Coral performance is comparable when transplanted to disparate reef sites despite divergent histories of reef decline and recovery

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ABSTRACT: As coral reefs degrade worldwide, researchers and managers need to determine whether corals can acclimatize to altered local conditions or whether their fixed phenotypes prevent coral persistence under these new environmental conditions. Fixed phenotypes could produce environmental mismatches that reduce population connectivity and exacerbate decline in the near-term, but a capacity for acclimatization could be harnessed in both passive and proactive coral restoration efforts. Here, we conducted a reciprocal transplant experiment in Moʻorea, French Polynesia, to test how intraspecific performance of 2 common coral species (*Acropora hyacinthus* and *Pocillopora verrucosa*) varied between a neighboring forereef and backreef that differed dramatically in trajectories of coral loss, resilience over decadal time scales, and cover of corals versus competing macroalgae. We also tested how corals responded to 2 common stressors — corallivory and macroalgal competition — and how this varied as a function of transplant location and the area of origin. Growth and survival of both coral species were affected by macroalgal competition, corallivory, transplant location, or some combination thereof, but we found limited evidence that the habitat of origin significantly impacted intraspecific performance. These results suggest that acclimatization capacity may outweigh local adaptation for these common reef-building species and could be leveraged to facilitate coral restoration.

KEY WORDS: Coral reef · Acclimatization · Restoration · *Pocillopora verrucosa* · *Acropora hyacinthus* · Adaptive management · Macroalgae · Coral−algal competition · Corallivory

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1. INTRODUCTION

Corals are declining on tropical reefs worldwide due to a variety of local (e.g. overfishing and nutrient pollution) and global disturbances (e.g. ocean warming and acidification) threatening vital ecosystem functions and the services that coral reefs provide (Bellwood et al. 2004, Eddy et al. 2021). However, coral loss is often spatially heterogeneous both at local and regional scales for reasons that remain inadequately understood (Kenkel et al. 2015, Schmitt et al. 2019). There are numerous examples of coral com-munities that have persisted or recovered following disturbances that reduced coral cover within neigh-boring reef systems (Idjadi et al. 2006, Graham et al. 2011, Roff et al. 2014, Edmunds 2018). These coral 'oases' (Guest et al. 2018, Elahi et al. 2022) or 'bright spots' (Cinner et al. 2016, Lester et al. 2020, Sully et al. 2022) are of considerable interest to managers as a tool and source population for restoring degraded reefs (Guest et al. 2018, Darling et al. 2019) — poten-tially via enhanced larval recruitment, assisted migra-tion, or assisted evolution (van Oppen et al. 2015, 2017, National Academies of Sciences, Engineering,

and Medicine 2019). However, identifying and predicting the conditions that will facilitate or undermine coral restoration efforts at localized scales remains a challenge.

The processes that influence local coral decline or recovery can be multifactorial and context-dependent, but connectivity among populations plays an integral role in the recovery of coral communities after a disturbance (Underwood et al. 2009, Graham et al. 2011, Edmunds et al. 2018, Holbrook et al. 2018, McManus et al. 2021). Connectivity of coral populations inherently depends on coral recruits — whether via natural- or human-mediated processes — successfully establishing and persisting to reproductive maturity in environments that may differ from parental environments. Numerous studies suggest that initial recruitment is not enough to guarantee successful recovery, and that differing physical conditions or biotic interactions across habitat types may prevent new recruits from surviving to reproduce unless the habitat is receptive and supportive of recruits (Burkepile & Hay 2008, Marshall et al. 2010, Mumby & Steneck 2008).

Eco-evolutionary processes at multiple spatial scales shape the structure, function, and resilience of coral reef ecosystems, and are expected to play critical roles in efforts to conserve corals in the Anthropocene (Colton et al. 2022). Increasing evidence suggests that local adaptation of corals and other benthic animals to increasingly disparate habitats may act as a barrier to connectivity (Rippe et al. 2021, Thomas et al. 2022) and recovery (Kenkel et al. 2015). If localized selection is strong, phenotypes may adapt to one environment at a cost of being able to persist in others. On coral reefs, such 'phenotype–environment mismatches' (Marshall et al. 2010) may prevent individuals from one site surviving to maturity under environmental contexts that differ from their reef of origin. If the traits that confer success at the reef of origin but failure in different environments are heritable, this can limit the ability of recruits from bright spots to successfully colonize and reach maturity on disturbed reefs in need of recruits to aid recovery (Shlesinger & Loya 2021). These phenotype–environment mismatches could help explain divergent coral community responses to, and trajectories after, disturbances at local scales (Kenkel et al. 2015, Thomas et al. 2022). Furthermore, such mismatches could pose challenges for active management and restoration of corals (e.g. assisted migration) in increasingly fragmented and disparate reef systems if larvae or transplants from healthy refuge sites are poorly adapted to settle, survive, or reach maturity on disturbed reefs.

Conversely, some studies on tropical reefs have found that corals transplanted to novel reefs with markedly different biological (e.g. coral vs. macroalgal dominance of the benthos; Clements et al. 2018) or physiochemical (e.g. pH, dissolved oxygen, sedimentation; Barott et al. 2021) conditions can perform equal to, or better than, local corals. This suggests that acclimatization can occur and could be harnessed to boost the fitness of recipient coral populations. Additional research is needed to determine the extent to which restrictive localized adaptation vs. acclimatization or broad physiological scope shapes coral fitness and demographics, as well as the external drivers that may shape these responses, across divergent sites.

Investigations of whether organisms are restrictively specialized to certain environments or have broad physiologies allowing success in a range of habitats most often involve reciprocal transplants between differing sites and comparing metrics of performance (e.g. growth, survival, bleaching susceptibility; Kenkel et al. 2015, Tamir et al. 2020, Barott et al. 2021, Baumann et al. 2021, Shlesinger & Loya 2021, Thomas et al. 2022). If local selection is strong and limits phenotype flexibility, individuals relocated away from their reef of origin should underperform compared to conspecifics that are transplanted back to their home reef. In contrast, if corals possess sufficient physiological range or ability to acclimatize, then performance could be comparable among conspecifics regardless of their reef of origin.

In Mo'orea, French Polynesia, we reciprocally transplanted colonies of 2 common coral species — *Acropora hyacinthus* and *Pocillopora verrucosa* — between a deeper forereef with high coral and low macroalgal cover and a shallower backreef with low coral and high macroalgal cover. Our main aim was to determine how growth and survival of transplanted corals varied between reef environments and whether coral origin differentially impacted performance. These nearby reef habitats differ dramatically in historical trajectories of coral loss and resilience over decadal time scales, with the forereef consistently returning to high coral cover following disturbance, and the backreef exhibiting consistent coral loss and increased macroalgal abundance over the same time period (Adjeroud et al. 2009, Trapon et al. 2010, Adam et al. 2011, Holbrook et al. 2018, Schmitt et al. 2022). We predicted that corals would exhibit a high degree of local adaptation. Accordingly, we expected that coral performance would be highest for corals transplanted to their reef of origin compared to a novel reef habitat.

