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Interactions between consumer access and nutrient enrichment have divergent impacts on two common Pacific corals

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ABSTRACT: As coral reefs face accelerating threats at global scales, examining how different coral species respond to local disruption from top-down and bottom-up forces can inform management at local scales. This may provide additional time for reducing global stressors. We conducted a full factorial experiment examining the effects of corallivory, herbivory, and fertilizer addition on 2 corals: *Acropora pulchra* and *Porites rus*, the former of which is faster-growing but more susceptible to predation, disease, and heat-induced mortality. Fertilizer addition enhanced corallivory but did not affect net coral growth. Consumer exclusion enhanced the net growth of *A. pulchra* by 18.1 times regardless of fertilizer treatment, while the net growth of *P. rus* did not differ among caging and fertilizer treatments. *A. pulchra* was rarely overgrown by algae regardless of treatment, while herbivore exclusion and fertilizer enrichment produced opposing effects on overgrowth of *P. rus*. In uncaged treatments, fertilizer enrichment led to greater herbivory but also 1.8 times greater algal overgrowth of *P. rus* relative to unfertilized treatments. However, in caged treatments, algal overgrowth of *P. rus* was 1.9 times higher in unfertilized versus fertilized treatments. Our results suggest that interactions between corallivory, herbivory, and fertilizer enrichment can have alternative effects on different coral species, with a hardier coral experiencing more negative impacts of fertilizer enrichment than a more sensitive coral, which was, in turn, more strongly suppressed by predation. Local stressors that disrupt top-down and bottom-up processes may increase the vulnerability of even the most robust corals, and it is these corals that have been predicted to become more common under future ocean scenarios.

KEY WORDS: Top-down · Bottom-up · Corallivory · Herbivory · *Acropora pulchra* · *Porites rus*

1. INTRODUCTION

Coral reefs face a multitude of stressors at both global and local scales (Carpenter et al. 2008, Mora et al. 2018, Donovan et al. 2021). Given the challenges and time lags involved with addressing global drivers of reef decline (e.g. Turner et al. 2010), identifying local factors that can enhance resilience is important for near-term management to allow time for addressing global stressors (Abelson 2020). Local stressors often alter the top-down and bottom-up processes that can affect reef community composition and ecosystem function, especially following disturbances (Smith et al. 2010, Adam et al. 2021, 2022). The relative strength of these factors can result in reefs flipping from coral- to algal-dominated states following disturbances (Schmitt et al. 2019, Adam et al. 2021). For example, top-down control of algae by herbivores has been cited widely as critical in promoting reef resilience and coral dominance (e.g. Burkepile & Hay 2006, Mumby & Steneck 2008, Hixon 2015), but herbivores are often targeted in local fisheries (Williams

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et al. 2008, Houk et al. 2018, Rassweiler et al. 2022), weakening resilience.

Bottom-up stressors in the form of fertilizer or nutrient runoff can have numerous direct and indirect impacts on reefs, such as the promotion of algal proliferation in the absence of adequate herbivory (Gruner et al. 2008, Burkepile & Hay 2009). This can lead to increased coral—algal interactions, resulting in reduced coral growth (Burkepile & Hay 2010) and increasing coral mortality and disease (Nugues et al. 2004, Rasher & Hay 2010, Bonaldo & Hay 2014). Nutrient enrichment can also promote coral diseases (Bruno et al. 2003, Vega Thurber et al. 2014) and increase coral susceptibility to thermal stress (Wiedenmann et al. 2013). However, corals may vary in their susceptibility to these effects (Carpenter et al. 2008, Bonaldo & Hay 2014, Swierts & Vermeij 2016). For example, coral—algal competitive outcomes often depend on factors such as coral morphology (Swierts & Vermeij 2016), algal chemistry (Rasher & Hay 2010), and coral—algal pairings (Bonaldo & Hay 2014), and while some studies have found that nutrient runoff increases the frequency of bleaching (e.g. Wiedenmann et al. 2013, Donovan et al. 2020), others have found that nutrient enrichment from fertilizer can enhance thermal tolerance in less turbid, lower light, nutrient-poor waters (Becker et al. 2021) Additionally, enhanced nutrients from bird and fish waste can promote coral growth and enhance reef resilience (Meyer et al. 1983, Shantz et al. 2015, Savage 2019, Benkwitt et al. 2023). Thus, examining the context-dependent and species-specific responses to differing top-down and bottom-up forces is necessary for understanding the resilience of both current and future reefs.

While prior work has independently or interactively assessed how fish exclusion and nutrient enrichment affect coral growth and/or benthic succession (e.g. Burkepile & Hay 2009, Smith et al. 2010, Rasher et al. 2012), few studies have addressed how bottom-up factors interact with coral predation, instead focusing on the impact of excluding herbivores. Corallivores (consumers that feed on live coral) can have significant impacts on coral growth and fitness (Rotjan & Lewis 2008, Cole et al. 2011, Clements & Hay 2018), which can have secondary impacts by suppressing coral reproductive potential (Henry & Hart 2005), enhancing coral disease (Gignoux-Wolfsohn et al. 2012), and increasing coral susceptibility to bleaching (Shaver et al. 2018). Given that nutrient enrichment often increases the consumption of less-preferred or more strongly defended prey species (Cruz-Rivera & Hay 2000, 2003) and can lead to increased consumption of macroalgae (Burkepile & Hay 2009, Shantz et al. 2017), and that nutrition is an important driver in corallivore prey preference (Cole et al. 2008), it seems plausible that nutrient enrichment also could increase predator consumption of corals.

