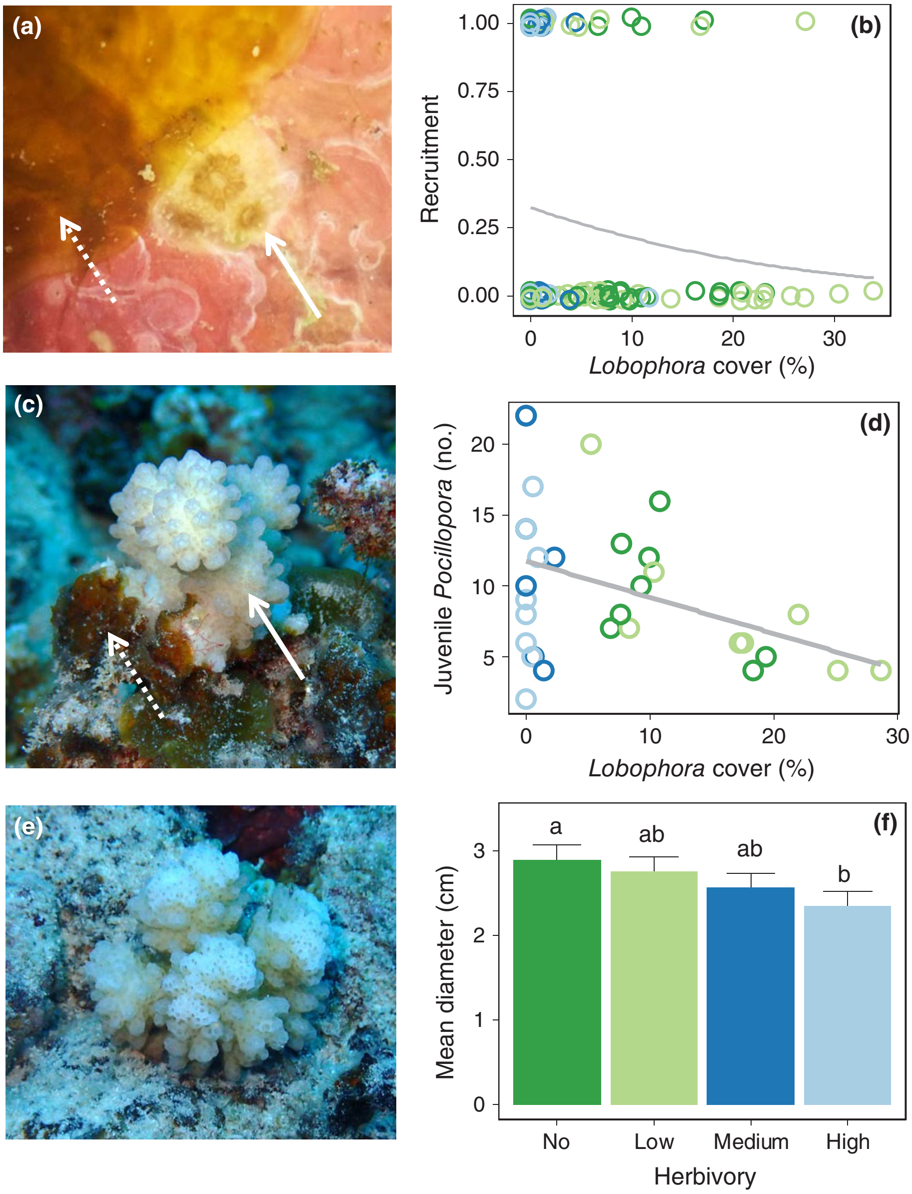

FIGURE 2 (a) Image of recently settled three-polyp coral recruit (solid arrow) being overgrown by *Lobophora* (dashed arrow) on a 10 cm × 10 cm settlement tile placed within a 1.25 m^2 exclosure. (b) Probability of successful coral recruitment on a settlement tile after 1 year as a function of the cover of *Lobophora* within a 50-cm radius ($N = 127$ tiles). (c) Image of an ~3 cm juvenile *Pocillopora* (solid arrow) on a natural substrate in a low herbivory treatment with *Lobophora* (dashed arrow) overgrowing the coral base. (d) Abundance of juvenile *Pocillopora* corals plotted against the cover of *Lobophora* for the experimentally disturbed plots ($N = 32$ exclosures). (e) Image of an ~3 cm juvenile *Pocillopora* in a high herbivory treatment showing evidence of corallivory (f) diameter (mean + SE) of juvenile *Pocillopora* corals in the experimentally disturbed plots for each of the four herbivory treatments ($N = 8$ exclosures per herbivory treatment). Letters represent significant differences ($p < 0.05$). Colors in all plots correspond to the four herbivory treatments as shown in Figure 1.