In addition to assessing the effects of coral origin and transplant location, we also tested how coral performance varied as a function of corallivore and herbivore exclusion (i.e. via caging), as well as macroalgal competition. These biotic interactions can be important determinants of coral fitness and are considered strong drivers of coral performance on the reefs of Mo'orea (Lenihan et al. 2011, Bulleri et al. 2013, 2018,

Schmitt et al. 2019, 2022, Ladd et al. 2021). In general, the more degraded backreef is characterized by higher cover of macroalgae and lower herbivory than the coral-dominated forereef (Adam et al. 2011, Schmitt et al. 2019), while corallivory is a chronic stressor on both the backreef (Lenihan et. al. 2011) and forereef, but tends to decline with depth (Ladd et al. 2021). From a management perspective, it will be useful to know if corals from the forereef, which has differed from the backreef in coral decline, algal proliferation, and other environmental conditions (e.g. depth-dependent light availability, corallivory, herbivory), could serve as sources to help damaged backreef sites recover.

2. MATERIALS AND METHODS

2.1. Study site

Our study was conducted from July to September of 2017 on the north coast of Mo'orea, French Polynesia, a high volcanic island in the central south Pacific 20 km west of Tahiti. We focused our efforts on 2 coral reef habitats that differ in their benthic community composition and response to coral-killing disturbances: (1) the forereef (i.e. outer slope) and (2) the neighboring backreef within the lagoon (Fig. 1). Despite periodic disturbances that dramatically reduced coral cover, the forereef has consistently exhibited a rapid return to high coral cover (~40%) and low abundances of macroalgae (<2%; Adjeroud et al. 2009, Trapon et al. 2010, Adam et al. 2011, Holbrook et al. 2018, Schmitt et al. 2022). In contrast, coral cover on the backreef has declined over the past several decades and has stabilized at low levels (<5%), while macroalgal cover consistently increased and remains elevated (20+%) across the north coast of Mo'orea (Schmitt et al. 2019, Adam et al. 2021). During the months of our study, temperatures averaged 27.05 ± 0.01°C (range = 23.97−29.03°C) on the backreef (2 m) and 27.08 ± 0.01°C (range = 26.26−27.84°C) on the forereef (10 m), indicating similar mean
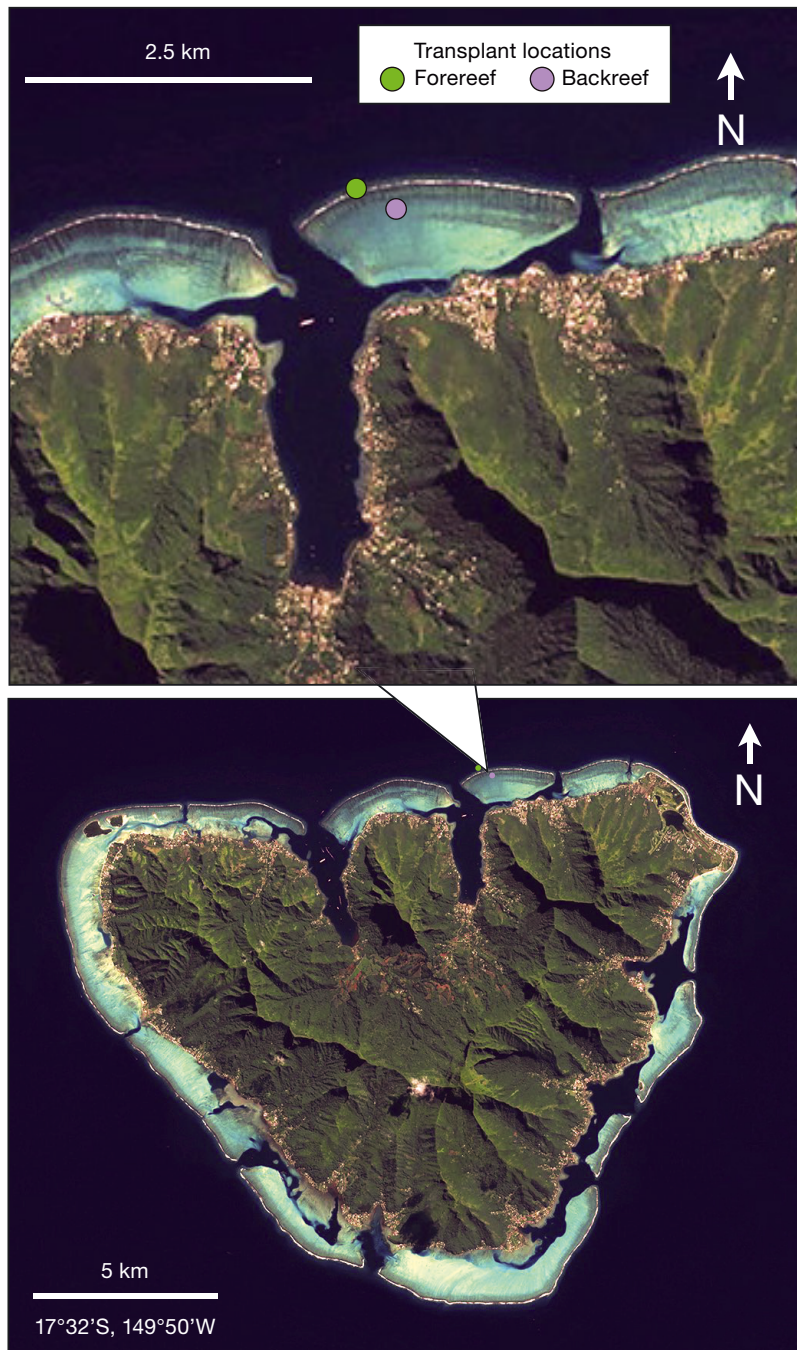

Fig. 1. Mo'orea, French Polynesia, showing the forereef and backreef locations where corals were collected from and transplanted to for this study

temperatures but large differences in temperature ranges between habitats (Moorea Coral Reef LTER et al. 2023). Underwater light intensity data during our study period are unavailable. As a proxy, we leveraged long-term records (P. J. Edmunds unpubl. data; May 2021 to January 2024; n = 918 d) of offshore seawater clarity at 17 m depth at our forereef site (recorded as the diffuse attenuation coefficient, KdPAR) and surface photosynthetically active radiation (PAR) to estimate mean ± SE light intensity of 30.10 ± 0.29 mol m^{-2} d^{-1} at our backreef site (2 m) and 15.10 ± 0.16 mol m^{-2} d^{-1} at our forereef site (10 m).