Here, we conducted a full-factorial field experiment to address how the exclusion of herbivorous and corallivorous fishes interacts with fertilizer enrichment to affect coral growth and turf algal overgrowth of 2 corals with different competitive abilities, life history traits, and tolerances to various physical and biotic stresses. We sought to answer (1) how fertilizer enrichment and the exclusion of larger fishes affect coral growth, (2) if this effect differs between coral species, (3) if fertilizer enrichment enhances corallivory and/or herbivory, and (4) if nutrient enrichment and the exclusion of herbivores and corallivores affect turf algal overgrowth of corals.

2. MATERIALS AND METHODS

Our study was conducted from 10 March to 13 April 2023 in the fringing reef lagoon on the north shore of Moʻorea, French Polynesia (17° 29′ 18.6″ S, 149° 52′ 53.9″ W), with the experiment deployed at ~1.5 m depth and ~100 m from shore on sand patches between coral 'bommies' (small patch reefs) that characterize the lagoons of Moʻorea. We conducted a full factorial experiment testing the independent and interactive effects of fish exclusion and fertilizer enrichment on 2 common corals: (1) *Acropora pulchra*, a fast-growing coral (Darling et al. 2012, Pratchett et al. 2015) that is often targeted by coral predators (White & O'Donnell 2010, Kamath et al. 2019, Kopecky et al. 2021), is susceptible to breakage and coral disease (Clements et al. 2024), and is a member of a genus that is globally threatened by climate change (Carpenter et al. 2008); and (2) *Porites rus*, a robust coral that is resistant to a multitude of stressors (Dizon & Yap 2005, Donner & Carilli 2019), is thermally resistant (Lenz & Edmunds 2017), and is thus likely to be more common on future reefs (Cannon et al. 2021). Given that fast-growing branching corals like *A. pulchra* often preferentially settle or survive in the algal gardens of territorial damselfish as a refuge from predation (White & O'Donnell 2010, Kamath et al. 2019), we hypothesized that these corals would be more sensitive to the effects of predation but less susceptible to algal overgrowth than *P. rus*. However, we predicted that fertilizer addition would enhance predation on both corals, potentially limiting coral growth in uncaged × fertilized treatments.

We collected 4 undamaged fragments (i.e. no visible skeletal or tissue abrasions, bite marks, etc.) from 12 separate colonies of *A. pulchra* and 12 separate colonies of *P. rus* in the study area, attached them into the inverted necks of plastic soda bottles using underwater epoxy (Z-spar Splash Zone Compound; see Clements & Hay 2015), screwed these bottlenecks into inverted bottle caps attached to cinder blocks (see below), and randomly assigned 1 fragment from each colony to prevent confounding treatment effects with colony effects.

Treatments were blocked spatially, where each replicate consisted of a single cinderblock (20.3 × 40.6 × 10.2 cm) with a fragment of each species of coral separated by 12 cm at one end of the cinderblock (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m750p053_supp.pdf), and each spatial block contained 1 replicate that was randomly assigned to one of the 4 treatments (i.e. control; consumer exclusion, 'caging'; fertilizer enrichment, 'fertilizer'; and caging × fertilizer; n = 12 per coral species per treatment). Caging treatments were implemented by affixing 5 × 5 × 10 cm cages of 1.3 cm mesh around coral fragments with cages cleaned every 3 d to prevent fouling. Cages and plots were checked daily as part of routine maintenance. Small animals that could pass through the mesh (amphipods, small crabs, etc.) could have fed preferentially during night hours, but during our daytime monitoring, we never observed small invertebrate herbivores or corallivores inside the cages during the experiment. Fertilizer treatments were implemented by attaching 2 nutrient diffusers containing 70 g of Osmocote (19-6-12, N-P-K) slow-release fertilizer to appropriate treatments, simulating nutrient enrichment. Each fertilizer diffuser was made of a 15 cm long, 4 cm diameter PVC tube with 8 holes (1 cm diameter) drilled into its sides at even intervals and then wrapped in plastic mesh. This design has been effective at elevating nutrients for 30–35 d with multiple kinds of slow-release fertilizers at this site and others (Vega Thurber et al. 2014, Zaneveld et al. 2016, Burkepile et al. 2020, Strader et al. 2022). In these previous experiments, plots treated with Osmocote fertilizer diffusers enhanced algal nitrogen content by 1.1–1.2 times and enhanced water column nitrogen and phosphorous content by 3–4 and 5–9 times, respectively relative to control areas (e.g. Vega-Thurber et al. 2014, Becker et al. 2021). The position of each coral fragment (left or right) at the end of the cinderblock was randomized between replicates, allowing us to compare treatment effects on the different corals as a paired assay (Fig. S1).