nearly four times as many bite scars as corals in the Medium Herbivory treatment (Tukey honestly significant difference, $p < 0.05$; Figure 4d). In contrast with corals in the High and Medium Herbivory treatments, corals in the Low and No Herbivory treatments rarely had bite scars (Figure 4d).

Despite competition with algae and predation by fishes, corals grew rapidly throughout the experiment, with corals increasing in area ~ 20-fold over 2 years. Yet growth differed significantly among treatments (ANOVA, $F_{3,27} = 21.4$, $p < 0.0001$; Figure 4e) with corals experiencing a ~ 30% reduction in growth in the High Herbivory treatment compared with the reduced herbivory treatments (Tukey HSD, $p < 0.05$; Figure 4e). In addition, corals grew at a ~20% greater rate in the Medium Herbivory treatment compared with the No Herbivory treatment (Tukey HSD, $p < 0.05$; Figure 4e). Approximately 90% of corals survived over the 2-year

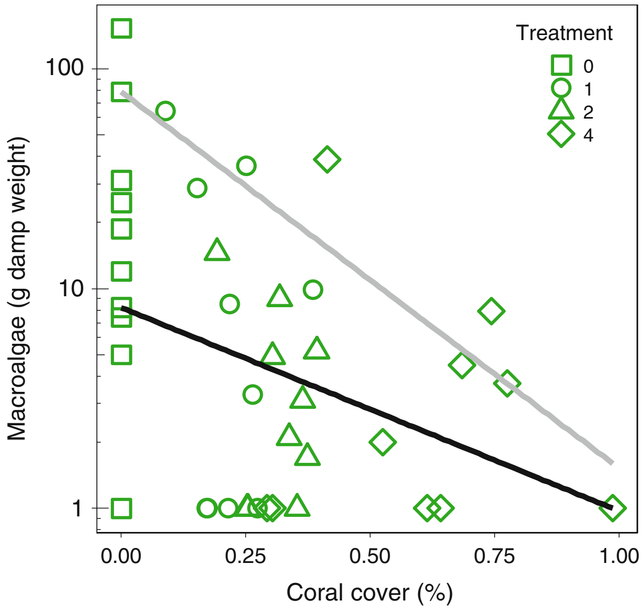

FIGURE 3 Damp weight of macroalgae plotted against coral cover after 2 years from Experiment III, in which the density of juvenile corals (*Pocillopora*) was manipulated on artificial substrate in small herbivore exclosures. Symbol shapes correspond to different initial density treatments (squares = 0, circles = 1, triangles = 2, diamonds = 4 corals per tile). Fits are from quantile regression on the median (black line) and the 85th quantiles (gray line). Note that one was added to all values to plot on a log scale.

study, with no significant differences among treatments (ANOVA, $F_{3,27} = 0.99$, $p = 0.41$, Figure 4f). Fast growth and low mortality rates resulted in corals rapidly occupying benthic space, with the rate of space occupancy accelerating after 8 months (Figure 5). Corals in the High Herbivory treatment occupied space more slowly compared with the reduced herbivory treatments, particularly during the first 16 months of the experiment (Figure 5). As a result, corals in the High Herbivory treatment only occupied ~65% of the space at the end of the experiment compared with ~90% for corals in the three reduced herbivory treatments (Figure 5).

DISCUSSION

Our experiments on the fore reef of Moorea revealed striking context-dependency in herbivore–algae–coral interactions. Like many prior studies, we found that control of macroalgae by herbivorous fishes facilitated the recruitment of juvenile corals following disturbances that reduced coral cover. Yet, we also found that established coral colonies, including small juveniles, suppressed the proliferation of macroalgae, even in the absence of herbivorous fishes. This surprising result indicates there is a strong priority effect in macroalgae–coral interactions, which has profound implications for the dynamics and resilience properties of the benthic community. For example, the ability of corals to suppress macroalgae could result in alternate community trajectories depending on the initial timing of coral and macroalgae recruitment following a disturbance. An unanticipated consequence of a strong priority effect between corals and macroalgae was that, once juvenile corals became established in high density aggregations, fishes had a net negative impact on these corals via predation. These results highlight how priority effects between corals and algae can create complex dynamics in how coral reef benthic communities respond following disturbances.