2.2. Field experiment

Between July and September 2017, we conducted a reciprocal transplant experiment to investigate how coral origin and transplant location interact with common ecological processes — algal competition, corallivory, and herbivory — to influence coral growth and survivorship. We chose *Acropora hyacinthus* and *Pocillopora verrucosa* because they represent coral genera that are important reef builders around Mo'orea and primary contributors to the recurrent coral recovery observed on the forereef following disturbances in recent years (Adjeroud et al. 2009, 2018, Edmunds 2018). In July 2017, we fragmented 8 branches (each ~6–8 cm in length) from 15 colonies of both *A. hyacinthus* and *P. verrucosa* from (1) a shallow backreef within the lagoon (~2.5 m depth, 17° 28′ 29″ S, 149° 48′ 54″ W) and (2) the neighboring forereef (~10 m depth, 17° 28′ 23″ S, 149° 49′ 09″ W) (Fig. 1). These sites were separated by a distance of approximately 500 m. To acquire samples broadly representative of these corals in each location, we collected samples from 15 colonies separated by at least 10 m from each other from an area spanning about 200 m × 80 m at each site. Branches from each colony were placed into labeled bags and transported in coolers filled with fresh seawater to onshore running seawater tables where each branch was epoxied (Z-Spar A-788 Splash Zone Epoxy) individually into the cutoff and inverted neck of a soda bottle. We have utilized this method extensively with more than 10 000 individuals representing 15 different species (see Clements & Hay 2015, Clements et al. 2020 for examples), and noted no signs of bleaching or tissue necrosis in response to the fragmentation or epoxy process. Each coral/bottleneck combination was individually labeled and buoyant-weighed following Davies (1989). Within 24 h of initial collection, corals were transplanted to their designated experimental backreef or forereef locations.

For each of the individual coral colonies from each experimental location, 4 fragments were transplanted to the other reef location and 4 were transplanted back onto their reef of origin. As a robust test of the hypothesis that corals might be disadvantaged by placement in a different environment, we did not allow corals to acclimatize slowly via small incremental changes over time but transplanted them to their respective experimental reefs within 24 h of initial collection.

To simultaneously test the influence of coral origin, transplant location, direct algal competition, and corallivory/herbivory on coral performance, 4 *P. verrucosa* and 4 *A. hyacinthus* originating from each reef area were randomly assigned to the following treatments when reciprocally transplanted to each reef area (n = 15 per treatment; Fig. 2):

(1) coral uncaged (i.e. exposed to consumers) and lacking algal contact,

(2) coral caged (i.e. protected from consumers) and lacking algal contact,

(3) coral uncaged and contacting ~8 cm tall portions of the alga *Turbinaria ornata*,

(4) coral caged and contacting *Turbinaria ornata*

Our experimental units consisted of 15.24 cm × 15.24 cm platforms made of PVC-coated mesh (hole size 2.54 cm × 2.54 cm) that were elevated ~8 cm above the substrate on all-thread posts, which were drilled into the reef framework and epoxied in place (Fig. 2b). Four inverted lids from plastic bottles were attached to the corners of the upper surface of each platform via a bolt that was driven through the center of the lid and secured with a 6 mm plywood washer. Corals could then be attached to the platform by screwing their bottleneck into their designated lid. Half of each platform was surrounded by a 15.24 cm × 7.62 cm × 10.16 cm PVC-coated mesh cage (hole size 2.54 cm × 2.54 cm) to prevent exposure to both corallivorous and herbivorous fishes in a manner similar to previous studies (Kopecky et al. 2021, Ladd et al. 2021).

Two corals from each species were attached to each platform via a bottle lid; one was within the enclosure and the other was attached to the uncaged portion of the platform, for a total of 4 corals per platform. On each platform, all corals were either in direct contact with 2 ca. 8 cm thalli of the brown alga *Turbinaria ornata* or lacked algal contact. *T. ornata* (hereafter *Turbinaria*) is the most abundant macroalgal species present in the backreefs of Mo'orea (Moorea Coral Reef LTER & Carpenter 2018), which is often considered *Turbinaria*-dominated (Schmitt et al. 2022). *Turbinaria* has been associated with reduced growth and recruitment of corals within the lagoon (Bulleri et al. 2013, 2018).
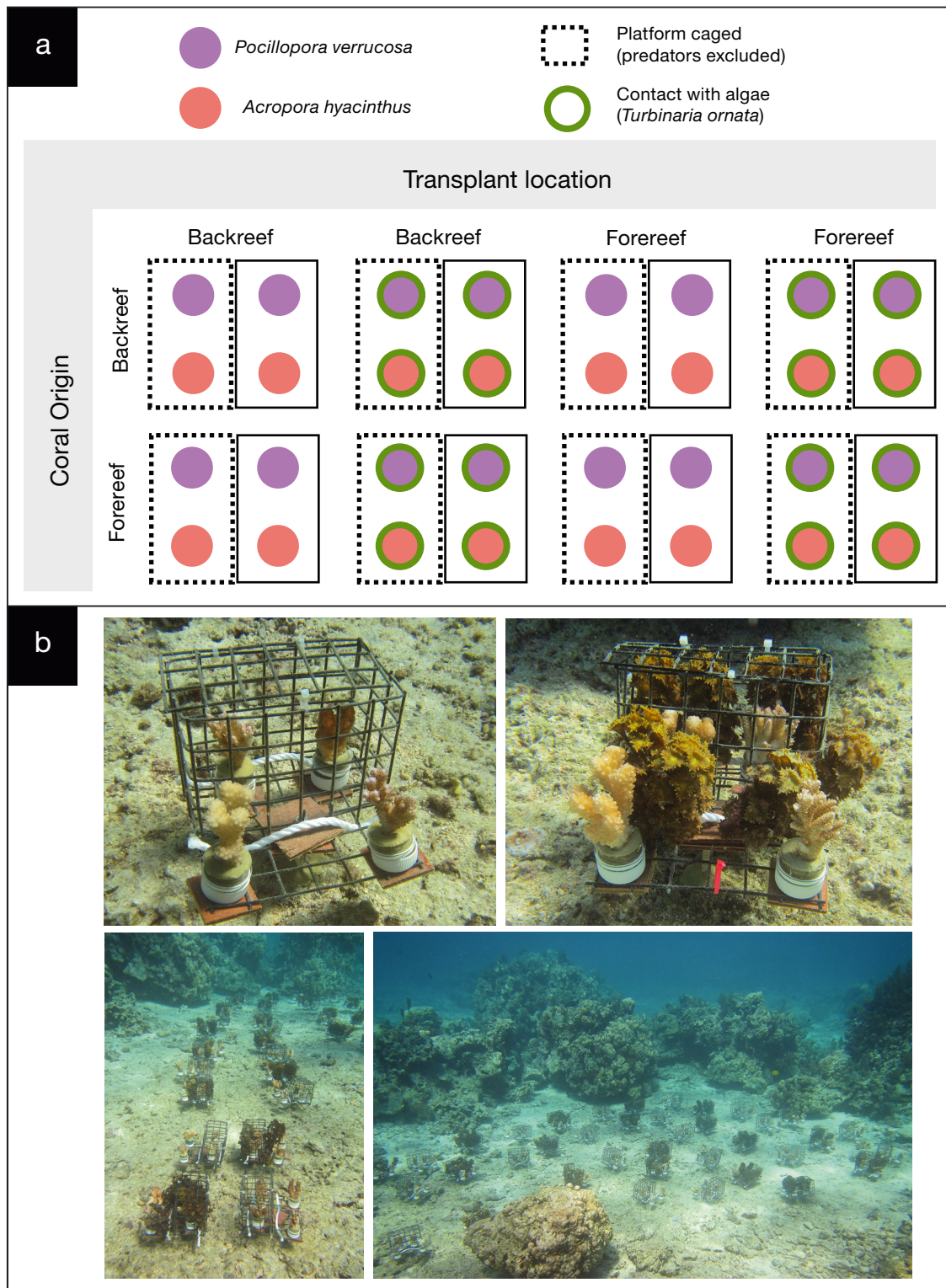
Fig. 2. (a) Schematic and (b) example photographs from the field depicting the experimental design for manipulations. Corals (*Acropora hyacinthus* and *Pocillopora verrucosa*) originating from the forereef and backreef were reciprocally transplanted to each area, and were either caged or uncaged (to test effects of corallivore and herbivore exclusion) and exposed or not exposed to the macroalga *Turbinaria ornata* (to test effects of macroalgal competition). In (b), top left and right images show an experimental unit with and without *Turbinaria*, respectively, and bottom left and right images show replicates in place within the backreef