We assessed treatment effects on net coral growth following methods outlined in Clements & Hay (2019, 2021). Briefly, corals were weighed prior to treatment application using a scale (OHAUS Scout Pro) enclosed in a plastic container elevated above the water on a tripod. Corals and bottlenecks were gently shaken 30 times to remove excess water, weighed, and then immediately placed back in the water. Corals were re-weighed 34 d later after gently removing all epiphytic algae and algal overgrowth from the corals and bottlenecks, providing coral growth or loss as the relative change in coral mass (% change). While this method precludes exact measurement of calcification via surface area-corrected buoyant weighing (Davies 1989), wet weighing on-site allows for rapid determination of weight that includes both changes in skeletal mass and coral tissue mass while minimizing stresses associated with removal from the reef, transport to and from a lab for buoyant weighing, and time spent in a non-natural aquarium setting during transport and before and after weighing.

Differences in coral growth were assessed using a linear mixed effects model (LMER) in R v.4.3.2 (R Core Team 2023) with 3-way interaction effects between coral species, fertilizer treatment, and caging treatment, and random effects to account for parent colony ID (1|Parent.colony) and spatial blocking (1|Block). Model assumptions (i.e. tests of dispersion and the normality and heterogeneity of residuals) were assessed using the 'DHARMa' package (Hartig 2022) and within-factor pairwise comparisons of the estimated marginal means were conducted with a Bonferroni correction using the 'emmeans' package (Lenth 2023).

To test the effect of fertilizer enrichment on herbivory and corallivory, we videoed all uncaged plots for 75–90 min immediately after deployment ('Week 0'), 2 wk post-deployment, and 4 wk post-deployment. We only filmed uncaged plots because exclusion cages prevented access of both herbivorous and corallivorous fishes. Herbivory was measured as the number of bites taken anywhere in the plot area, excluding coral fragments, while corallivory was measured as the number of bites taken directly on coral fragments. Herbivory data were underdispersed, largely due to low grazing during Week 0, where 7 out of 24 videos contained no bites and 15 out of 24 videos contained fewer than 100 bites. We assumed that this was due to minimal algal growth on plots immediately following deployment, and there-fore we removed all Week 0 data for comparisons of grazing rates between fertilized and unfertilized plots, focusing only on the videos from Weeks 2 and 4, giving fertilizer effects time to be expressed. We modeled treatment effects on grazing rates using a negative binomial generalized linear mixed effects model (GLMER) in the 'glmmTMB' package in R (Brooks et al. 2017) with a random effect to account for spatial blocking and (1+Week|Plot.ID) as a random slope and intercept to account for temporal autocorrelation.

Corallivory data were strongly zero-inflated. We assumed that fertilizer effects on corals were not yet present in Week 0, so these data were again removed from the analysis. We also were interested in whether rates of predation differed between coral species (i.e. not just between fertilized vs. unfertilized treatments), so we compared corallivory rates between coral × fertilizer treatments using a zero-inflated negative binomial model to account for overdispersion and with the model intercept specified as the zero-inflation component and random effects or repeated measures specified as above in the herbivory model. The highest bite rate in the unfertilized *A. pulchra* treatment was 12.1 times greater than the next-highest observation in this treatment, so this outlier was removed from the analyses. Results from the model that includes this datum can be found in Tables S1 & S2. DHARMa model diagnostics indicated that residuals of the corallivory data were underdispersed following the removal of the outlier, so these data were fit using a Conway-Maxwell-Poisson model link. The zero-inflation component and random effects were specified as above in the model that included all data. Coral × fertilizer interaction effects were assessed using the 'emmeans' package (Lenth 2023).

Finally, we assessed treatment effects on coral tissue mortality and algal overgrowth following 34 d of treatment by taking pictures of the front and back of each fragment prior to cleaning the corals for reweighing. Using ImageJ, we traced the outline of each skeleton, the outline of algal overgrowth, and the outline of any coral mortality that extended beyond the area of coral overgrowth. We then averaged the area of overgrowth and mortality for the front and back of each coral to estimate % overgrowth and % tissue mortality for each coral fragment. We compared proportional overgrowth and overgrowth + mortality between each coral × caging × fertilizer treatment with a beta regression using the 'glmmTMB' package in R (Brooks et al. 2017) with random effects to account for parent colony ID and spatial blocking. Multiple fragments had no mortality or overgrowth or were completely overgrown, so data were transformed according to Smithson & Verkuilen (2006):

$$x' = \frac{x(N-1)+s}{N}$$

where x is proportion overgrowth/mortality, N is the sample size, and s is a constant between 0 and 1 (set to 5×10^{-6} for our data to minimize the effects of the transformation) to allow for modeling via beta regression on data that include zeroes and ones. Results were almost identical between models examining only overgrowth and overgrowth + mortality, as only 16 out of 192 fragments displayed mortality beyond overgrowth. As such, only the results from the latter model (overgrowth + mortality) are presented below (hereafter 'overgrowth'). One outlier in the caged *P. rus* treatment was removed from the analysis. Results from the model that include this datum can be found in Tables S3 & S4. Pairwise comparisons and interaction effects were conducted using the 'emmeans' package (Lenth 2023).