Mechanisms and consequences of priority effects

Priority effects resulting from preemption of resources (e.g., space, light, nutrients) are common in nature and can result in divergent community trajectories following a disturbance (Fukami, 2015). In addition to preemption, early colonists often modify the environment in ways that favor their persistence, creating feedbacks that can inhibit new colonizers (Connell & Slatyer, 1977; Orrock et al., 2008; Peterson, 1984; Yelenik & D'Antonio, 2013). Large numbers of studies have shown that abundant algae can inhibit coral recruitment by preempting space and by creating an environment that is hostile to coral colonists (e.g., Bulleri et al., 2018; Evensen et al., 2021; Hughes et al., 2007; Mumby et al., 2016; Schmitt et al., 2021). In particular, the dominant alga that proliferated under reduced herbivory conditions in our study, the creeping foliose brown alga *Lobophora*, can inhibit coral recruitment by suppressing the settlement of coral larvae (Baird & Morse, 2004; Evensen, Doropoulos, Morrow, et al., 2019; Evensen, Doropoulos, Wong, et al., 2019; Kuffner et al., 2006; Morrow et al., 2017) and by killing newly settled corals via overgrowth and allelopathy (Evensen, Doropoulos, Wong, et al., 2019; Johns et al., 2018; Rasher & Hay, 2010). Consistent with previous studies, we found that the presence of abundant *Lobophora* severely inhibited early coral recruitment, with recruitment to settlement tiles being reduced approximately five-fold when *Lobophora* were abundant. Similarly, high cover of *Lobophora* was associated with a three-fold reduction in the abundance of juvenile *Pocillopora* corals on natural substrate, probably indicating a negative effect of *Lobophora* on the survivorship of newly recruited corals as they emerge from their cryptic settlement locations.

In contrast with the effects of macroalgae on corals, few studies have investigated how corals may impact