To create standardized units of coral—algal contact, *Turbinaria* thalli were attached to the upper surface of their respective platforms via a 3-strand rope that was threaded between holes of the PVC-coated mesh (Fig. 2b). Corals not assigned to treatments involving macroalgal contact received a rope without algae. All *Turbinaria* were collected from the backreef area surrounding our study site, and *Turbinaria* was not present at our forereef site. We used representative-sized *Turbinaria* that are common on the backreef, and intact, whole thalli were used to avoid stress compounds that might be released if seaweeds were clipped. Platforms with or without *Turbinaria* were interspersed haphazardly within the ~100 m^2 study area at each transplant location (for example, see Fig. 2b).

After 60 d (28 July to 26 September), corals were detached from their experimental platforms and transported in coolers filled with fresh seawater to onshore water tables. At this time, we also collected all algae from caged and uncaged portions of the platforms to quantify the impact of *Turbinaria* addition and herbivore exclusion in our manipulations and to quantify any additional algae that had recruited during the 60 d experiment. On shore, bottle lid bases were cleaned of epibionts and each coral was buoyant-weighed and tissue mortality assessed visually into 10% classes (0, 10, 20, … 100%). Algae were wet-weighed to the nearest 0.1 g after removing excess water using a salad spinner (15 revolutions per sample). Following assessments, all corals were transplanted back to their original backreef or forereef locations.

2.3. Statistical analyses

We used permutation-based, mixed-effects models in the R (R Core Team 2020) package 'predictmeans' (Luo et al. 2020) to separately compare differences in percentage mass change and percentage tissue mortality of *P. verrucosa* and *A. hyacinthus* as a function of coral origin (backreef vs. forereef), transplant location (backreef vs. forereef), exposure to corallivores/herbivores (caged vs. uncaged), and algal competitors (initial addition of *Turbinaria* vs. no addition). Permutation-based analyses have the benefit of utilizing an empirical distribution created from permutations of the observed data — rather than a theoretical distribution — for testing hypotheses (Kabacoff 2022). Our approach takes advantage of this while also incorporating random effects into the structure of our models. In each analysis, coral origin, transplant location, cag-

ing status, and algal addition were treated as interacting fixed effects, with coral colony treated as a random effect to account for coral branches collected from the same coral colony that were allocated to separate treatments. When appropriate, subsequent comparisons were conducted via a post hoc permutation test for multiple comparisons using the R package 'predictmeans'. Two individual *P. verrucosa* and 2 *A. hyacinthus* corals that became dislodged from their epoxy base during collection and transport were excluded from the analyses. To compare differences in algal mass as a function of transplant location, algal addition, and caging status, we used a permutation-based linear model and post hoc permutation test for multiple comparisons using the R package 'predictmeans'.

3. RESULTS

Overall, the evidence that the origin of a coral impacted its performance was limited and context dependent. Origin did not consistently impact growth and survival across either species, and the few significant pairwise differences that were observed involved interactions with external biotic effects incorporated into our manipulations. For example, *Acropora hyacinthus* growth ranged from a high of 30.3 ± 1.7% (mean ± SE; backreef origin, backreef transplant location, caged, *Turbinaria* not added) to a low of 13.3 ± 1.3% (backreef origin, forereef transplant location, caged, *Turbinaria* added). *A. hyacinthus* growth differed as a function of transplant location (p = 0.019), caging status (p = 0.040), and algal contact (p = 0.001), but not coral origin (p = 0.123); however, 2 of these main effects were qualified by a significant interaction between caging status and contact with algae (p = 0.002) (Table 1A). This was reflected in post hoc analyses; in general, *A. hyacinthus* growth was suppressed when in contact with algae, and this was exacerbated when corals were caged (Fig. 3). Furthermore, there were no instances where growth differed between corals originating from different reefs when controlling for transplant location, caging status, and algal contact.

A. hyacinthus tissue mortality did differ as a function of coral origin (p = 0.012) and transplant location (p = 0.004), but these were qualified by significant interactions between coral origin and transplant location (p = 0.026), and caging status and algal contact (p = 0.047; Table 1B). There were also marginal to nonsignificant interactions among coral origin, transplant location, and algal contact (p = 0.098; Table 1B), as

Table 1. Permutation-based mixed-effects model results for *Acropora hyacinthus* (A) growth and (B) tissue mortality as a function of coral origin, transplant location, caging status, and contact with the alga *Turbinaria*. Degrees of freedom = 1 for all main effects; p-values defined as significant at a threshold of 0.05 are highlighted in **bold**

Main effects	SS	MS	*F*	Perm p
(A) *Acropora hyacinthus* growth				
Coral origin	160.242	160.242	2.754	0.123
Transplant location	346.375	346.375	5.953	**0.019**
Caging status	247.840	247.840	4.260	**0.040**
Algal contact	3833.232	3833.232	65.879	**0.001**
Coral origin × Transplant location	60.095	60.095	1.033	0.311
Coral origin × Caging status	24.181	24.181	0.416	0.521
Transplant location × Caging status	192.291	192.291	3.305	0.066
Coral origin × Algal contact	35.760	35.760	0.615	0.455
Transplant location × Algal contact	35.873	35.873	0.617	0.404
Caging status × Algal contact	511.541	511.541	8.792	**0.002**
Coral origin × Transplant location × Caging status	21.748	21.748	0.374	0.564
Coral origin × Transplant location × Algal contact	1.194	1.194	0.021	0.887
Coral origin × Caging status × Algal contact	35.396	35.396	0.608	0.462
Transplant location × Caging status × Algal contact	20.047	20.047	0.345	0.583
Coral origin × Transplant location × Caging status × Algal contact	4.841	4.841	0.083	0.777
(B) *Acropora hyacinthus* tissue mortality				
Coral origin	706.303	706.303	4.667	**0.012**
Transplant location	764.545	764.545	5.052	**0.004**
Caging status	222.628	222.628	1.471	0.114
Algal contact	155.145	155.145	1.025	0.379
Coral origin × Transplant location	693.957	693.957	4.585	**0.011**
Coral origin × Caging status	185.022	185.022	1.223	0.187
Transplant location × Caging status	219.189	219.189	1.448	0.131
Coral origin × Algal contact	120.972	120.972	0.799	0.558
Transplant location × Algal contact	149.936	149.936	0.991	0.377
Caging status × Algal contact	641.085	641.085	4.236	**0.047**
Coral origin × Transplant location × Caging status	178.713	178.713	1.181	0.203
Coral origin × Transplant location × Algal contact	118.632	118.632	0.784	0.559
Coral origin × Caging status × Algal contact	573.829	573.829	3.791	0.098
Transplant location × Caging status × Algal contact	630.445	630.445	4.166	0.050
Coral origin × Transplant location × Caging status × Algal contact	563.188	563.188	3.721	0.109