3. RESULTS

3.1. Effects of nutrient enrichment on coral growth and corallivory

There was a significant interaction between caging and coral species on coral net growth (LMER, F = 82.8, $p < 0.0001$; Fig. 1). In caged plots, net growth of *Acropora pulchra* (mean ± SE: 13.0 ± 0.92%) was 1.9 times greater than net growth of *Porites rus* (6.9 ± 0.77%) regardless of fertilizer treatment ('emmeans', fertilized: t-ratio = −4.1, $p = 0.002$; unfertilized: t-ratio = −3.5, $p = 0.013$; Fig. 1) but the pattern was reversed in uncaged plots, with the net growth of *P. rus* (9.1 ± 0.64%) being 12.6 times greater than that of *A. pulchra* (0.72 ± 0.99%) (fertilized: t-ratio = 5.0, $p < 0.0001$; unfertilized: t-ratio = 5.6, $p < 0.0001$). *A. pulchra* net growth was 18.1 times greater in caged treatments than in uncaged treatments regardless of fertilization treatment ('emmeans', fertilized: t-ratio = −7.6, $p < 0.0001$; unfertilized: t-ratio = −6.7, $p < 0.001$). Mean net growth of *P. rus* was statistically indistinguishable across treatments ('emmeans', fertilized: t-ratio = 1.0, $p = 1$; unfertilized: t-ratio = 1.4, $p = 1$). Fertilizer treatment had no detectable effect on the net growth of either coral (LMER, F = 0.2, $p = 0.698$) and did not produce any significant interactions with other factors (Fig. 1).

Although fertilizer had no detectable effect on coral growth, it increased the rate at which fishes fed on corals (zero-inflated GLMER, $\chi^2 = 10.6$, $p < 0.0001$;

Fig. 2). Bite rates on *P. rus* were 11.2 times greater in the fertilized versus unfertilized treatment ('emmeans', *z*-ratio = 2.4, p = 0.004) and bite rates on *A. pulchra* were 39.3 times greater in the fertilized versus unfertilized treatment ('emmeans', *z*-ratio = 3.9, p = 0.003). However, the inclusion of a single outlier altered the results such that attacks on *A. pulchra* no longer rose significantly when the coral was fertilized

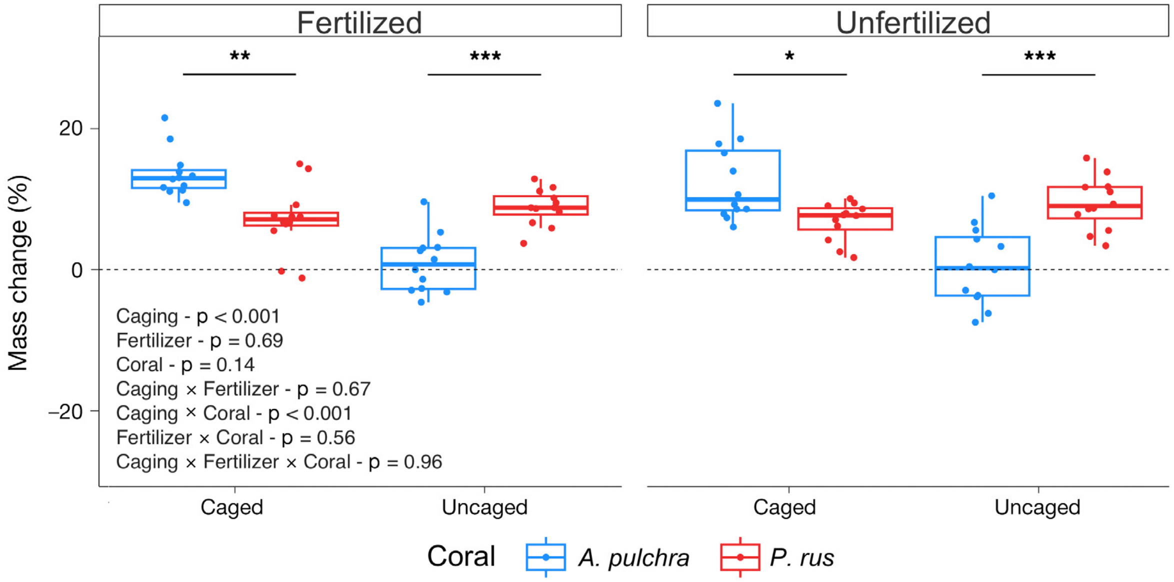

Fig. 1. Growth of corals *Acropora pulchra* and *Porites rus* after 5 wk of treatment. Boxes display the lower quartile, median, and upper quartile of the data; whiskers: total range of the data; points: 1.5× the interquartile range. Asterisks indicate significant differences from within-factor pairwise comparisons using 'emmeans' (*p < 0.05; **p < 0.01; ***p < 0.0001)

