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Farmerfish Interactions Help Buffer Stony Corals Against Marine Heat Waves

A thesis submitted in partial satisfaction of the

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by

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June 2022

The thesis of Randi N. Honeycutt is approved.

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June 2022

Abstract

Farmerfish Interactions Help Buffer Stony Corals Against Marine Heat Waves

by

Randi N. Honeycutt

With marine heat waves increasing in intensity and frequency due to climate change, it is important to understand how thermal disturbances will alter coral reef ecosystems, which are highly susceptible to thermally-induced, mass bleaching events. In Moorea, French Polynesia, we evaluated the response and fate of stony coral following a major thermal stress event in 2019 that caused a substantial amount of branching coral (dominantly *Pocillopora*) to bleach and die. We investigated whether *Pocillopora* colonies that occurred within territorial gardens protected by the farmerfish *Stegastes nigricans* were less susceptible to or survived bleaching better than *Pocillopora* on adjacent, undefended substrate. Bleaching prevalence (proportion of the sampled colonies affected) and severity (proportion of a colony's tissue that bleached), which were quantified for >1,100 colonies shortly after they bleached, did not differ between colonies within or outside of defended gardens. By contrast, the fates of 399 focal colonies followed for a year revealed that a bleached coral within a garden was a third less likely to suffer complete colony death and, for survivors, about twice as likely to recover to its pre-bleaching cover of living tissue compared to *Pocillopora* outside of a farmerfish garden. Our findings indicate that while residing in a farmerfish garden may not reduce the bleaching susceptibility of a coral during thermal stress, it does help buffer a bleached coral against severe outcomes. This oasis effect of farmerfish gardens,

where survival and recovery of thermally-damaged corals are enhanced, is another mechanism that helps explain why large *Pocillopora* colonies are far more abundant in farmerfish territories than elsewhere in the lagoons of Moorea, despite gardens being much less common. As such, farmerfish may have a growing role in maintaining the resilience of branching corals as the frequency and intensity of marine heat waves continue to increase.

Introduction

Climate change is intensifying disturbances such as marine heat waves that increasingly are impacting shallow ocean ecosystems (Jacox et al. 2022), including coral reefs (Hughes et al. 2018). Marine heat waves (MHWs) can trigger a coral 'bleaching' event where thermal stress breaks down the mutualistic relationship between a coral host and its endosymbiotic algae (Symbiodiniaceae), which are expelled from the host (Loya et al. 2001; Pratchett et al. 2013; Hughes et al. 2017). A bleached coral will die if it does not regain its endosymbionts (Lesser 2011; LaJeunesse et al. 2018; Speare et al. 2022). During the past several decades, episodes of mass mortality of corals from MHWs have contributed to the widespread decline of stony corals (Hughes and Connell 1999; Hughes et al. 2018; Speare et al. 2022). There is ample evidence that the frequency, severity, and geographical extent of coral bleaching induced by MHWs have increased since the first such reported mass coral mortality event in the early 1980's (Glynn 1984; Baker et al. 2008; Lough et al. 2018; Sully et al. 2019). Hence, understanding the abiotic and biotic factors that influence the ability of stony corals to buffer the effects of MHWs is critical for developing management strategies that will enhance the resilience of coral to recurring periods of thermal stress (Gochfeld 2010; Hughes et al. 2018; Donovan et al. 2020, 2021).

Stony coral in parts of the Indo-Pacific can benefit by local interactions with a farming damselfish, the Dusky Gregory *Stegastes nigricans* ('farmerfish'), that can result in enhanced recruitment, growth, and survival of coral colonies (Gleason 1996; Gochfeld 2010; White and O'Donnell 2010; Johnson et al. 2011; Pruitt et al. 2018; Kamath et al. 2019). *S. nigricans* is a group-living damselfish that occurs on tropical reefs from the western Indian Ocean to the eastern Pacific (Randall 2005). Territorial groups of this fish cultivate algal

gardens for food that they vigorously defend against herbivores as well as corallivorous fishes (Johnson et al. 2011). By protecting their gardens, farmerfish provide coral that recruit into the garden an associational defense against coral predators, which can enhance coral growth and survival and ultimately can result in a great number and diversity of corals within a garden compared to adjacent areas that are not defended by farmerfish (Gleason 1996; Gochfeld 2010; White and O'Donnell 2010; Kamath et al. 2019). In addition to the moderating influence of *S. nigricans* on top-down effects on coral within their territory, farmerfish also can potentially strengthen bottom-up forcing via local fertilization of coral. Several experimental studies have revealed that group-living damselfishes can benefit stony corals and anthozoans by excreting nitrogenous waste that enhance their growth rate and/or reduce their probability of dying (Holbrook and Schmitt 2004; 2005; Holbrook et al. 2008, 2011; Shantz and Burkepile 2014; Burkepile et al. 2019). What has not been explored is whether coral-farmerfish interactions might buffer coral against MHWs, or alternatively, exacerbate the thermal stress to increase a coral's probability of bleaching and not recovering.

There are *a priori* reasons to hypothesize that coral-farmerfish interactions could either benefit or harm coral colonies during a MHW. For example, the reduction in photosynthetically supplied energy a coral colony suffers due to fewer endosymbionts during a MHW might be offset to some degree by a reduced need to allocate energy to wound repair because farmerfish lessen corallivory. Similarly, recycled nitrogen excreted by farmerfish that enhance algal growth within their territories (Blanchette et al. 2019) also might fuel a rapid increase in the density of the algal endosymbionts a bleached coral needs, and thus lower the probability it would starve to death (Shantz and Burkepile 2014; Burkepile et al.

2019). There also are situations where too much nitrogen can stimulate an excess production of photosynthetic products that can increase the susceptibility to or severity of coral bleaching (Donovan et al. 2020; Detmer et al. 2022). Both empirical and theoretical studies that have examined nutrient enrichment in relation to bleaching severity suggest that the relationship switches from beneficial at lower levels to harmful at higher levels of enrichment (Burkepile et al. 2019; Donovan et al. 2020; Detmer et al. 2022).

The aim of this study was to evaluate whether the response and fate of stony coral to a major thermal stress event depended on whether the colony occurred within a territorial garden protected by *Stegastes nigricans* or on adjacent, undefended reef substrate. At our study location (Moorea, French Polynesia), *Stegastes nigricans* live in shallow lagoon habitats. In early 2019, a prolonged marine heat wave in Moorea kept sea surface temperatures well above average for several months, which caused a substantial fraction of branching corals (mostly in the genera *Pocillopora* and *Acropora*) to bleach (Speare et al. 2022). The present study focused on *Pocillopora* spp. because they have been the dominant branching coral on reefs of Moorea for the past several decades (Burgess et al. 2021), and they commonly occur within farmerfish territories (Gochfeld 2010). The responses (i.e., bleaching prevalence, bleaching severity) of *Pocillopora* colonies within and outside of farmerfish gardens on haphazardly selected lagoon patch reefs (hereafter bommies) were evaluated immediately after coral had bleached but before the bleached tissued had died. The fate of colonies that bleached (i.e., proportion that completely died, proportion that recovered) within and outside of farmerfish gardens was assessed by following 399 individually marked colonies for a year. Our findings indicate that gardens defended by

Stegastes nigricans may serve as a thermal stress oasis for branching coral that enhances their chances of buffering marine heat waves.

Methods

Study Site, Study Organisms, and the Thermal Stress Event

Moorea, French Polynesia (17° 30'S, 149° 50'W) is a high volcanic island in the central South Pacific Ocean ~ 20 km west of Tahiti. Moorea is protected by a barrier reef approximately 1 km offshore that encircles the ~ 60 km perimeter of the island, which creates a continuous series of shallow (~ 3 m depth) lagoons. Shoreward of the barrier reef crest are numerous patch reefs ('bommies') separated by sand, coral rubble, and reef pavement.