well as among transplant location, caging status, and algal contact (p = 0.050; Table 1B). Post hoc pairwise comparisons revealed that percent tissue mortality was greatest among corals originating from the fore-reef that were outplanted to the backreef, uncaged, and in contact with *Turbinaria* (Fig. 4). However, overall mortality was limited. None of the corals transplanted to the forereef exhibited partial mortality, 7 corals (6%) transplanted to the backreef exhibited 10−100% mortality (mean of all *A. hyacinthus* transplanted to the backreef = 3.6 ± 1.7%), and only 4 of these 7 corals experienced 100% mortality — all of which were forereef corals transplanted to the backreef. We observed evidence of corallivory on ~8.4% (10 of 120) corals transplanted to the forereef, but in all cases, corals were already healing and did not exhibit partial mortality. On the backreef, ~11.8% (14 of 120) of corals exhibited evidence of recent corallivory, including 11 corals that were already healing (i.e. no

partial mortality) and 3 that exhibited 10% tissue mortality.

Pocillopora verrucosa growth ranged from a high of 19.2 ± 1.3% (forereef origin, forereef transplant location, uncaged, both *Turbinaria* present and absent) to a low of 7.5 ± 1.1% (backreef origin, forereef transplant location, caged, *Turbinaria* present). *P. verrucosa* growth differed as a function of caging status (p = 0.001) and algal contact (p = 0.001; Table 2A), but not coral origin (p = 0.089) or transplant location (p = 0.087). However, main effects were qualified by significant interactions between caging status and contact with algae (p = 0.002), as well as 3-way interactions among (1) coral origin, caging status, and algal contact (p = 0.004) and (2) transplant location, caging status, and algal contact (p = 0.009; Table 2A). As with *A. hyacinthus*, post hoc comparisons revealed that algal contact consistently suppressed *P. verrucosa* growth and was exacerbated when corals were
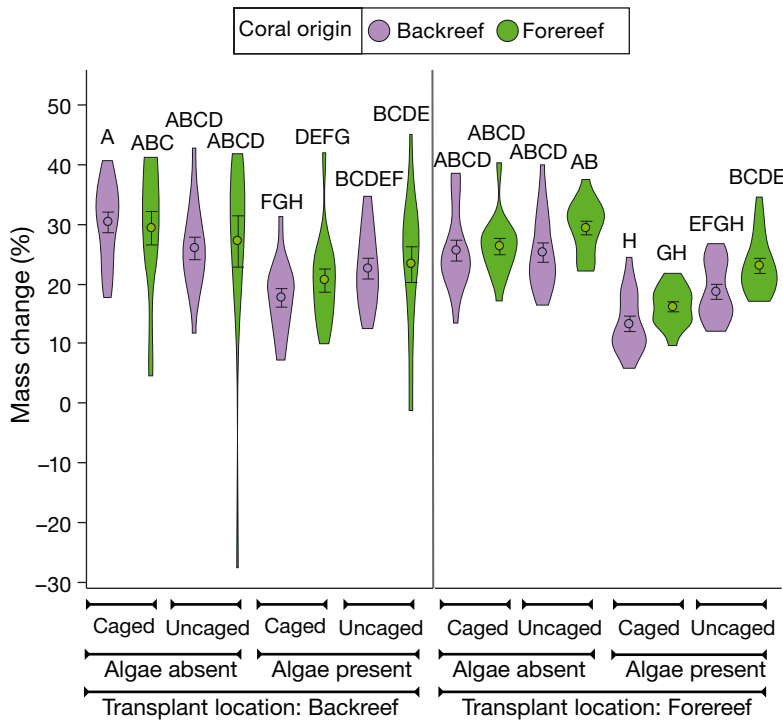
Fig. 3. Percent growth of *Acropora hyacinthus* (mean ± SE) as a function of coral origin, transplant location, caging status, and contact with algae (*Turbinaria*). Letters above violin plots indicate significant groupings based on post hoc permutation test for multiple comparisons. Colors depict coral origin to highlight comparisons assessing local adaptation vs. acclimatization of coral transplants. p-values obtained from post hoc tests were adjusted using the Benjamini-Hochberg method to control the false discovery rate, and treatments were considered significantly different if the adjusted p-value was less than 0.05
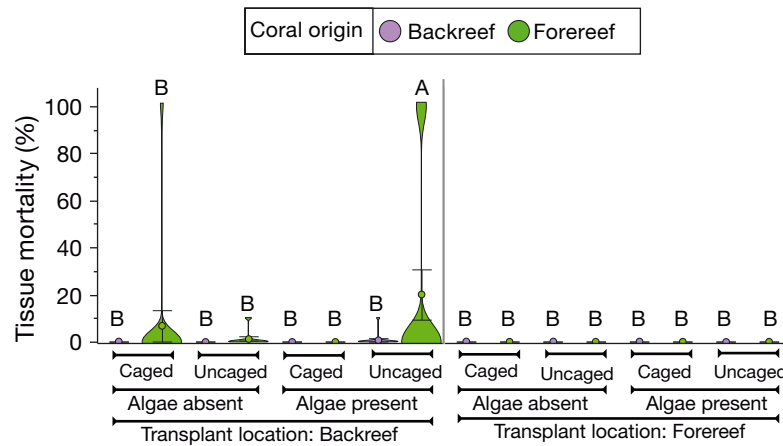

Fig. 4. Percent tissue mortality of *Acropora hyacinthus* (mean ± SE) as a function of coral origin, transplant location, caging status, and contact with algae (*Turbinaria*). Other details as in Fig. 3

caged with algae. On the backreef, caging suppressed growth more among corals originating from the backreef compared to conspecifics from the forereef, both with and without algal contact (Fig. 5).

P. verrucosa tissue mortality also differed as a function of transplant location (p = 0.001) and caging status (p = 0.009) but was again qualified by significant interactions between transplant location and caging status (p = 0.026), as well as between transplant location and algal contact (p = 0.031; Table 2B). Post hoc comparisons revealed that percent tissue mortality tended to be greater among corals outplanted on the backreef, and this was exacerbated when corals were uncaged and in contact with algae (Fig. 6). No significant differences in mortality were observed between corals originating from different reefs when controlling for transplant location, caging status, or algal contact. Only 7 of the 120 corals (~5.8%) transplanted on the forereef exhibited signs of corallivory, but all were already healing and did not exhibit partial tissue mortality. In contrast, 21 of the 120 corals (~17.8%) in the backreef exhibited evidence of recent corallivory, including 8 corals that were already healing (i.e. no partial mortality) and 13 that exhibited 10–50% tissue mortality.