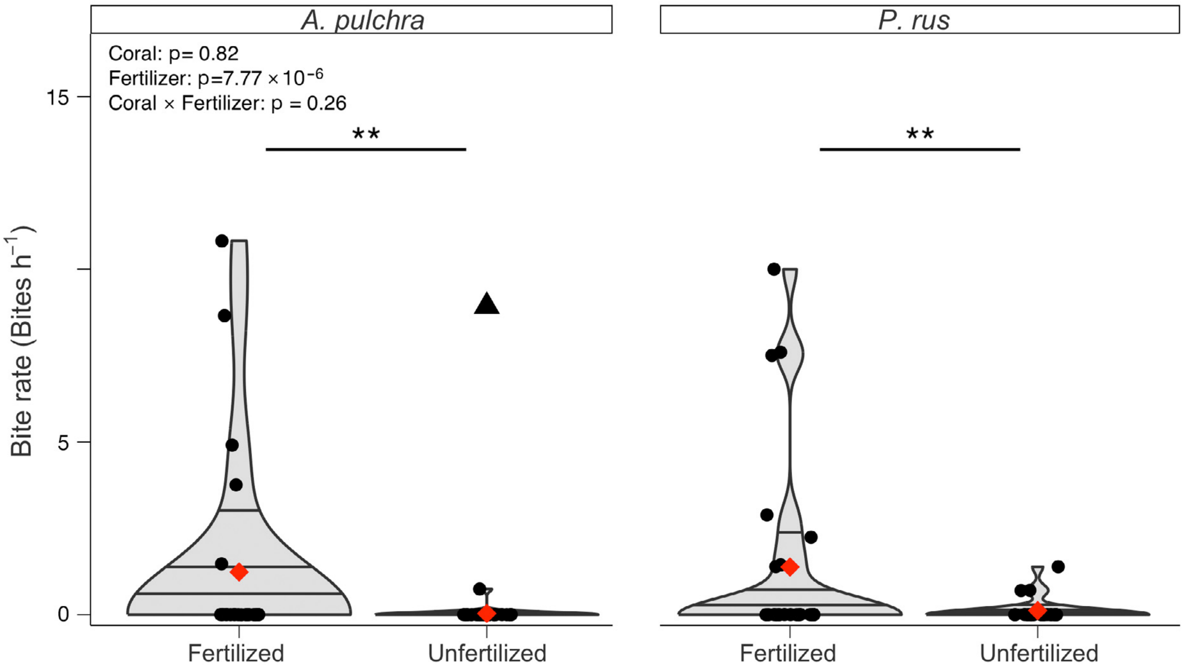

Fig. 2. Impact of fertilizer addition on the frequency with which *Acropora pulchra* and *Porites rus* are bitten by fishes. Horizontal lines: lower quartile, median, and upper quartile of the distribution; points: data from both Weeks 2 and 4. The triangle is an influential outlier that was removed from the reported statistics. Violin widths: kernel probability density to highlight the zero-inflation of the data; red diamonds: mean bite rate following the removal of the outlier. Asterisks indicate significant differences from a within-factor pairwise comparison using 'emmeans' (**p < 0.01)

(z-ratio = 3.4, $p = 1.00$; Table S1). A full list of pairwise comparisons between treatments when the outlier was and was not included can be found in Tables S1 & S5, respectively. In our videos, observed instances of fishes feeding on corals were uncommon and the zero-inflated model was highly significant (zero-inflated GLMER, $z = 1.3$, $p < 0.0001$), with only 19 of 72 videos showing fish feeding events. A total of 54% of observed predation events came from the butterflyfish *Chaetodon lunulatus*, although we also observed bites from *Balistapus undulatus*, *Ctenochaetus striatus*, and roving schools of juvenile *Scarus psittacus* and *Chlorurus spilurus.* Despite rarely being captured in videos, feeding scars on *A. pulchra* indicated that all uncaged fragments experienced skeletal loss due to predation from excavating fish such as *B. undulatus* within the first 2 wk of the experiment regardless of fertilizer treatment. Thus, predation kept the net growth of *A. pulchra* at or near zero regardless of fertilizer treatment (Fig. 1), while fertilization of *P. rus* increased the rate at which it was attacked (Fig. 2) but without producing a detectable suppression of its net growth.

3.2. Algal overgrowth of corals: effects of fertilization, herbivory, and coral species

Algal overgrowth of corals differed significantly between coral species (GLMER, $\chi^2 = 46.1$, $p < 0.0001$; Fig. 3), with *A. pulchra* largely resistant to being overgrown by algae regardless of treatment (Fig. 3, Table S4) while *P. rus* experienced mean overgrowth rates of 6–24% of its surface during this 34 d experiment. There was a significant 3-way interaction between coral species, fertilizer treatment, and caging treatment ($\chi^2 = 11.0$, $p < 0.001$) driven by the variable effects of caging and fertilizer on turf overgrowth of *P. rus*. When caged, overgrowth of *P. rus* was 1.9 times greater in the unfertilized relative to the fertilized treatment ('emmeans', z-ratio = 4.7, $p < 0.0001$) but the effect of fertilizer on algal overgrowth was reversed when *P. rus* occurred uncaged. In uncaged treatments, overgrowth was 1.8 times higher on fertilized relative to unfertilized *P. rus* (z-ratio = −1.4, $p = 0.011$). A full list of interaction effects for models where the outlier was and was not included are shown in Tables S4 & S6, respectively. We observed 13 different fish grazing on our plots, although 5 species were responsible for 95% of bites: *C. striatus* was responsible for 31% of the bites, *Acanthurus triostegus* for 25%, *Zebrasoma scopas* for 21%, *Acanthurus blochii* for 11%, and *S. psittacus* for 7%. Fertilizer addition also increased rates of grazing by herbivorous fishes by 1.6 times relative to grazing rates on unfertilized plots (zero-inflated GLMER, $\chi^2 = 5.7$, $p = 0.017$; Fig. 4).