Dispersed throughout the lagoons of Moorea are colonies of the group-living Dusky Gregory, which tend to be most common from the mid-lagoon to fringing reef in the cross-shore direction (Gochfeld 2010). *Stegastes nigricans* actively farm gardens of palatable turf algae by selectively weeding out undesired algae (Hata et al. 2010), enhancing productivity of their farm by fertilizing the garden with their nitrogenous waste (Blanchette et al. 2019), and defending the garden vigorously against intruders, particularly herbivorous and corallivorous fishes (Hata and Kato 2002, 2004; Gobler et al. 2006; Hata et al. 2010; Johnson et al. 2011). In Moorea, farmerfish territories are mainly established on dead portions of mounding coral bommies (*Porites* spp.) and reef pavement (Gochfeld 2010; White and O'Donnell 2010), but also within thickets of living staghorn coral *Acropora pulchra* (Johnson et al. 2011). As a consequence of the protection gained against corallivores, farmerfish territories on bommies tend to serve as recruitment 'nurseries' for branching (most commonly *Pocillopora* spp.) and other types of coral (Gochfeld 2010; White and O'Donnell

2010), as well as potential reservoirs of coral repopulation following large disturbances (Done et al. 1991; Gleason 1996).

In 2019, reefs of Moorea were subjected to the largest thermal stress event in at least the previous 14 years (Speare et al. 2022). Over the Austral summer of 2019, an unusually warm water event resulted in an accumulative thermal stress ($\sim$ 6 weeks above 29° C, the temperature threshold that predicts thermal stress for corals in Moorea) that was roughly twice that recorded in 2007, which was the highest recorded in any of the 14 years preceding 2019. The 2019 thermal event peaked in April - May, at which time a substantial proportion of (mostly branching) coral in the lagoon and shallower (< 12 m) depths on the outer fore reef bleached (Burgess et al. 2021; Speare et al. 2022). The present study was initiated in June 2019, after corals had bleached but before bleached tissues died, and continued until August 2020 to determine the fate of corals that had bleached. The study site was located over a 2 km longshore stretch of the lagoon at the eastern-most corner of the north shore of Moorea, between Avaroa Pass and Irihonu Pass; in the cross-shore direction, habitats were surveyed between the fringing reef to the mid-lagoon region, which is where *S. nigricans* gardens are abundant. The study focused on branching coral in the genus *Pocillopora* because they were by far the most common type of branching coral found in Moorea (Burgess et al. 2021), including in *Stegastes* gardens (Gochfeld 2010).

Resistance to Bleaching: Patterns of Bleaching Prevalence and Severity

A field survey to assess whether patterns of bleaching of *Pocillopora* differed between colonies within a farmerfish garden (territory) and those on adjacent, unprotected substrate was conducted during June – July 2019 before bleached tissues of coral died or recovered. Divers assessed all *Pocillopora* colonies found on 178 haphazardly encountered

bommies that were scattered throughout the 2 x 0. 5 km study polygon. The bommies varied in the amount of their surface covered by *Stegastes* gardens, from lacking gardens altogether to those that were partially to completely covered. Gardens were readily identified by their lush growth of turf red algae (commonly *Polysiphonia* spp.) and the presence of *Stegastes*; the substrate surface not defended by farmerfish typically had closely cropped turf and/or crustose coralline algae. All surveyed bommies were measured (l x w x h) and the location of *Pocillopora* colonies noted (outside or inside of a garden if present). All *Pocillopora* colonies on each surveyed bommie were sized into 5 diameter categories (< 3 cm, 3 - 10 cm, 11 - 20 cm, 21 - 30 cm, > 30 cm dia; see Donovan et al. 2020), and the colony position inside or outside a *Stegastes* garden was noted. Each *Pocillopora* was photographed, and the proportion of the colony that was (1) alive and unbleached, (2) alive but bleached (i.e., tissues transparent and underlying skeleton visibly white), and (3) dead (no tissue and skeleton overgrown with algae from previous partial mortality) was estimated visually in the field (the 3 categories sum to 1). The live but bleached category was defined as tissue that had substantially lower or no pigmentation (due to lower levels of Symbiodiniaceae) relative to the rest of the colony and followed the Australian Coral Watch Coral Health Chart for scoring coral bleaching (https://coralwatch.org). Quantification of bleaching was made by the same individual (RH). If present on a bommie, *Stegastes* garden sizes were measured, and the number of adult farmerfish enumerated. A total of 1,137 *Pocillopora* colonies was assessed on the 178 bommies surveyed.

Due to the need for a rapid assessment of bleached corals, the total amount of the two 'substrate types' (inside vs outside farmerfish territories) in the study area was not estimated in the June - July 2019 survey. This is because not all the non-garden area of a bommie was

suitable for occupancy by *Pocillopora*; some varying portions of the *Porites* coral bommies were still alive and/or occupied by other benthic space holders such as macroalgae. Thus, we used a recent survey of benthic habitats of the study site in 2016 to estimate the relative areas of garden vs non-garden habitats that were suitable for occupation by *Pocillopora* as an approximation of the relative sampling effort for the two habitat types in 2019. The 2016 benthic survey consisted of 24 band transects each 20 x 5 m where the substrate / space holder was identified at every 0.5 m point on the grid (i.e., 492 point samples per band transect). The benthic categories quantified included, among others, *Stegastes* gardens, other turf algae / crustose coralline algae (CCA), live coral (by genus or species), live portions of *Porites* bommies, and macroalgae (by genus or species). The 24 transects were distributed more or less evenly from the mid-lagoon to fringing reef along the 2 km span of the study site. These data were used to estimate the mean proportion of hard substrate at the study site that was covered by farmerfish gardens, and the mean proportion of non-garden hard substrate that was or could have been occupied by branching corals (i.e., cover of branching coral + cover of cropped turf algae / CCA on bommies).

In addition to exploring how *Pocillopora* responded to the bleaching event as a function of its position within or outside a farmerfish territory, responses as a function of colony size also were explored as other studies in Moorea have shown that for a variety of reasons, larger and smaller colonies of *Pocillopora* can have different susceptibilities to bleaching (Burgess et al. 2021, Speare et al. 2022). Accordingly, the 1,137 surveyed corals were divided into two size classes, small ($\leq$ 10 cm dia) and large (> 10 cm dia). Several statistical tests were conducted to explore relationships between *Pocillopora* colony size and location (inside or outside of a garden) with two metrics of bleaching (prevalence and

severity, see below). All analyses were performed using the R language for statistical computing version 4.1.1 (R Core Team 2016).

Proportion of Large vs Small colonies as a Function of Garden 'Status.' A Pearson's chi-square contingency analysis with Yates' continuity correction was used to test whether the proportion of large vs small *Pocillopora* colonies differed between those found within and outside farmerfish gardens. For each garden 'status' (inside or outside), the number of colonies in a size class (large or small) was divided by the total number of colonies in that location category.

Bleaching Prevalence. Bleaching prevalence is the proportion of the total colonies in a sample that had bleached. For this analysis, a colony was categorized as bleached if $\geq 5\%$ of its live tissue was deemed to be bleached using the criteria described earlier. To determine whether bleaching prevalence differed as a function of garden status (inside or outside) and colony size, Pearson's chi-square contingency analyses with Yates' continuity correction were used to test for garden status effect separately for small and large size classes. For each size class and garden status, the number of colonies categorized as bleached was divided by the total number of colonies (bleached + unbleached) in the respective size and garden status group.