Consumer exclusion within caged portions of our platforms had significant impacts on macroalgal abundances within our manipulations. Algal mass at 60 d differed as a function of transplant location (p = 0.001), caging status (p = 0.001), and initial addition of *Turbinaria* algae (p = 0.001), but these main effects were qualified by significant interactions between transplant location and caging status (p = 0.047), and caging status and addition of *Turbinaria* (p = 0.023), as well as a 3-way interaction among transplant location, caging status, and initial addition of *Turbinaria* algae (p = 0.001; Table 3). Post hoc comparisons revealed that algal mass was greatest within caged areas on the backreef where *Turbinaria* was initially added (59.4 ± 3.8 g), followed by caged areas with added *Turbinaria* on the forereef (44.9 ± 3.3 g; Fig. 7). These were followed by caged areas on the backreef where *Turbinaria* was not added (34.0 ± 4.2 g) and uncaged areas on the

Table 2. Permutation-based mixed-effects model results for *Pocillopora verrucosa* (A) growth and (B) tissue mortality as a function of coral origin, transplant location, caging status, and contact with *Turbinaria* algae. Degrees of freedom = 1 for all main effects; p-values defined as significant at a threshold of 0.05 are highlighted in **bold**

Main effects	SS	MS	*F*	Perm p
(A) *Pocillopora verrucosa* growth				
Coral origin	55.2448	55.2448	3.0596	0.089
Transplant location	56.5471	56.5471	3.1317	0.087
Caging status	368.5255	368.5255	20.4099	**0.001**
Algal contact	1613.381	1613.381	89.3533	**0.001**
Coral origin × Transplant location	6.8768	6.8768	0.3809	0.525
Coral origin × Caging status	60.8702	60.8702	3.3712	0.079
Transplant location × Caging status	2.233	2.233	0.1237	0.735
Coral origin × Algal contact	22.298	22.298	1.2349	0.268
Transplant location × Algal contact	57.2438	57.2438	3.1703	0.079
Caging status × Algal contact	187.1113	187.1113	10.3627	**0.002**
Coral origin × Transplant location × Caging status	129.2735	129.2735	7.1595	**0.004**
Coral origin × Transplant location × Algal contact	19.728	19.728	1.0926	0.313
Coral origin × Caging status × Algal contact	3.509	3.509	0.1943	0.633
Transplant location × Caging status × Algal contact	120.0166	120.0166	6.6468	**0.009**
Coral origin × Transplant location × Caging status × Algal contact	52.6669	52.6669	2.9168	0.097
(B) *Pocillopora verrucosa* tissue mortality				
Coral origin	0.7787	0.7787	0.0067	0.916
Transplant location	2096.177	2096.177	18.1255	**0.001**
Caging status	768.7401	768.7401	6.6473	**0.009**
Algal contact	329.4118	329.4118	2.8484	0.107
Coral origin × Transplant location	21.4138	21.4138	0.1852	0.675
Coral origin × Caging status	19.4357	19.4357	0.1681	0.672
Transplant location × Caging status	579.8387	579.8387	5.0138	**0.026**
Coral origin × Algal contact	16.3368	16.3368	0.1413	0.688
Transplant location × Algal contact	494.052	494.052	4.272	**0.031**
Caging status × Algal contact	230.4868	230.4868	1.993	0.159
Coral origin × Transplant location × Caging status	66.0114	66.0114	0.5708	0.456
Coral origin × Transplant location × Algal contact	64.4083	64.4083	0.5569	0.493
Coral origin × Caging status × Algal contact	76.7517	76.7517	0.6637	0.450
Transplant location × Caging status × Algal contact	369.0836	369.0836	3.1914	0.081
Coral origin × Transplant location × Caging status × Algal contact	166.3738	166.3738	1.4386	0.275

backreef with added *Turbinaria* (30.7 ± 3.6 g), which did not differ significantly from each other. Algal mass was least, and statistically indistinguishable among, uncaged areas on the backreef where *Turbinaria* was not added (0.0 ± 0.0 g), and on the forereef in both uncaged (0.1 ± 0.1 g) and caged (4.8 ± 2.8 g) areas where *Turbinaria* was not added (Fig. 7). Only platforms on the backreef held algae other than *Turbinaria* (predominantly *Rosenvengia* and *Dictyota* spp.); masses of these 'other algae' ranged from 0.0 ± 0.0 g in uncaged areas where *Turbinaria* was not added, to 34.0 ± 4.2 g in caged areas where *Turbinaria* was not added.

4. DISCUSSION

As coral reef systems around the world continue to degrade, there is an urgent need to assess if, and to what extent, coral populations adapt vs. acclimatize to altered environmental conditions. If adaptation (strong localized selection) is the predominant driver of demographic change, this could lead to phenotype—environment mismatches that reduce coral population connectivity, limit recovery from disturbance, and hinder coral restoration efforts if corals or larvae are added from sites not similar to the one in need of recovery (Dewitt et al. 1998, Marshall et al. 2010). In contrast, if acclimatization or broad ecological tolerance is common, then natural processes (e.g. recruitment from 'coral oases') or human intervention (e.g. assisted migration) could be leveraged more quickly to aid coral recovery (Palumbi et al. 2014, Barott et al. 2021).

We found limited evidence for localized adaptation limiting the success of transplants between habitats, despite the backreef and forereef areas we used differing dramatically in trajectories of coral cover and resilience over the past 40 yr (Adjeroud et al. 2009, Trapon
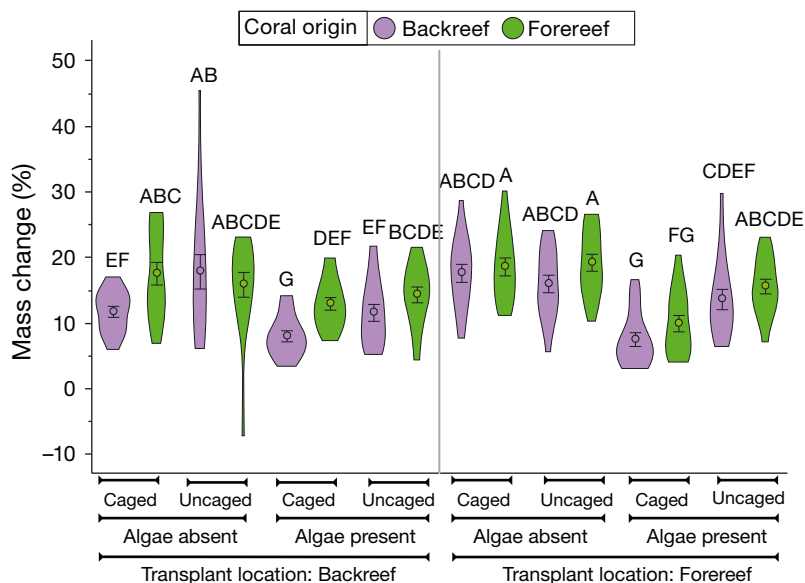
Fig. 5. Percent growth of *Pocillopora verrucosa* (mean ± SE) as a function of coral origin, transplant location, caging status, and contact with algae (*Turbinaria*). Other details as in Fig. 3
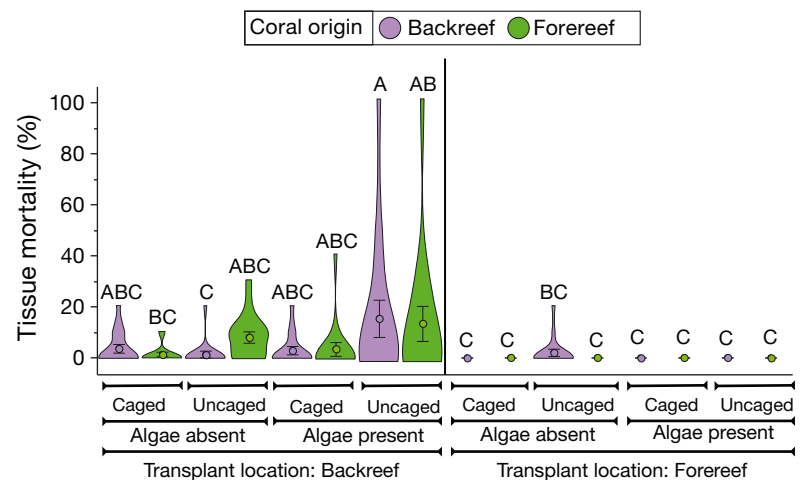