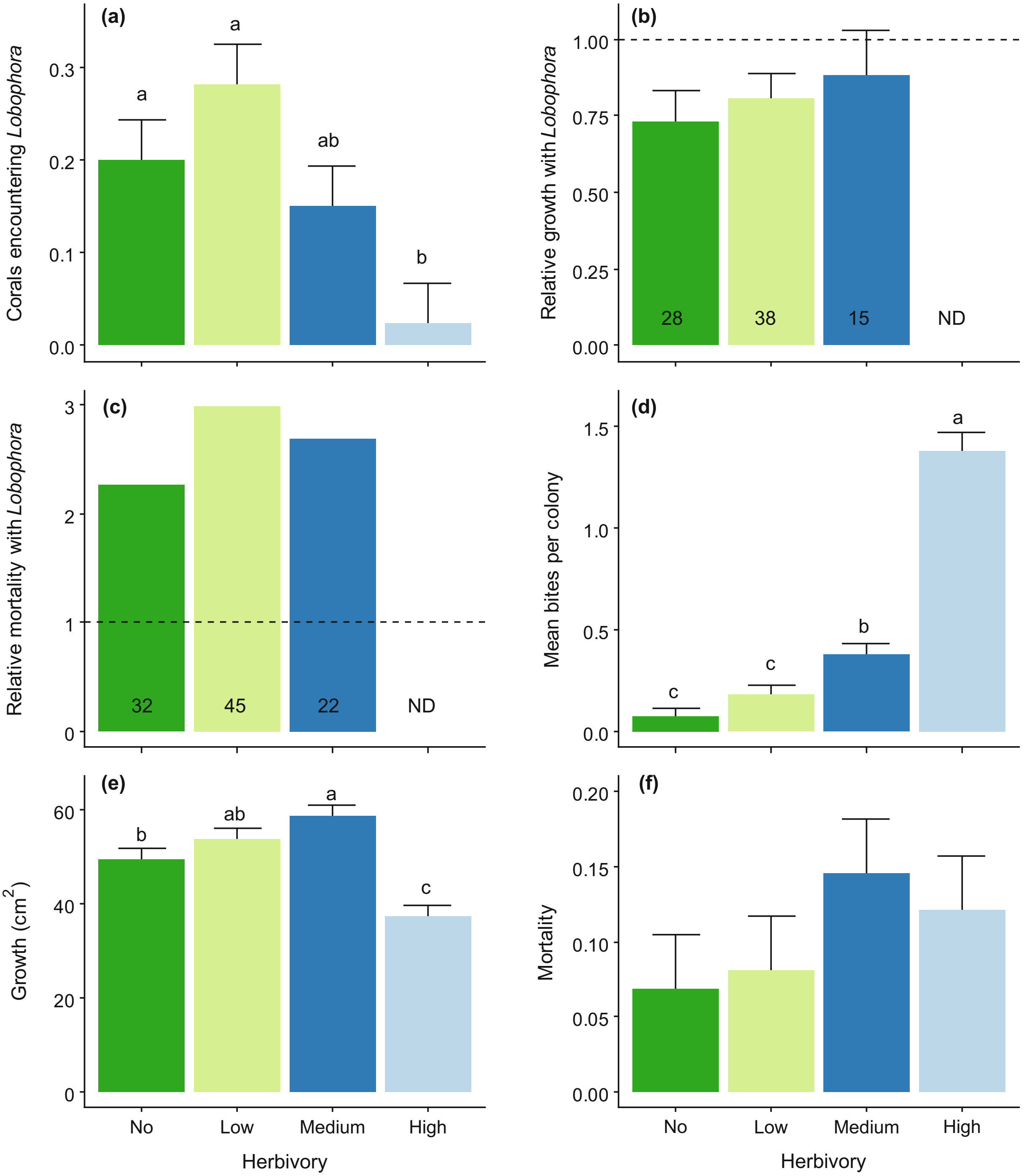

FIGURE 4 Patterns of growth and mortality for juvenile *Pocillopora* corals after 2 years of exposure to four herbivory treatments in Experiment IV. (a) Proportion (mean + SE) of juvenile *Pocillopora* corals that encountered *Lobophora* at some point during the experiment ($N = 10$ replicates per treatment with 16 corals per replicate). Relative (b) growth (mean + SE) and (c) mortality rates of juvenile *Pocillopora* that encountered *Lobophora* at some point during the experiment compared with corals that did not encounter foliose *Lobophora*. Dashed lines represent the values if growth and mortality were equal in the presence and absence of *Lobophora*. Numbers on the bars are the sample sizes. In panel (c), N represents the total number of corals in each treatment that encountered *Lobophora*. N is smaller in panel (b) because growth was only assessed for corals that survived until the end of the experiment. (d) Bite marks (mean + SE) from corallivorous fishes on juvenile *Pocillopora* corals during the first year of the experiment. (e) Growth (mean + SE) and (f) mortality (mean + SE) rates of juvenile *Pocillopora* corals during the experiment. Growth rates are expressed as change in areal cover. Values in (d) are back transformed. Letters represent significant differences ($p < 0.05$) as determined from post hoc Tukey tests.

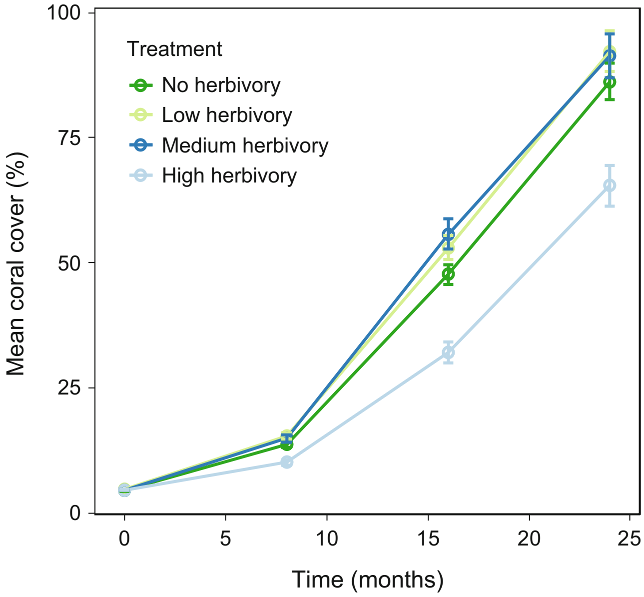

FIGURE 5 Time series of coral cover (mean ± SE) on artificial substrate for the four herbivore treatments over 2 years in Experiment IV that manipulated herbivore access to juvenile corals.