4. DISCUSSION

The relative importance of local factors that disrupt top-down control of algae by herbivores and potential interactions with bottom-up factors like

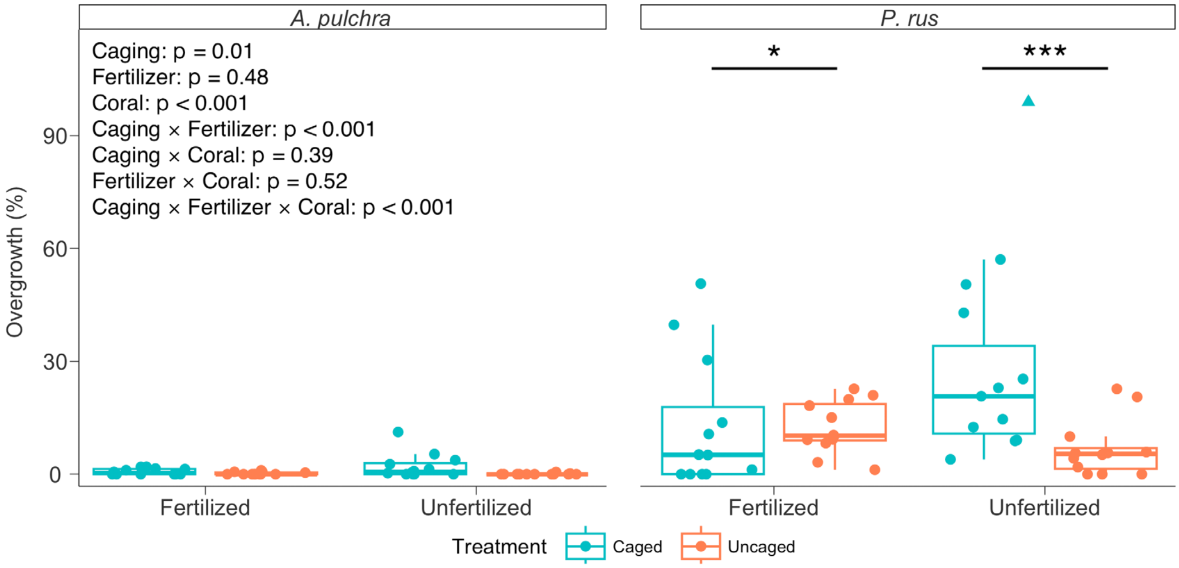

Fig. 3. Algal overgrowth of the corals *Acropora pulchra* and *Porites rus* as a function of caging and fertilizer treatments. Colors represent caging treatment. Boxes, points, and significant differences as in Fig. 1

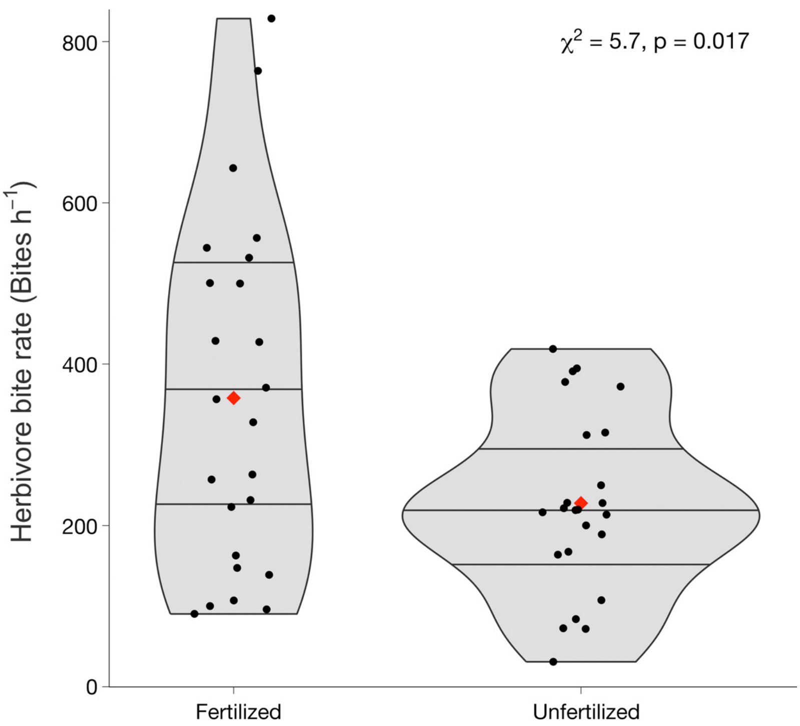

Fig. 4. Treatment effects of fertilizer addition on herbivore grazing of experimental plots. Plot widths, bars, and symbols as in Fig. 2