Fig. 6. Percent tissue mortality of *Pocillopora verrucosa* (mean ± SE) as a function of coral origin, transplant location, caging status, and contact with algae (*Turbinaria*). Other details as in Fig. 3

et al. 2010, Adam et al. 2011, Holbrook et al. 2018, Schmitt et al. 2019, 2022). The statistically discernible influence of coral origin on growth and survival was only evident when co-occurring with other experimentally manipulated stressors (e.g. algal competition). For example, coral origin significantly influenced *A. hyacinthus* mortality, but pairwise comparisons revealed that mortality was only significantly greater among corals originating from the fore-reef that were transplanted to the back-reef, uncaged, and in contact with *Turbinaria*; no other differences were observed among treatment groupings. Similarly, the influence of coral origin on *P. verrucosa* growth was statistically significant in higher-level interactions, but the only pairwise comparisons that differed between comparable treatment groupings involved greater growth among corals originating from the fore-reef, transplanted to the backreef, and caged with or without *Turbinaria*. In the latter case, this is the opposite of what we would expect if corals were selected to be most fit in their home site — corals originating from the backreef should have had strong home-site advantages compared to conspecifics relocated from the forereef (where they do not co-occur with *Turbinaria*).

In contrast to the disparate evidence for localized adaptation discussed above, we found consistent evidence for acclimatization when controlling for other experimentally manipulated stressors. There were no instances of differential performance among con-

Table 3. Permutation-based mixed-effects model results for algal mass as a function of transplant location, caging status, and initial addition of *Turbinaria* algae. Degrees of freedom = 1 for all main effects; p-values defined as significant at a threshold of 0.05 are highlighted in **bold**

| Main effects	SS	MS	*F*	Perm p
Transplant location	11186.88	11186.88	48.4767	**0.001**
Caging status	31224.02	31224.02	135.3047	**0.001**
Turbinaria addition	34692.71	34692.71	150.3358	**0.001**
Transplant location × Caging status	4698.762	4698.762	20.3614	**0.001**
Transplant location × *Turbinaria* addition	39.1037	39.1037	0.1695	0.664
Caging status × *Turbinaria* addition	1070.066	1070.066	4.637	**0.023**
Transplant location × Caging status × *Turbinaria* addition	3222.081	3222.081	13.9624	**0.001**
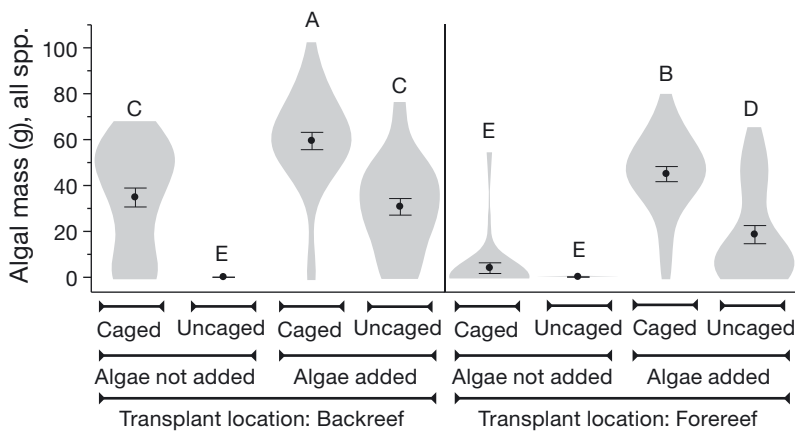
Fig. 7. Mass of algae (all spp.) after 60 d on experimental platforms as of function of transplant location, caging status, and initial addition of *Turbinaria* algae. Letters above violin plots indicate significant groupings based on post hoc permutation tests for multiple comparisons. p-values obtained from post hoc tests were adjusted using the Benjamini-Hochberg method to control the false discovery rate, and treatments were considered significantly different if the adjusted p-value was less than 0.05

specifics originating from different reefs that were simply transplanted to the same reef, uncaged, and lacked algae. The lack of strong origin effects could be due to corals having the physiological ability to function well across the ranges of these environments or to acclimatize once moved. These patterns suggest that corals from either of these sites could serve as effective sources for corals and larvae if these beneficial traits are heritable to help restore the other site if it experienced differential disturbance. Differential disturbance has happened in the past when crown-of-thorns outbreaks devastated forereef corals but rarely impacted those on the reef flat (Adam et al. 2011).

Caging corals with the macroalga *Turbinaria* consistently suppressed performance of both coral species. This is unsurprising — a large body of work documents how algal competitors, including macroalgae such as *Turbinaria* spp., impact coral fitness via reductions in coral growth, survival, fecundity, and recruitment (McCook et al. 2001, Beatty et al. 2018, Clements et al. 2018, 2020). Coral growth can differ as a function of algal abundance (Clements et al. 2018), which was greater in caged portions of our platforms and likely suppressed coral growth compared to uncaged conspecifics. Even in cases where *Turbinaria* was not added, caged corals often exhibited reduced growth (e.g. Fig. 5), likely associated with increased algal mass due to herbivore exclusion (Fig. 7).