Bleaching Severity. Bleaching severity is the proportion of the tissue on an individual colony that bleached. A two-way analysis of variance was used to test the effect of colony size (small or large) or location (inside or outside a garden) on the severity of bleaching. Data were arcsine-transformed to meet assumptions of normality; the interaction term in the full model was non-significant *(p = 0.24),* so the analysis was rerun without the interaction term.

Fate of Bleached Coral: Patterns of Mortality and Recovery

Bleached tissue on a coral will eventually die if it does not recover a sufficient complement of algal symbionts. To assess the post-bleaching fate of *Pocillopora* at the study site, focal colonies were selected and followed for a year. In July 2019, 399 *Pocillopora* colonies that had some level of bleaching (5-100%) were selected and uniquely tagged using combinations of colored cable ties that were attached to u-nails affixed to the adjacent substrate. The focal colonies, which were spread among 148 bommies, included 263 that occurred within farmerfish gardens and 136 that were on bommie surfaces outside of *Stegastes* gardens. Focal colonies were resampled after 6 months (January 2020) and again after 13 months (August 2020), at which times the proportion of each colony that was alive or had died was quantified.

Complete Colony Death. A subset of the focal corals suffered complete colony mortality between July 2019 and August 2020. Pearson's chi-square contingency analyses with Yates' continuity correction were used to test whether the proportion of corals that suffered complete colony mortality differed depending on whether they were inside or outside of a garden. The total number of dead colonies both inside and outside of gardens was divided by the total number of colonies in those categories. To explore whether smaller and larger sizes had different fates depending on their garden status, a Fischer's exact test was used to test if colony size and garden status influenced whether a colony had complete mortality. The number of colonies within each garden status and size class was divided by the total number of colonies within those respective categories.

Colony Recovery. For colonies that were still at least partially alive after a year, we explored whether garden status influenced whether the amount of living tissue on a colony

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after a year was equal to or greater than the initial amount in 2019, immediately after they bleached. Corals that met this criterion were considered 'recovered.' Pearson's chi-square contingency analyses with Yates' continuity correction were used to test if the proportion of colonies that recovered depended on whether they were inside or outside of a garden. The total number of colonies that recovered within a respective garden status was divided by the total number of colonies in that category. A Fischer's exact test was used to test whether recovery of large and small corals differed depending on garden status. The number of colonies within each garden status and size category (large vs small) was divided by the total number of colonies within those respective categories.

Results

Patterns of *Pocillopora* Distribution

Estimates of benthic microhabitats in 2016 reveal that in the years just before the bleaching event, the mean proportion of bommie surfaces covered by *Stegastes* gardens was 0.30 (± 0.4 SE) within the study site, whereas the mean proportion of bommie surfaces that either were occupied by or suitable for branching corals was 0.49 (± 0.4). This suggests that in the 2019 survey of bleached coral on bommies, the suitable area sampled for *Pocillopora* outside of farmerfish gardens may have been as much as 1.6 times greater than the total area of farmerfish gardens sampled. Despite this likely sampling bias toward more non-garden habitat, only 32% of the *Pocillopora* colonies encountered (361 of 1,137) in the census of the 178 bommies were found outside of farmerfish territories. Perhaps even more striking, there was a marked shift in proportional representation of small versus large colonies between garden and non-garden habitats (Fig. 1). About 60% of all smaller *Pocillopora* encountered in the survey occurred within gardens, which rose to 86% of the larger colonies (Fig. 1). This

shift between the size classes was highly significant ($X^2_{(1, 1137)} = 66.76$, $p < 0.001$) and is a pattern consistent with enhanced survivorship and/or growth of coral within *Stegastes* territories relative to colonies on adjacent, non-garden substrates.

Resistance to Bleaching: Patterns of Bleaching Prevalence and Severity

Bleaching Prevalence. Occurring in a garden did not have a statistically significant effect on the proportion of all small ($X^2_{(1, 796)} = 2.35$, $p = 0.12$) or all large colonies ($X^2_{(1, 341)} = 0.02$, $p = 0.88$) that bleached (i.e., bleaching prevalence), although for both size classes there was a trend for bleaching prevalence to be slightly higher inside gardens (Fig. 2). Overall, a higher proportion of the total number of large colonies sampled bleached relative to smaller corals ($X^2_{(1, 1137)} = 63.1$, $p < 0.0001$). Bleaching prevalence was about twice as great for large relative to small corals (Fig. 2).

Bleaching Severity. With respect to bleaching severity (i.e., the proportion of a colony's tissue that bleached), the interaction between garden status and colony size was not significant ($F_{1, 203} = 1.35$, $p = 0.24$). Similar to prevalence, occurring in a garden did not alter how much of an individual colony's tissue bleached, given that at least some tissue did ($F_{1, 203} = 1.03$, $p = 0.31$; reduced model without interaction term) (Fig. 3). As with prevalence, colony size did have a significant effect on bleaching severity (Fig. 3) ($F_{1, 203} = 8.16$, $p < 0.005$; reduced model without interaction term). Overall, small colonies had an approximate mean severity that was roughly 40% greater than that of large colonies (Fig. 3, Table 1). Taken together, these findings indicate that occurring in a farmerfish territory did not reduce or increase the probability of or degree to which *Pocillopora* tissue bleached in response to prolonged thermal stress.

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Fate of Bleached Coral: Patterns of Mortality and Recovery

The 399 bleached colonies followed for a year showed qualitatively identical patterns of bleaching severity as the larger collection of 1,137 colonies surveyed in June 2019 (Table 2). *Complete Colony Death.* Garden status had a strong effect on whether a bleached colony completely died ($X^2_{(1, 399)} = 19.6$, $p < 0.0001$). Just over 67% of bleached colonies outside of gardens did not survive the year compared to only 44% in gardens (Fig. 4). Thus, bleached colonies associated with farmerfish territories were ~ 34% less likely to die. As expected, small colonies were more likely to die compared to large colonies (Table 3). Also as predicted, small colonies were less likely to die when they were associated with a farmerfish garden ($p = 0.03$; 1-tailed test). Large colonies exhibited the same (non-significant; $p = 0.36$, Table 4) trend with garden status, although we caution that the much lower number of large corals followed may have precluded a robust test.

Colony Recovery. For the subset of focal colonies that were at least partially alive after a year, being associated with a farmerfish garden increased the chances that the proportional area of a colony covered by live tissue after a year was equal to or greater than at the time it bleached in 2019 ($X^2_{(1, 399)} = 7.53$, $p < 0.01$). Using this threshold metric of recovery, 33% of bleached colonies recovered inside gardens compared to just 19% of bleached, non-garden corals (Fig. 5, Tables 5 and 6). This indicates that the 'recovery' advantage of dwelling in a farmerfish garden was almost double. Overall, proportionately more large colonies (47%) had met our recovery threshold compared to smaller *Pocillopora* (21%).