macroalgae (but see De Ruyter Van Steveninck et al., 1988; Jompa & McCook, 2002; Nugues & Bak, 2006). Our experiments revealed that some corals, including small juvenile corals that collectively occupied little space, can suppress macroalgae. For example, macroalgae never became abundant in any of our experiments when coral cover was >40%, even in the absence of significant herbivory. Although we expected that adult corals would inhibit algae to some degree by preempting space, the ability of small juvenile corals to suppress algae was surprising. Previous studies have found large negative effects of macroalgae on the growth and survivorship of juvenile corals (Box & Mumby, 2007; Ferrari et al., 2012), but these studies did not test the impacts of corals on macroalgae. When we manipulated the density of juvenile *Pocillopora*, we found that these corals effectively suppressed macroalgae. By limiting encounters with *Lobophora* and other macroalgae, juvenile corals in high density aggregations were able to thrive in the absence of herbivory. Therefore, if corals are able to colonize a reef in large numbers they may be able to suppress macroalgae, even under low levels of herbivory. In this case, the recovery trajectory of a reef may be determined by the initial colonization and growth rates of corals and algae.

Space preemption by juvenile and adult corals is likely to be one key mechanism limiting macroalgae in our experiments. Algal propagules are unable to colonize living coral tissue (Diaz-Pulido & McCook, 2004), and healthy corals are often able to prevent overgrowth from neighboring macroalgae (McCook et al., 2001; Nugues & Bak, 2006). Therefore, as corals increase their areal coverage (either through growth of existing colonies or recruitment of new individuals) less space is available for algal colonization and expansion. In our experiment manipulating herbivore access to juvenile corals, corals exposed to low levels of herbivory occupied the majority of substrate within ~16 months, significantly limiting the amount of space available for algae to colonize. Nonetheless, space preemption alone cannot explain the magnitude of algal suppression we observed in our experiments. For example, in Experiment I, all plots had at least 40% of the substrate available for algal colonization. Yet, macroalgae were nearly absent in the high coral cover plots. Similarly, in our experiment manipulating the densities of juvenile corals, the upper quantile of algal biomass was an order of magnitude lower on substrate with 50% coral cover compared with substrate with no corals despite there being only a two-fold difference in available space. Therefore, mechanisms in addition to space preemption appear to be limiting the ability of macroalgae to proliferate when corals are abundant.

Corals may limit macroalgae either by preventing algal settlement or by inhibiting the expansion of established plants. Although both mechanisms may be operating, small encrusting *Lobophora* were observed close to corals in all of our experiments. However, when coral cover was dense, these algae usually did not take on the three-dimensional foliose form associated with detrimental impacts on corals. The near ubiquitous presence of encrusting *Lobophora* adjacent to corals suggests that corals are likely to be limiting *Lobophora* by inhibiting the expansion of existing thalli. Corals may prevent algal expansion via a number of mechanisms, including mechanical damage by mesenterial filaments or sweeper tentacles (De Ruyter Van Steveninck et al., 1988; Nugues et al., 2004), allelopathy (Ben-Ari et al., 2018), the involvement of coral exosymbionts that defend coral margins (Dixson & Hay, 2012, Stachowicz & Hay, 1999), or possibly via microbial mechanisms. In addition to interference competition, corals may also outcompete macroalgae for limiting resources such as light or nutrients. Irrespective of the specific mechanisms, the ability of corals to inhibit the expansion of macroalgae into unoccupied space could be an important yet overlooked feedback helping to maintain reefs in a coral-dominated state; in theory, this would enhance the potential for coral and macroalgae states to be bistable over some range of herbivory (Briggs et al., 2018).