Furthermore, algal-induced differences in light may also help explain the lone pairwise comparison where coral origin positively influenced coral growth; specifically, *P. verrucosa* originating from the forereef

outperformed conspecifics originating from the backreef when transplanted to the backreef, caged, and both with or without *Turbinaria* addition (Fig. 5). Numerous coral species can modulate autotrophic or heterotrophic mechanisms used to obtain energy based on local environmental conditions, such as depth-related light availability (Roth 2014). Physiological changes to the coral animal (e.g. skeletal morphology; Kramer et al. 2022b) or its endo-symbionts (e.g. changes in Symbiodiniaceae clade, density, chlorophyll concentrations, and location within host tissues; Winters et al. 2009) can help regulate photosynthetic efficiency (i.e. photoacclimation) at varying depths, and previous studies involving transplantation of corals between shallow and deeper reefs reported photoacclimation among coral transplants (Cohen & Dubinsky 2015, Einbinder et al. 2016, Tamir et al. 2020). It is possible that *P. verrucosa* originating from, and initially photoacclimated to, the deeper forereef were less affected by lower light conditions associated with caging/algal competition and this translated into enhanced growth during our study. That said, it is interesting to note that in previous studies, putative photoacclimation among transplants from other habitats did not lead to comparable macroscale coral fitness metrics (e.g. calcification, Cohen & Dubinsky 2015; survivorship, Tamir et al. 2020). When accounting for algal contact and caging in our experiment, corals transplanted away from their home reefs exhibited growth and survival comparable to native outplants. Our findings suggest that forereef and backreef populations of each of these corals are physiologically capable of growing well in either habitat and have largely similar performances when algal competition is limited. Thus, if major disturbances differentially impacted forereef or backreef populations, individuals from the less damaged habitat could be transplanted to speed the recovery of the more impacted population.

The impacts of macroalgal competition on coral tissue mortality were less pronounced than on growth, consistent with previous studies (Clements & Hay 2015, Clements et al. 2018, 2020). For *A. hyacinthus*, no corals exposed to algal competition exhibited ≥10% mortality without also being exposed to corallivory and even then constituted less than 2% of our coral outplants (4 of 238). In cases that were statisti-

cally distinguishable, we found that *P. verrucosa* mortality was greater when corals transplanted to the backreef were exposed to a combination of algal competition and corallivory (i.e. uncaged; Fig. 6). While previous studies have highlighted the potential for macroalgae to protect corals from predators (Venera-Ponton et al. 2011, Clements & Hay 2015, Brooker et al. 2016, 2017), others have documented how macroalgal competition can increase corallivore predation (Wolf & Nugues 2013) and synergize with other stressors (e.g. microbial dysbiosis; Zaneveld et al. 2016) to increase coral mortality. The mechanistic interplay between these stressors is beyond the scope of the present study, but merits investigation.

Corallivory is a considerable biological stressor that can reduce coral growth and survivorship, sometimes dramatically (Miller & Hay 1998, Kayal et al. 2012), via direct consumption, disease vectoring, and synergistic impacts with other stressors (Rotjan & Lewis 2008, De'ath et al. 2012, Rice et al. 2019). Previous studies conducted in the backreef lagoon and forereef of Mo'orea found that corallivory can significantly impact coral fitness and may influence coral recovery following disturbance and shifts in coral community composition (Lenihan & Edmunds 2010, Lenihan et al. 2011, Kayal et al. 2012, Kopecky et al. 2021, Ladd et al. 2021). However, in contrast to previous studies, we did not find compelling evidence that exposure to corallivory outweighed the adverse growth effects of caging for either *A. hyacinthus* or *P. verrucosa*. Growth of caged corals was comparable to or less than that of uncaged individuals, and in instances where significant differences between otherwise analogous pairs did occur, growth was greater among uncaged corals. This was true both for our *Turbinaria* additions (e.g. *P. verrucosa* originating from the backreef and forereef, transplanted to the backreef; Fig. 5) and when these additions were absent (e.g. *P. verrucosa* originating from the backreef, transplanted to the backreef; Fig. 5). It should also be noted that macroalgal mass was significantly greater in the caged vs. uncaged areas of the backreef site by the end of the experiment even in those cages where we did not add *Turbinaria* (Fig. 7). This suggests that adverse effects of excluding herbivores likely outweighed advantages of excluding corallivores — a finding of interest that merits further investigation (Mumby 2009).

Similarly, the statistically distinguishable influence of corallivory on coral mortality involved interactions with our *Turbinaria* additions (*A. hyacinthus*; Table 1B) or transplant location (*P. verrucosa*; Table 2B). The limited evidence of corallivory that we observed overall could be due to the coral species used, the location of manipulations (e.g. near the substrate vs. tops of bommies), or other aspects of our experimental set-up. For example, Lenihan et al. (2011) found that caging vs. exposure to corallivores influenced *P. verrucosa* growth, but this varied by transplant location(s); protection from corallivores enhanced growth of corals transplanted to elevated bommies, but caging either had no effect (location: backreef) or reduced growth (location: mid-lagoon) of those transplanted close to the substrate (i.e. similar to our manipulations). Similarly, Lenihan & Edmunds (2010) found that *P. verrucosa* growth was greater among caged vs. uncaged transplants on mid-lagoon bommies, but did not differ when transplanted to the adjacent seafloor. Our visual assessments of corallivory only account for bites from bio-eroding corallivores (e.g. triggerfishes, pufferfishes, and parrotfishes), but not those that target soft tissues and leave limited evidence of predation (e.g. butterflyfishes), despite the latter being able to exact a considerable energetic cost (Cole et al. 2011), transmit diseases while feeding (Raymundo et al. 2009), and induce defenses that can limit future corallivory in targeted coral species (Gochfeld 2004).

As reefs continue to degrade, there is increasing interest in utilizing corals from deeper, less-disturbed, and seemingly more resilient reefs to replenish shallow-water reefs that are disproportionately impacted by more frequent and severe disturbances (Baumann et al. 2021, Kramer et al. 2022a). The forereef and backreef sites where we conducted our study exemplify these divergent habitats and trends in disturbances and recoveries, with the forereef consistently returning to high coral cover following successive disturbances and backreef increasingly characterized by coral decline and macroalgal increase (Adjeroud et al. 2009, Trapon et al. 2010, Adam et al. 2011, Holbrook et al. 2018). Our findings suggest that, in most cases, *A. hyacinthus* and *P. verrucosa* can acclimatize to, or innately withstand, environmental conditions on the degraded backreef and in some scenarios even outperform backreef conspecifics (Fig. 5). Although transplants from the forereef did underperform in one instance, this also involved exposure to combinations of biotic stressors tested in our manipulations (i.e. corallivore/herbivore exclusion and macroalgal competition; Fig. 4). Whether the trends we observed are consistent over longer time scales, during different environmental conditions (e.g. ambient temperatures vs. heat stress events; Barott et al. 2021), or for different life stages (e.g. recently settled recruits; Kramer et al. 2022a) requires further investigation. However, our findings suggest that local specialization may

play less of a role in coral decline than differential disturbance regimes among these habitats (Kenkel et al. 2015, Baumann et al. 2021). This is encouraging, since the latter could be partially remediated by restoring important ecosystem processes, such as herbivory (Schmitt et al. 2019), or using other human-assisted approaches (Ceccarelli et al. 2018, Smith et al. 2022, 2023). Furthermore, our study species represent 2 coral genera that have largely driven recovery of local coral communities on Moʻorea (Bramanti & Edmunds 2016, Tsounis & Edmunds 2016, Adjeroud et al. 2018, Edmunds 2018) and elsewhere in the Pacific (Ortiz et al. 2021, Khen et al. 2022, Palacio-Castro et al. 2023). Insights from our manipulations thus increase our understanding of the fundamental ecology within these systems and have practical implications for proactive conservation and restoration efforts.

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