Discussion

Like many coral reefs worldwide in recent years, those surrounding Moorea recently experienced an intense thermal stress event that caused widespread bleaching and death of

mainly branching corals (Leichter et al. 2022; Burgess et al. 2022; Speare et al. 2022). For reefs in the lagoons of Moorea, mass mortality of coral can trigger a regime shift from coral to macroalgae that is challenging to reverse (Schmitt et al. 2019, 2022), making it important to understand factors that enhance the resilience of coral to marine heat waves. Here we found that colonies of *Pocillopora* that were associated with defended gardens of the farmerfish *Stegastes nigricans* had the same susceptibility to bleaching, both in terms of prevalence and severity, compared to adjacent corals on closely cropped turf algae and/or crustose coralline algae outside of farmerfish territories. Similarly, Smith et al. (2022) found that branching coral under canopies of macroalgae (primarily *Sargassum* spp.) on fringing reefs of Magnetic Island on the Great Barrier Reef had the same susceptibility to bleaching as those in nearby plots where macroalgae had been removed well before the thermal event. With respect to post-bleaching recovery, we found that a bleached *Pocillopora* colony in a farmerfish garden had a substantially lower probability of completely dying (about one third less) and about twice the probability of recovering (having as much or more live tissue a year later) compared to their counterparts on open substrate outside of *Stegastes* territories. This rescue effect of dwelling in a farmerfish garden of filamentous red algae stands in sharp contrast to the generally adverse effect that macroalgae have on the recovery of bleached coral (Donovan et al. 2021; Smith et al. 2022).

It is well known that the territorial gardens cultivated by *Stegastes nigricans* can enhance recruitment and growth of branching and other corals (Gleason 1996; Gochfeld 2010; White and O'Donnell 2010; Johnson et al. 2011; Pruitt et al. 2018; Kamath et al. 2018), which ultimately can result in a greater number and diversity of corals within a garden relative to adjacent reef substrate of the same area (Gleason 1996; Gochfeld 2010; White and

O'Donnell 2010). While we also found a much greater density of individual *Pocillopora* colonies within gardens, our surveys also revealed that in the lagoons of Moorea, > 85% of the larger-sized colonies (i.e., > 10 cm dia) occurred in *Stegastes* territories despite that microhabitat accounting for < 40% of the reef substrate suitable for coral (i.e., surfaces with closely cropped turf algae or otherwise occupied by coral) at our study site. This suggests that *Pocillopora* in farmerfish gardens grew faster, survived better, or both. We found that overall, bleached corals survived and recovered better if they occurred in a garden. As the frequency of thermal stress events continues to increase, the rescue effect of bleached coral in farmerfish gardens (lowered death rate, accelerated recovery of survivors) will likely further skew the distribution of large *Pocillopora* colonies even more towards *Stegastes* territories. Large colonies are the primary source of sexually produced propagules on reefs (Hall and Hughes 1996). Further, Johnston et al. (2020) found that smaller *Pocillopora* sp. colonies that recovered from bleaching suffered a prolonged period of reproductive impairment that was not observed in larger conspecifics. These aspects have profound population-level consequences that will further amplify the importance of farmerfish garden oases in enhancing the resilience of coral communities as the thermal stress regime continues to intensify.

Although dwelling in farmerfish gardens can have a positive influence on growth and survivorship of stony coral, we found that susceptibility to bleaching was related to colony size and not whether it occurred within or outside of a *Stegastes* territory. Like others (e.g., Nakamura and van Woesik 2001; Johnston et al. 2020; Speare et al. 2022), we found that bleaching prevalence (proportion of total colonies that showed any level of bleaching) was greater for larger relative to smaller *Pocillopora* colonies, but that bleaching severity

(proportion of tissue of an individual colony that bleached) was much greater for smaller rather than larger corals. The size and morphology of a coral can affect its susceptibility to bleaching because it influences its mass transfer capability during thermal stress via water-flow rates and passive diffusion (Nakamura and van Woesik 2001; van Woesik et al. 2012). During periods of thermal stress, the photosymbionts of coral produce harmful metabolites (oxygen radicals) that accumulate within the host coral, and if not diffused away, can lead to oxidative stress and coral bleaching (Downs et al. 2002; Lesser 2011). The more complex flows and longer water residence times within the branches of larger corals facilitate gas exchange and feeding opportunities that enable large colonies to more effectively manage both bleaching susceptibility and survival after bleaching when energy reserves are limited (Nakamura and van Woesik 2001; Johnston et al. 2020). Consistent with this mechanistic understanding, we found that smaller *Pocillopora* were more severely bleached and had a much greater probability of dying compared to larger colonies. This conforms with the typical pattern observed where rates of coral mortality decrease with increasing colony size (Hughes and Connell 1987; but see Burgess et al. 2021; Speare et al. 2022). Thus, one explanation for the enhanced ability of bleached coral in farmerfish gardens to buffer the thermal event was that proportionately more of the colonies were large.

The observed rescue effect of farmerfish territories on bleached *Pocillopora* was not just due to the difference in the colony size distributions between garden and non-garden habitats; small corals that bleached were significantly more likely to survive and recover if they occurred in a *Stegastes* garden. Because smaller colonies have lower energetic reserves than larger colonies (Oren et al. 2001), the underlying mechanism accounting for the enhanced survival and recovery of small *Pocillopora* in farmerfish territories may be related

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to how *Stegastes* interactions help bleached coral conserve energy needed for recovery and/or speed energy production. One possible mechanism is the protection corals in farmerfish garden gain against corallivorous fishes, which *Stegastes nigricans* aggressively exclude from their garden (Johnson et al. 2011). Corallivory generally reduces colony growth and survivorship (e.g., Lenihan et al., 2011; Kopecky et al., 2021), and several studies have shown that corals protected by farmerfish incurred substantially lower rates of corallivory that resulted in greater growth and survivorship than adjacent, unprotected colonies (e.g., Gochfeld 2010; White and O'Donnell 2010). Repair of wounds from corallivores and other agents of damage is a high priority for *Pocillopora* (see Johnston et al., 2020; Rice at al., 2019), and smaller colonies heal more slowly than larger conspecifics due to high energetic demand relative to available reserves (Counsell et al. 2019). Bleaching greatly reduces the already limited energy supply of a small coral such that colonies protected from corallivory by farmerfish may gain a fitness advantage by needing to devote less energy to wound repair.

In addition to farmerfish interactions potentially lowering energetic demands of bleached coral, they may enhance the production of energy either via heterotrophic or autotrophic pathways. While the ambient flux of zooplankton appears sufficient to meet the basic heterotrophic needs of *Pocillopora* at our study location when colonies are not thermally stressed (Alldredge et al. 2013), it can become a crucially important source of energy when corals are severely bleached (Palardy et al. 2008). In the field experiments reported by Adam et al. (in review) where reduced predation on *Pocillopora* resulted in faster growth, the polyps of corals in lower predation treatments were consistently observed to be extended and feeding throughout the day, whereas diurnal feeding was not observed for corals exposed to ambient levels of predation (pers obs.). This suggests that thermally-

stressed corals protected by farmerfish may be able to increase their metabolic carbon intake by feeding on zooplankton without great risk during the day, and not just at night. Alternatively, local fertilization of corals by nitrogenous excretions from damselfishes can enhance the growth rates of coral, including *Pocillopora* in Moorea (Holbrook et al. 2008; Holbrook et al. 2011). Fish excretion in the form of recycled ammonia and urea has been shown to increase the density of algal endosymbionts in bleached coral, which recovered faster and survived better than bleached colonies exposed to other forms of nitrogen (Burkepile et al. 2019). There also is compelling evidence that excess nitrogen and/or the wrong form of nitrogen (e.g., nitrates / nitrites) can adversely affect the health of a coral colony by over-stimulating the production of photosynthate, making the host coral more liable to bleach (Burkepile et al. 2019; Donovan et al. 2020; Detmer et al. 2022). While increases of nitrogen at low levels can be beneficial, an excess can become an added stressor to coral (Burkepile et al. 2019; Donovan et al. 2020; Detmer et al. 2022). While the mechanisms underlying the positive effect of *Stegastes nigricans* on post-bleaching recovery of small coral remain to be explored, our study adds yet another pathway by which the fitness of stony coral can be enhanced by associating with farmerfish.