nutrient enrichment in influencing benthic trajectories on coral reefs has long been debated (Burkepile & Hay 2006, Smith et al. 2010, Evensen et al. 2021). While manipulative experiments often find stronger evidence for the importance of top-down forces in mitigating transitions to macroalgal-dominated reef states (Burkepile & Hay 2009, Rasher et al. 2012, Fong et al. 2020), surveys at broader scales often find correlations of nutrient enrichment with algal increases and coral declines (Sandin et al. 2008, Adam et al. 2021). Here, we found that fertilizer addition interacted with herbivory and corallivory to produce complex and species-specific impacts on corals.

The impacts of fish exclusion on net coral growth were largely based on coral susceptibility to predation. Accumulation of *Acropora pulchra* mass was strongly enhanced by caging, likely due to the exclusion of excavating corallivores like the triggerfish *Balistapus undulatus*. While these impacts may have been exacerbated by out-planting relatively small fragments of *A. pulchra* into a previously coral-depauperate region, prior work has found that impacts of biotic enemies on small coral outplants predict effects for larger colonies as well (Bonaldo & Hay 2014). Our results are also consistent with previous studies that found that excavating corallivores such as balistids preferentially target the apical tips of fast-growing acroporids and pocilloporids (Cole et al. 2008, White & O'Donnell 2010) and that growth and survival of these corals are enhanced when they are protected from predation by territorial damselfishes (Gochfeld 2010, White & O'Donnell 2010, Kamath et al. 2019). In stark contrast, caging did not enhance the net growth of *Porites rus*. This is consistent with the lack of observed bites from excavating corallivores on this species and previous work noting that excavating corallivores primarily target pocilloporids and acroporids in the Indo-Pacific (Cole et al. 2008). However, we could not evaluate predation from browsing corallivores that do not remove coral skeletons (e.g. *Chaetodon lunulatus*; Rotjan & Lewis 2008, Cameron & Edmunds 2014) and fish that do not typically target corals (e.g. *Ctenochaetus striatus*). It is possible that impacts of these predation events or differences in coral growth rates might be more apparent via the use of potentially more accurate measurements of growth and skeletal accumulation, such as surface area-corrected buoyant weighing (Davies 1989), or over longer experimental periods. Regardless, our results suggest that *P. rus* is not immune to predation but seems to suffer minimal damage due to fish corallivores. Given that browsing corallivores can have long-term effects on coral fitness (Rotjan & Lewis 2008, Cole et al. 2011) and that this study had a relatively short duration, the effects of chronic predation on *P. rus* growth and *A. pulchra* regrowth over longer periods warrant further investigation.

Fertilizer addition did not impact the net growth of either coral in our experiment. While enhanced nutrient supply can stimulate coral growth (Meyer et al. 1983, Savage 2019), it appears that corals can better utilize nutrients from natural sources (e.g. bird and fish wastes) as opposed to anthropogenic sources such as fertilizer (Shantz & Burkepile 2014, Savage 2019, Burkepile et al. 2020). Fertilizer addition may also harm corals by enhancing disease (Bruno et al. 2003) and bleaching sensitivity (Wiedenmann et al. 2013, Burkepile et al. 2020), and these impacts may be exacerbated by exposure to predators (Shaver et al. 2017). However, no bleaching occurred during our experiment and we rarely observed mortality extending beyond the boundaries of algal overgrowth, suggesting that neither disease nor bleaching played a noticeable role in affecting the coral performance we documented here.

Although we did not explicitly test how fertilizer addition affected the nitrogen content of corals or their holobiont (e.g. Becker et al. 2021), fertilizer addition did increase bite rates on both *A. pulchra* and *P. rus* by corallivores, possibly by increasing the nutritional value of these corals, similar to what has been observed in other systems (e.g. Cruz-Rivera & Hay 2000, 2003, Burkepile & Hay 2009). We detected no evidence of predator impacts on *P. rus* growth during our experiment but cannot rule out the possibility that enhanced predation on fertilized individuals might impact this coral over longer periods (Cole et al. 2011) or might do so indirectly via disease transmission by corallivores (Raymundo et al. 2009). Additionally, the inclusion of a single outlier altered our results such that there was no longer a significant difference in the rates of predation between fertilized and unfertilized replicates of *A. pulchra*. Regardless, these results suggest that nutrient runoff alone may not have direct deleterious effects on physiological aspects of growth for these corals. Given the relatively short duration of this experiment compared to others that have examined the impacts of nutrient enrichment (e.g. Sotka & Hay 2009, Vega Thurber et al. 2014), further investigation into the differential effects of chronic fertilizer enrichment on coral growth, frequency of disease, the dynamics of algal—coral interactions as well as differences in how corals use and assimilate these nutrients is warranted.