An unexpected result of our study was the negative effect of nutrient enrichment on the abundance of macroalgae. Many studies have shown that macroalgae benefit from nutrient enrichment, particularly in the absence of herbivory (Burkepile & Hay, 2006). However, other long-term experiments manipulating nutrients on coral reefs suggest the effects of nutrients on algal communities can be slow to develop and may take years to be fully realized (Zaneveld et al., 2016). A limitation of our study is that the 1 year time frame of our experiment may not have allowed sufficient time for all treatment effects to be fully realized, particularly given the impacts from the bleaching event and the likelihood that algal and coral communities were still responding to the event. Furthermore, modest nutrient enrichment can have positive effects on coral growth and physiology (Becker et al., 2021; Gil, 2013; Shantz & Burkepile, 2014). Indeed, we found a positive effect of nutrients on coral cover, suggesting that nutrients were facilitating coral growth. Therefore nutrient enrichment may have increased the overall competitive ability of corals, thereby preventing the establishment and growth of macroalgae and representing a further priority effect.

Fish consumers as coral facilitators and inhibitors

When we manipulated access to juvenile *Pocillopora* corals by fishes, we found that juvenile corals were more likely to be in contact with *Lobophora* and other macroalgae under reduced herbivory conditions compared with high herbivory conditions. Increased encounters with *Lobophora* had strong growth and mortality costs, with corals that were in close proximity to *Lobophora* at any point during the 2-year experiment suffering an ~20% reduction in growth and an ~2.5 fold increase in mortality compared with corals that were never in close proximity to *Lobophora*. Yet, on average, juvenile corals grew significantly faster and survived as well or better in reduced herbivory treatments relative to High Herbivory controls despite more encounters with macroalgae. Corals exposed to high levels of herbivory were frequently preyed on by excavating corallivores (including parrotfish, pufferfish, and filefish) as evidenced by bite scars where coral tissue and skeleton had been removed. Therefore our results indicate that once corals emerge from their cryptic settlement locations, the direct negative effects of predation can outweigh the benefit of reduced competition with algae. Nonetheless, juvenile corals performed best at intermediate levels of herbivory, in which the trade-off between reduced competition with macroalgae and increased predation by fishes was likely to be optimized. This is consistent with a number of recent studies that found that grazing fishes can increase coral recruitment by controlling algae while also inflicting high levels of mortality on juvenile corals (Doropoulos et al., 2016; McCauley et al., 2010; Mumby et al., 2016; Shantz et al., 2020). Therefore, the net impact of fishes on small corals will be determined by the balance between the positive indirect effects of herbivores via the control of algae and the direct negative effects of predation.

Similar dynamics arise in a wide variety of marine, aquatic, and terrestrial systems, in which consumers can act as indirect mutualists of their prey by removing consumer-susceptible species that otherwise would be competitively dominant (Hay et al., 2004; Lubchenco, 1983; Wootton, 1994). Although these indirect mutualisms are common in nature, they have seldom been explored in the context of priority effects in which the outcomes of competitive interactions between prey species are variable and depend on their order of arrival. Our results indicate that the presence of strong priority effects can alter the relationships between consumers and their prey by changing the relative magnitudes of direct consumptive and indirect facilitative effects.

Generality of results and implications for management

Reef-building corals and macroalgae exhibit a wide range of life history strategies yet, in general, macroalgae tend to be faster colonizers compared with corals. In fact, when uncontrolled by herbivores, macroalgae can become abundant on newly available substrate in a matter of months (Adam et al., 2011; Roff & Mumby, 2012; Vieira, 2019). By contrast, it takes years to decades for corals to dominate substrate following a disturbance even in systems with high rates of coral recruitment (Colgan, 1987; Doropoulos et al., 2022; Gilmour et al., 2013; Holbrook et al., 2018). Such a large disparity in the ability of macroalgae to colonize and subsequently dominate new substrate compared with corals suggests that priority effects between corals and macroalgae will often favor macroalgae. However, the ability of corals to inhibit macroalgae could still be an important mechanism influencing coral dynamics, particularly in systems with high rates of coral recruitment or in which coral–algal competition is highly asymmetric in favor of corals. For example, in the Keppel Islands on the southern Great Barrier Reef, a mass bleaching event caused significant coral mortality and facilitated a large bloom of *Lobophora*, which quickly colonized the dead coral skeletons. Yet, remnant tissue that survived bleaching and the subsequent *Lobophora* bloom was able to rapidly regenerate, outcompeting and largely replacing *Lobophora* within a year (Diaz-Pulido et al., 2009). In this case, coral recovery on the Keppel Islands was driven by the regeneration of coral tissue on existing coral colonies rather than the recruitment of new individuals and was enabled by the highly asymmetric competitive abilities between the fast growing *Acropora* corals and the competitively inferior macroalga.