Marine heat wave events that induce mass coral bleaching will continue to occur more frequently and with greater intensity as the climate continues to warm (Hughes et al. 2018; Sulley et al. 2019; Donovan et al. 2020). As such, climate-related bleaching mortality of coral is now considered to be the one greatest threat to coral reefs in the foreseeable future (Hughes et al. 2018; Sulley et al. 2019). This places a premium on understanding factors that either moderate or exacerbate the impact of thermal stress on corals (Burkepile et al. 2019; Smith et al. 2022). Branching corals that recruit to defended territories of the Dusky Gregory

Stegastes nigricans are buffered to a greater degree against the most severe outcomes of thermal stress relative to colonies on adjacent substrate because smaller, more thermally-sensitive sizes are more likely to survive and recover, and because they are more likely to grow to larger, less sensitive sizes. The importance to coral resilience of this rescue effect of farmerfish oases will continue to grow as thermal-stress events become more frequent in the coming decades.

Acknowledgments

References

Adam, T.C, S.J. Holbrook, D.E. Burkepile, K.E. Speare, A.J. Brooks, M.C. Ladd, A.A. Shantz, R. Vega Thurber, and R.J. Schmitt. Priority effects in coral-macroalgae interactions can drive alternate community paths in the absence of top-down control. Ecology In review.

Alldredge, A.L., S.J. Holbrook, R.J. Schmitt, A.J. Brooks, and H. Stewart. 2013. Skeletal growth of four scleractinian corals is not enhanced by in situ mesozooplankton enrichment. Marine Ecology Progress Series 489:143-153.

Baker, A.C., P.W. Glynn, and B. Riegl. 2008. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuarine, Coastal and Shelf Science 80:435-371.

Blanchette, A., T. Ely, A. Zeko, S.A. Sura, R. Turba, and P. Fong. 2019. Damselfish *Stegastes nigricans* increase algal growth within their territories on shallow coral reefs via enhanced nutrient supplies. Journal of Experimental Marine Biology and Ecology 513:21-26.

Burgess, S.C., E.C. Johnston, A.S.J. Wyatt, J.J. Leichter, and P.J. Edmunds. 2021. Response diversity in corals: hidden differences in bleaching mortality among cryptic *Pocillopora* species. Ecology 102(6):e03324.

Burkepile, D.E., A.A. Shantz, T.C. Adam, K.S. Munsterman, K.E. Speare, M.C. Ladd, M.M. Rice, L. Ezzat, S. McIlroy, J.C.Y. Wong, D.M. Baker, A.J. Brooks, R.J. Schmitt, and S.J. Holbrook. 2019. Nitrogen identity drives differential impacts of nutrients on coral bleaching and mortality. Ecosystems 23:798-811.

Counsell, C.W.W., E.C. Johnston, and T.L. Sale. 2019. Colony size and depth affect
wound repair in a branching coral. Marine Biology 166:148.

Detmer, A.R., R. Cunning, F. Pfab, A.L. Brown, A.C. Stier, R.M. Nisbet, and H.V.
Moeller. 2022. Fertilization by coral-dwelling fish promotes coral growth but can
exacerbate bleaching response. Journal of Theoretical Biology 541:111087.

Done, T.J., P.K. Dayton, A.E. Dayton, and R. Steger. 1991. Regional and local
variability in recovery of shallow coral communities: Moorea, French Polynesia
and central Great Barrier Reef. Coral Reefs 9:183-192.

Donovan, M.K., T.C. Adam, A.A. Shantz, K.E. Speare, K.S. Munsterman, M.M. Rice,
R.J. Schmitt, S.J. Holbrook, and D.E. Burkepile. 2020. Nitrogen pollution
interacts with heat stress to increase coral bleaching across the seascape.
Proceedings of the National Academy of Sciences 117(10):5351-5357.

Donovan, M.K., D.E. Burkepile, C. Kratochwill, T. Shlesinger, S. Sully, T.A. Oliver,
G. Hodgson, J. Freiwald, and R. van Woesik. 2021. Local conditions magnify
coral loss after marine heat waves. Science. 372(6545):977-80.

Downs, C.A., J.E. Fauth, J.C. Halas, P. Dustan, J. Bemiss, and C.M. Woodley. 2002.
Oxidative stress and seasonal coral bleaching. Free Radical Biology and Medicine
33(4):533-543.

Gleason, M.G. 1996. Coral recruitment in Moorea, French Polynesia: the importance of
patch type and temporal variation. Journal of Experimental Marine Biology and
Ecology 207:79-101.

Glynn, P.W. 1984. Widespread coral mortality and the 1982-83 El Nino warming
event. Environmental Conservation 11:133-146.

Gobler, C.J., D.B. Thibault, T.W. Davis, P.B. Curran, B.J. Peterson, and L.B. Liddle. 2006. Algal assemblages associated with *Stegastes* sp. territories on Indo-Pacific coral reefs: Characterization of diversity and controls on growth. Journal of Experimental Marine Biology and Ecology 336:135-145.

Gochfeld, D.J. 2010. Territorial damselfishes facilitate survival of corals by providing an associational defense against predators. Marine Ecology Progress Series 398:137-148.

Hall, V.R., and T.P. Hughes. 1996. Reproductive strategies of modular organisms: Comparative studies of reef- building corals. Ecology 77:950-963.

Hata, H., and M. Kato. 2002. Weeding by the herbivorous damselfish *Stegastes nigricans* in nearly monocultural algae farms. Marine Ecology Progress Series 237:227-231.

Hata, H., and M. Kato. 2004. Monoculture and mixed-species algal farms on a coral reef are maintained through intensive and extensive management by damselfishes. Journal of Experimental Marine Biology and Ecology 313:285-296.

Hata, H., K. Watanabe, and M. Kato. 2010. Geographic variation in the damselfish-red alga cultivation mutualism in the Indo-West Pacific. BMC Evolutionary Biology 10:185.

Holbrook, S.J. and R.J. Schmitt. 2004. Population dynamics of a damselfish: effects of a competitor that also is an indirect mutualist. Ecology 85:979-985.

Holbrook, S.J. and R.J. Schmitt. 2005. Growth, reproduction, and survival of a tropical sea anemone (Actiniaria): benefits of hosting anemonefish. Coral Reefs 24:67-73.

Holbrook, S.J., A.J. Brooks, R.J. Schmitt, and H.L. Stewart. 2008. Effect of sheltering

    fish on growth of their host corals. Marine Biology 155:521-530.

Holbrook, S.J., R.J. Schmitt, and A.J. Brooks. 2011. Indirect effects of species

    interactions on habitat partitioning. Oecologia 166:739-749.

Hughes, T.P., and J. H. Connell. 1999. Multiple stressors on coral reefs: A long-term

    perspective. Limnology and Oceanography 44:932-940.

Hughes, T.P., et al. 2017. Global warming and recurrent mass bleaching of corals.

    Nature 543(7645):373-377.

Hughes, T.P., et al. 2018. Spatial and temporal patterns of mass bleaching of corals in

    the Anthropocene. Science 359:80-83.

Jacox, M.G., M.A. Alexander, D. Amaya, E. Becker, S.J. Bograd, S. Brodie, E.L.

    Hazen, M.P. Buil, and D. Tommasi. 2022. Global seasonal forecasts of marine

    heat waves. Nature 604:486-490. https://doi.org/10.1038/s41586-022-04573-9

Johnson, M.K., S.J. Holbrook, R.J. Schmitt, and A.J. Brooks. 2011. Fish communities

    on staghorn coral: Effects of habitat characteristics and resident farmerfishes.