Our cages excluded both coral- and algal-eating fishes, and herbivore removal can limit coral growth by allowing the proliferation of algal competitors (Burkepile & Hay 2010, Rasher et al. 2012). While the effect of our exclusion cages on coral growth seemed largely limited to predator impacts, herbivore exclusion did lead to differential impacts of algal overgrowth on corals. *A. pulchra* was rarely overgrown by algae regardless of treatment, and this is consistent with previous work suggesting that this species is a strong competitor against turf algae (Darling et al. 2012, Swierts & Vermeij 2016). In contrast, algal overgrowth of *P. rus* was impacted by caging and fertilization. While these trends may have been exacerbated by manipulating small fragments as opposed to large corals, White & O'Donnell (2010) found that acroporids preferentially recruit to and persist in the algal gardens of territorial damselfish, whereas the presence of these fishes suppresses *Porites* cover, suggesting that *Porites* may be more susceptible to algal overgrowth. This suggestion is further supported by previous work in which we found that *P. rus* was more strongly impacted by contact with turf algae than *A. pulchra* (Altman-Kurosaki et al. 2024).

Although we had expected *P. rus* to be more strongly impacted by herbivore removal than *A. pulchra*, we did not predict the manner in which caging and fertilizer addition would affect algal overgrowth. In uncaged treatments, fertilizer addition led to more overgrowth of *P. rus* than in unfertilized treatments; however, this trend was reversed in caged treatments, where *P. rus* fragments without fertilizer experienced more turf overgrowth. This result was contrary to our expectations. While nutrient enrichment can favor algae in coral—algal interactions (Vermeij et al. 2010), multiple reviews and manipulative experiments have found that nutrient enrichment generally leads to increased algal abundance only in areas of reduced herbivory (Burkepile & Hay 2006, 2009, 2010, Gruner et al. 2008, Rasher et al. 2012), as top-down control by herbivores can overwhelm the ability of nutrient additions to foster greater cover or mass of primary producers (Silliman & Zieman 2001, Burkepile & Hay 2009, Rasher et al. 2012). Our observation that herbivory was higher on fertilized plots is consistent with this expectation. While herbivory at our site could potentially have been reduced to the extent that herbivores were unable to control enhanced algal productivity (Knowlton & Jackson 2008, Houk et al. 2018), this would not explain why unfertilized *P. rus* experienced greater overgrowth inside fish exclusion cages.

Our fertilized exclosures may have attracted grazing amphipods, crabs, or other small herbivores that could enter the cage mesh (Altman-Kurosaki et al. 2018). These invertebrates might have preferentially migrated to and survived in the caged and fertilized treatments due to the lower risk of predation and increased nutrient content of algae on those plots (Cruz-Rivera & Hay 2000), similar to the herbivorous fishes that we observed feeding selectively on our fertilized plots. We did not assay for such herbivores but noted no obvious among-treatment differences in these while monitoring and maintaining the experiment. It is also possible that enhanced predation on fertilized *P. rus* outside of cages created small lesions that were rapidly overgrown by algae (Gerhart 1990, Raymundo et al. 2016, Shaver et al. 2017), which more readily utilize nutrients from fertilizer than corals (den Haan et al. 2016). On larger coral heads, coral morphology itself could potentially have prevented fish access to feeding on some colony portions and produced between-species differences in the consumption of algae in refuge spaces (Bennett et al. 2010, Poray & Carpenter 2014), but this would not be the case with the smaller and more structurally simple branches used in our experiments; fishes could approach all portions of these corals (Fig. S1). Additionally, some algae alter their morphology and growth strategy as a function of herbivory, investing more into lateral runners and less into upright structures when herbivory is higher (Lewis et al. 1987). It is possible that following fertilizer addition in the uncaged plots, the more frequent grazing caused algae to prioritize lateral spread over upright growth, resulting in increased algal overgrowth of corals in the fertilized uncaged treatments. When caged and fertilized, these algae were ungrazed and may have prioritized growth of upright versus lateral creeping branches and thus covered less adjacent coral tissue. Regardless of the mechanisms involved, the complex and interactive effects of herbivore exclusion and nutrient enrichment on corals suggest that this area warrants further research.

Despite the threats coral reefs face at global scales, understanding and managing the impact of local stressors can enhance near-term resilience (Donovan et al. 2021). Here, we found divergent responses to simulated local stressors between 2 corals with different traits and life history strategies (Darling et al. 2012). Given that many faster-growing corals like *A. pulchra* are increasingly threatened by global stressors such as ocean warming (Carpenter et al. 2008, Hughes et al. 2018) and that some acroporids are already endangered (Miller et al. 2022), the increased vulnerability of slower-growing, hardier taxa like *P. rus* (Lenz & Edmunds 2017) to algal overgrowth under some conditions is worrisome. The corollary to this is that effective policy to manage these stressors at local scales might increase reef resilience and resistance to stressors at larger scales. For example, mitigating nutrient runoff could minimize algal overgrowth of hardier corals like *P. rus* that are becoming characteristic of disturbed reefs following bleaching events (Donner & Carilli 2019, Cannon et al. 2021), thus maintaining live coral structure and 'buying time' for future reefs. Increased understanding of taxa-specific coral responses to shifts in fish assemblage, nutrient regimes, and their interactions may facilitate better conservation and management of reefs in the Anthropocene.

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