Our results have several important implications for the management and restoration of coral reefs. A common tool used in coral reef restoration is to transplant juvenile corals (or coral fragments) to disturbed areas to promote reef recovery by overcoming recruitment bottlenecks (Ladd et al., 2018). Studies on the restoration of the endangered Caribbean coral, *Acropora cervicornis*, have found positive effects of coral density on growth, with hypothesized mechanisms ranging from density-dependent impacts on water flow to impacts on nutrient cycling via the attraction of fish (Huntington et al., 2017; Ladd et al., 2016; Shaver & Silliman, 2017). Our results also suggest that coral density could be an important factor to consider during restoration if high density aggregations are better able to suppress macroalgae. A second tool used in coral reef restoration is the manual removal of macroalgae to reduce competition with corals and provide space for coral recruitment (Ceccarelli et al., 2018). Removal of macroalgae is labor intensive and likely to be impractical if macroalgae quickly regrow following removal. Our findings indicate that restoration practitioners could leverage priority effects by pairing algae removals with coral transplantation. Such paired interventions may be more likely to succeed than only the removal of macroalgae.

Many researchers have emphasized the need to protect herbivorous fishes on coral reefs to control the proliferation of algae while also recognizing that herbivorous fishes can have direct negative impacts on corals (Adam et al., 2015; Bellwood et al., 2012). Although low levels of consumer pressure can benefit corals under some conditions, our results emphasize that priority effects are likely to become increasingly important when herbivory rates are low. Studies of community assembly in disparate ecosystems, including ponds (Chase et al., 2009; Morin, 1984) and grasslands (Alberti et al., 2017; Germain et al., 2013), have shown that the presence of consumers (predators and herbivores) can reduce the importance of priority effects, resulting in more deterministic community development. Consumers can reduce the importance of priority effects in part by favoring species that are resistant to consumption (Chase et al., 2009; Germain et al., 2013). We found that this may also be the case on coral reefs. Under high levels of herbivory, macroalgae remain uncommon, favoring the recruitment and growth of corals that are preyed on to a lesser degree than macroalgae. But when herbivory is reduced, community development may be more variable. Corals may suppress macroalgae following a disturbance if enough corals survive the disturbance or if there is a large recruitment event resulting in high enough densities of juvenile corals. However, in the absence of sufficient densities of corals, macroalgae may proliferate, inhibiting further coral recruitment and reinforcing an algae-dominated state. Therefore, whereas our results suggest that loss of fish consumers to overfishing could benefit corals under certain conditions, consumer loss would also increase the importance of priority effects between corals and macroalgae, leading to a cryptic loss of resilience and greater chances of unwanted ecological surprises.

AUTHOR CONTRIBUTIONS

All authors designed and conducted the experiments. Thomas C. Adam analyzed the data and wrote the first draft of the manuscript. All authors contributed to manuscript revisions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available in the Environmental Data Initiative repository as follows: Moorea Coral Reef LTER et al. (2022), https://doi.org/10.6073/pasta/593324912dc7858b7090e18541f21637; Moorea Coral Reef LTER and Alldredge (2019), https://doi.org/10.6073/pasta/9328a024f2bf16ecc66024f07dbcc574; Moorea Coral Reef LTER and Brooks (2021), https://doi.org/10.6073/pasta/a667eed481d9743c69c4209f6479acb4; Moorea Coral Reef LTER and Edmunds (2020), https://doi.org/10.6073/pasta/10ee808a046cb63c0b8e3bc3c9799806.

ORCID

Thomas C. Adam https://orcid.org/0000-0001-6146-0260
Sally J. Holbrook https://orcid.org/0000-0002-3015-3484
Deron E. Burkepile https://orcid.org/0000-0002-0427-0484
Kelly E. Speare https://orcid.org/0000-0002-0016-3606
Andrew J. Brooks https://orcid.org/0000-0002-6651-1204
Mark C. Ladd https://orcid.org/0000-0002-8024-5811
Andrew A. Shantz https://orcid.org/0000-0001-5641-8914
Rebecca Vega Thurber https://orcid.org/0000-0003-3516-2061
Russell J. Schmitt https://orcid.org/0000-0002-9674-4244

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SUPPORTING INFORMATION

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

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