    Environmental Biology of Fishes 91:429-448.

Johnston, E.C., C.W.W. Counsell, T.L. Sale, S.C. Burgess, and R.J. Toonen. 2020. The

    legacy of stress: Coral bleaching impacts reproduction years later. Functional

    Ecology 34:2315-2325.

Kamath, A., J.N. Pruitt, A.J. Brooks, M.C. Ladd, D.T. Cook, J.P. Gallagher, M.E.

    Vickers, S.J. Holbrook, and R.J. Schmitt. 2019. Potential feedback between coral

    presence and farmerfish collective behavior promotes coral recovery. Oikos

    128:482-492.

Kopecky, K.L., D.T. Cook, R.J. Schmitt, and A.C. Stier. 2021. Effects of corallivory

    and coral colony density on coral growth and survival. Coral Reefs 40:283-288.

LaJeunesse, T.C., J.E. Parkinson, P.W. Gabrielson, H.J. Jeong, J.D. Reimer, C.R.

    Voolstra, and S.R. Santos. 2018. Systematic revision of Symbiodiniaceae

    highlights the antiquity and diversity of coral endosymbionts. Current Biology

    28(16):2570-2580.e6.

Leichter, J., T. Adam, K. Seydel, and C. Gotschalk. 2022. Benthic Water Temperature,

    ongoing since 2005 ver 15. Environmental Data Initiative.

    https://doi.org/10.6073/pasta/b8b3c1a927b7639459a244ff2ceef4e2.

Lenihan, H.S., S.J. Holbrook, R.J. Schmitt, and A.J. Brooks. 2011. Influence of

    corallivory, competition, and habitat structure on coral community shifts. Ecology

    92:1959-1971.

Lesser, M.P. 2011. Coral bleaching: Causes and mechanisms. Pp. 405-419 in Z.

    Dubinsky and N. Stambler (Eds.). Coral Reefs: An Ecosystem in Transition.

    Springer.

Lough, J.M., K.D. Anderson, and T.P. Hughes. 2018. Increasing thermal stress for

    tropical coral reefs: 1871–2017. Scientific Reports 8:6079.

Loya, Y., K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, and R. van Woesik. 2001.

    Coral bleaching: The winners and the losers. Ecology Letters 4:122-131.

    https://doi.org/10.1046/j.1461- 0248.2001.00203.x

Nakamura, T., and R. van Woesik. 2001. Water-flow rates and passive diffusion

    partially explain differential survival of corals during the 1998 bleaching event.

    Marine Ecology Progress Series 212:301-304.

Oren, U., Y. Benayahu, H. Lubinevsky, and Y. Loya. 2001. Colony integration during regeneration in the stony coral *Favia favus*. Ecology 82: 802-813.

Palardy, J.E., L.J. Rodrigues, and A.G. Grottoli. 2008. The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. Journal of Experimental Marine Biology and Ecology 367:180-188.

Pratchett, M.S., D. McCowan, J.A. Maynard, and S.F. Heron. 2013. Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. PLoS ONE 8(7):e70443.

Pruitt, J.N., C.N. Keiser, B.T. Banka, J.S. Leidle, A.J. Brooks, R.J. Schmitt, and S.J. Holbrook. 2018. Collective aggressiveness of an ecosystem engineer is associated with coral recovery. Behavioral Ecology 29:1216-1224.

R Development Core Team. 2016. R: A Language and Environment for Statistical Computing. Version 1.4.1106. R Foundation for Statistical Computing, Vienna, Austria.

Randall, J.E. 2005. Reef and Shore Fishes of the South Pacific: New Caledonia to Tahiti and the Pitcairn Islands. University of Hawai'i Press, Honolulu, HI.

Rice, M.M., L. Ezzat, and D.E. Burkepile. 2019. Corallivory in the Anthropocene: Interactive effects of anthropogenic stressors and corallivory on coral reefs. Frontiers in Marine Science 5:10.3389.

Schmitt, R.J., S.J. Holbrook, S.L. Davis, A.J. Brooks, and T.C. Adam. 2019. Experimental support for alternative attractors on coral reefs. Proceedings of the National Academy of Sciences 116:4372-4381.

Schmitt, R.J., S.J. Holbrook, A.J. Brooks, and T.C. Adam. 2022. Evaluating the precariousness of coral recovery when coral and macroalgae are alternative basins of attraction. Limnology and Oceanography 67:S285-S297.

Shantz, A.A., and D.E. Burkepile. 2014. Context-dependent effects of nutrient loading on the coral-algal mutualism. Ecology 95:1995-2005.

Smith, H.A., T. Prenzlau, T. Whitman, S.E. Fulton, S. Borghi, M. Logan, S.F. Heron, and D.G. Bourne. 2022. Macroalgal canopies provide corals limited protection from bleaching and impede post-bleaching recovery. Journal of Experimental Marine Biology and Ecology 553:151762.

Speare, K.E., T.C. Adam, E.M. Winslow, H.S. Lenihan, and D.E. Burkepile. 2022. Size-dependent mortality of corals during marine heat wave erodes recovery capacity of a coral reef. Global Change Biology 28:1342-1358.

Sully, S., D.E. Burkepile, M.K. Donovan, G. Hodgson, and R. van Woesik. 2019. A global analysis of coral bleaching over the past two decades. Nature Communications 10:1264.

van Woesik, R., A. Irikawa, R. Anzai, and T. Nakamura. 2012. Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. Coral Reefs 31:633- 639.

White, J.-S.S., and J.L. O'Donnell. 2010. Indirect effects of a key ecosystem engineer alter survival and growth of foundation coral species. Ecology 91:3538-3548.

Table 1: The mean (± SE) proportion of live tissue of an individual coral colony and mean (± SE) bleaching severity (i.e., proportion of live tissue bleached) as a function of coral colony size class (small: ≤ 10 cm dia; large > 10 cm) and farmerfish garden status (inside vs outside); N = 1,137 *Pocillopora* colonies encountered on 178 bommies; corals were categorized as bleached if ≥ 5% of live tissue was bleached.

Colony size	Garden	No. of colonies bleached	Mean proportion of live tissue	SE	Bleaching severity	SE
Small	Inside	105	0.91	0.02	0.53	0.04
Small	Outside	53	0.98	0.01	0.54	0.05
Large	Inside	126	0.78	0.02	0.32	0.03
Large	Outside	20	0.79	0.06	0.45	0.07

Table 2: The initial mean (± SE) proportion of live tissue, the proportional change in live tissue after 1 year, and the initial bleaching severity for 399 uniquely marked colonies followed for a year post bleaching as a function of coral colony size class (small: ≤ 10 cm dia; large > 10 cm) and farmerfish garden status (inside vs outside).

Colony size	Garden	No. of colonies	Initial mean proportion alive	SE	Proportional change in live tissue after 1 year	SE	Initial mean bleaching severity	SE
Small	Inside	172	0.93	0.01	-0.63	0.03	0.43	0.03
Small	Outside	123	0.94	0.01	-0.72	0.04	0.45	0.03
Large	Inside	91	0.88	0.02	-0.12	0.03	0.24	0.02
Large	Outside	13	0.88	0.06	-0.26	0.1	0.29	0.07

Table 3: The proportion of alive and completely dead small colonies ('colony state') after one year as a function of farmerfish garden status.

Small colonies

Garden	Colony state	No. of colonies	Proportion of colonies by garden status
Inside	Alive	65	0.38
Inside	Dead	107	0.62
Outside	Alive	33	0.27
Outside	Dead	90	0.73

Table 4: The proportion of alive and completely dead large colonies ('colony state') after one year as a function of farmerfish garden status.

Large colonies

Garden	Colony state	No. of colonies	Proportion of colonies by garden status
Inside	Alive	83	0.91
Inside	Dead	8	0.09
Outside	Alive	11	0.85
Outside	Dead	2	0.15

Table 5: The proportion of surviving small colonies that either did or did not recover to at least their initial amount of live tissue after a year as a function of farmerfish garden status.

Small colonies

Garden	Recovered	No. of colonies	Proportion of colonies by garden status
Inside	Yes	42	0.24
Inside	No	130	0.76
Outside	Yes	21	0.17
Outside	No	102	0.83

Table 6: The proportion of surviving large colonies that either did or did not recover to at least their initial amount of live tissue after a year as a function of farmerfish garden status.

Large colonies

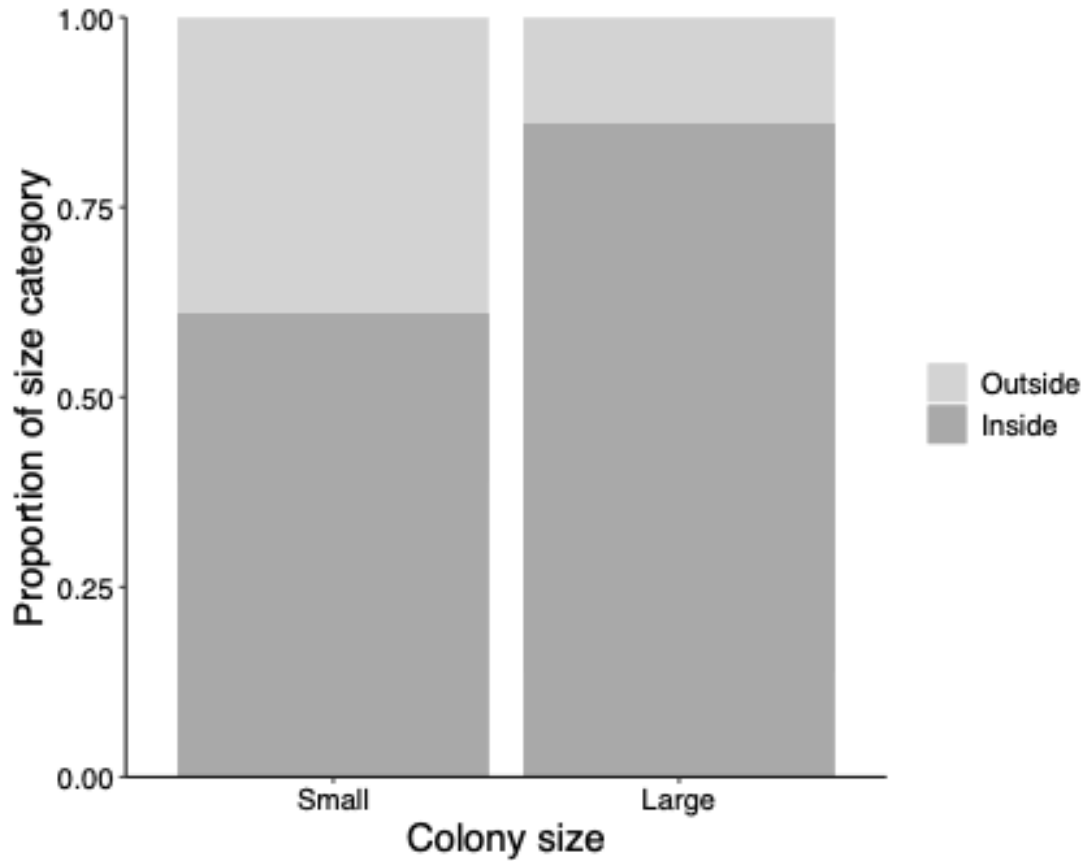| Garden	Recovered	No. of colonies	Proportion of colonies by garden status
Inside	Yes	44	0.48
Inside	No	47	0.52
Outside	Yes	5	0.38
Outside	No	8	0.62

Figure 1: The proportion of small and of large *Pocillopora* colonies encountered inside and outside of farmerfish gardens (small: ≤ 10 cm dia; large > 10 cm) of the 1,137 colonies surveyed on 178 bommies.
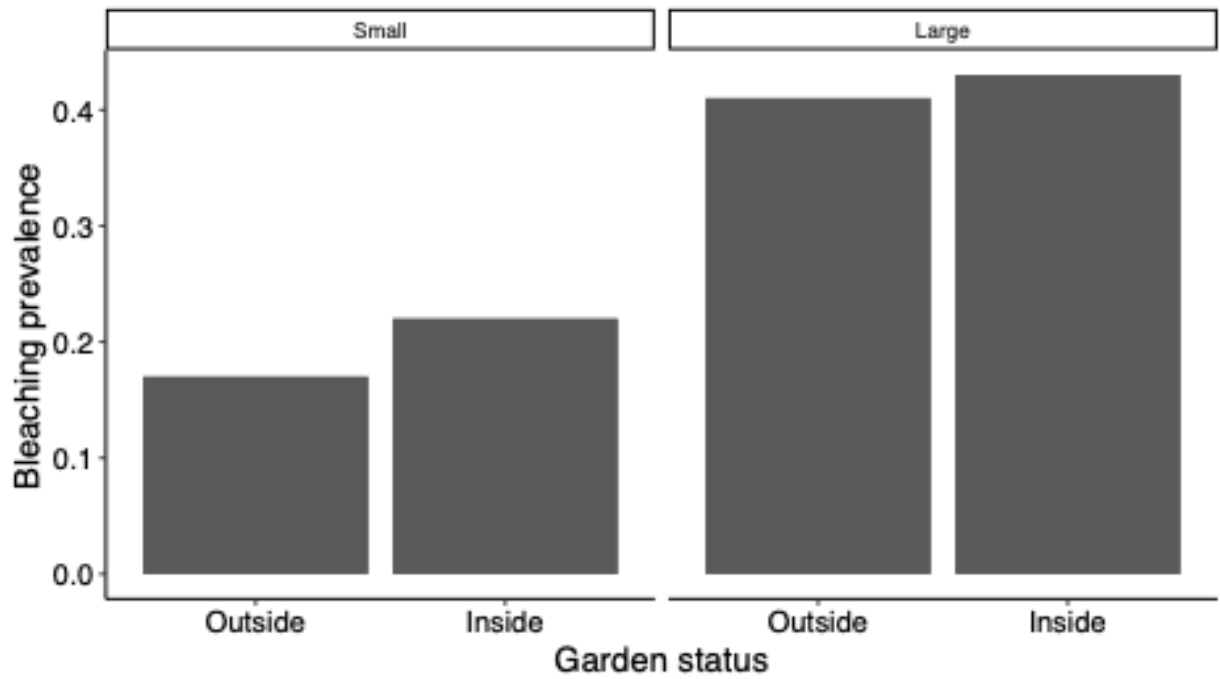
Figure 2: Bleaching prevalence (proportion of the sampled colonies showing at least 5% bleaching) by colony size class as a function of farmerfish garden status for the 1,137 *Pocillopora* encountered on 178 bommies.
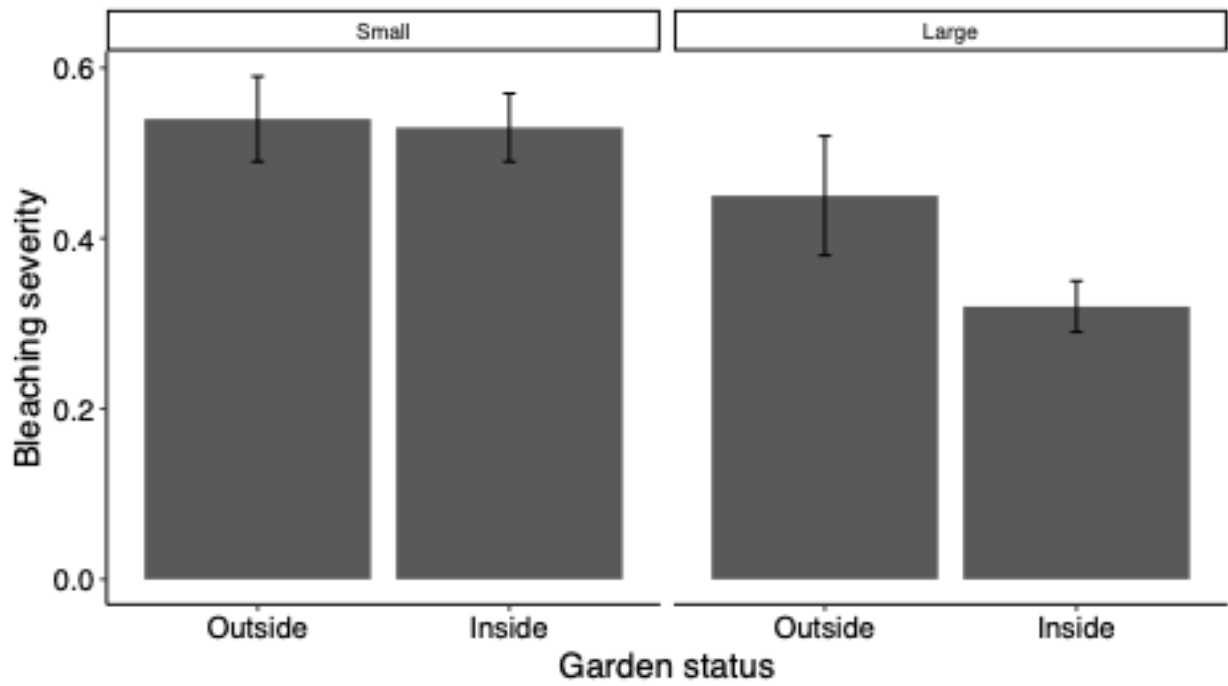
Figure 3: For colonies with ≥ 5% bleached tissue, the mean (± SE) bleaching severity (proportion of a colony's tissue that bleached) by colony size class as a function of farmerfish garden status.
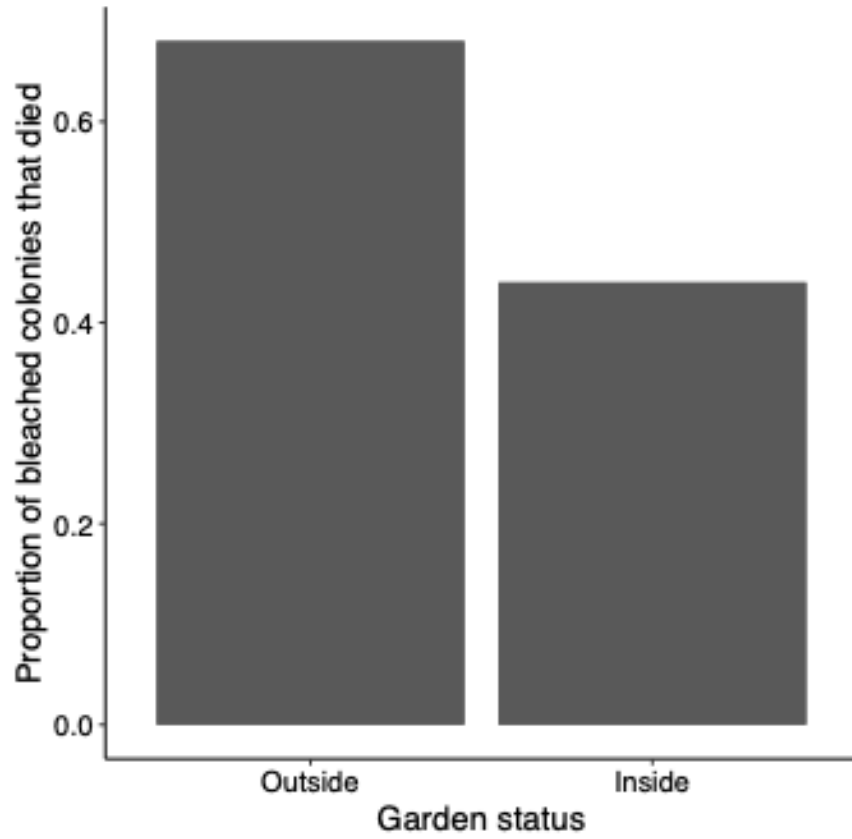
Figure 4: Proportion of bleached colonies that completely died after one year as a function of garden status. Colonies were considered dead if they lost all living tissue.
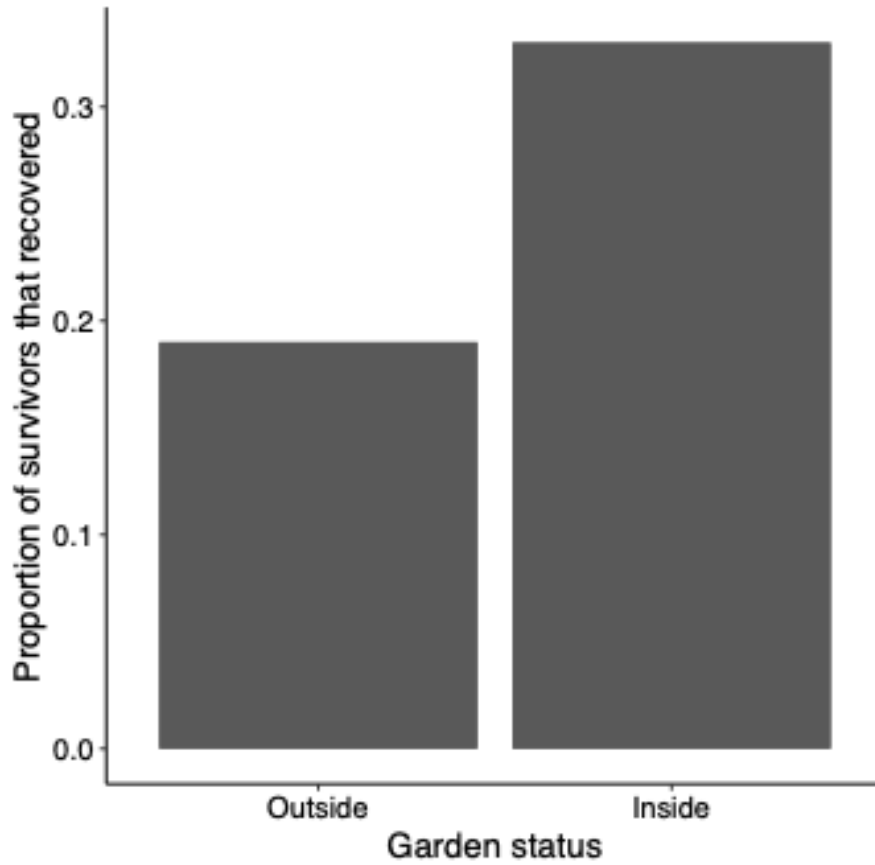
Figure 5: Proportion of surviving bleached colonies that recovered after 1 year as a function of farmerfish garden status; a colony was deemed recovered if it had as much or more live tissue as it had in the initial post-bleaching survey.