



NOTE

Effects of corallivory and coral colony density on coral growth and survival

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Abstract A suite of processes drive variation in coral populations in space and time, yet our understanding of how variation in coral density affects coral performance is limited. Theory predicts that reductions in density can send coral populations into a predator pit, where concentrated corallivory maintains corals at low densities. In reality, how variation in coral density alters corallivory rates is poorly resolved. Here, we experimentally quantified the effects of corallivory and coral density on growth and survival of small colonies of the staghorn coral *Acropora pulchra*. Our findings suggest that coral density and corallivory have strong but independent effects on coral performance. In the presence of corallivores, corals suffered high but density-independent mortality. When corallivores were excluded, however, vertical extension rates of colonies increased with increasing densities. While

we found no evidence for a predator pit, our results suggest that spatio-temporal variation in corallivore and coral densities can fundamentally alter population dynamics via strong effects on juvenile corals.

Keywords Density dependence · Coral fundamental traits · Corallivory · Staghorn coral

Introduction

The density of stony corals varies across multiple spatial and temporal scales, yet we lack a core understanding of how changes in coral colony density (hereafter, coral density) alter dynamics of coral populations. Ecological theory holds that the long-term persistence of populations is facilitated when population density alters one or more demographic rates (Murdoch and Walde 1989). Specifically, a negative relationship between density and population growth rate can bound populations at high density and promote population growth at low density. By contrast, a very low or negative per capita growth rate at low population densities has a destabilizing influence and can lead to extirpation (Courchamp et al. 1999). Consequently, lower colony densities may reduce competitive dynamics within or among species and allow coral populations to rebound. Alternatively, declines in coral density may lead to negative per capita growth rates, which would destabilize coral populations and increase risk of extinction. Therefore, resolving the link between coral fundamental traits like colony growth or survival and coral density will sharpen our ability to forecast the capacity of coral populations to rebound following major declines in density.

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We comprehensively reviewed studies from 1996 to 2020 documenting links between coral density and coral fundamental traits (Table S1). Our review revealed that, to date, corallivory has received relatively limited attention as a mechanism that alters fundamental traits, despite mounting evidence for its importance to coral (Rotjan and Lewis 2008; Lenihan et al. 2011, 2015) and theory highlighting the role predators can have in shaping density dependence in demographic rates (Murdoch 1994). Predators can regulate growth of prey populations by increasing the per capita mortality of prey at higher prey densities (Janzen 1970; Connell 1971; Murdoch 1994; Schmitt and Holbrook 2007) through increases in foraging rates of individual predators, aggregation of predators to areas of higher prey density, and/or an overall increase in abundance via a demographic response to an increased food supply. Alternatively, increases in prey density can positively affect per capita survival of prey, where high prey densities dilute predator effects (Murdoch 1994). Lastly, predators can reduce the capacity of prey populations to recover when predators concentrate their foraging on low density prey populations, a situation known as a predator pit (Bakun 2006). Therefore, how predators respond to variation in prey density has the potential to either stabilize or destabilize dynamics of prey populations.

Studies have shown that highly mobile corallivores can aggregate in areas of higher coral density (Shantz et al. 2011) and that the feeding rate of an individual corallivore can increase as coral density increases (Roff et al. 2011). However, it is unclear whether the observed responses of these corallivores to variation in coral density acted to regulate or destabilize coral populations because the link between the behavioral responses and effects on per capita mortality of coral was not explored. In the present study, we tested the hypothesis that corallivory is a key mechanism underlying the effects of coral density on coral growth and survival. Specifically, we quantified how the skeletal growth and colony survival of the staghorn coral, *Acropora pulchra*, varied with density in the presence and absence of corallivores. We focused on small-sized colonies for two related reasons. First, they represent a critical phase in the establishment of a new thicket of staghorn, either via sexual reproduction or asexual fragmentation, where the risk of whole-colony mortality is much greater than for larger colonies. Second, as *A. pulchra* colonies increase in size, they become protected by territorial farmlandfishes that ward off both herbivorous and corallivorous species of fishes (Johnson et al. 2011). Therefore, a small (juvenile) life stage is most susceptible to complete removal (and thereby extirpation) by corallivores and thus provides a more direct test of the predator pit hypothesis in this system.

Materials and methods

Study site, species, and experimental design

We conducted a 30-day experiment on the northern shore of Moorea, French Polynesia (17.5388° S, 149.8295° W) from July–August, 2018. Moorea's shallow lagoons (1–4 m depth) are characterized by patch reefs formed by live and dead colonies of mounding species of *Porites* interspersed with sand and coral rubble. Branching *Acropora* corals commonly grow on the tops of these *Porites* reefs and vary naturally in density (Johnson et al. 2011; Lenihan et al. 2011). Our study focused on *A. pulchra* due to this known variation in density, as well as its high growth rate and sensitivity to predation pressure (Kamath et al. 2019).

To quantify how corallivory pressure changes as a function of coral density, we used a factorial experimental design crossing three levels of coral density with two levels of corallivore exposure (Fig. 1). We harvested *A. pulchra* coral nubbins, each 70–80 mm in length with no secondary branches (i.e., to mimic a young juvenile), from 6 thickets of adult colonies in a lagoon near our experimental site. We then affixed the nubbins to artificial bases using underwater epoxy (Z-Spar A-788 Splash Zone Epoxy), and measured their vertical extension (VE), total linear extension (TLE), and buoyant mass (Davies 1989) before deployment. We then randomized their assignment to the three density treatments, using the average density of branch tips ($\sim 350 \text{ m}^{-2}$) in nearby natural staghorn patches as the high density treatment (see Supplemental Materials). The low density treatment consisted of a single nubbin (affixed to a base 'platform' to facilitate deployment) ($n = 12$ for each corallivore treatment); the medium density had 4 nubbins evenly spaced 13 cm apart on a square platform (equivalent to $\sim 172 \text{ nubbins m}^{-2}$; $n = 8$); and high density had 8 nubbins spaced in the same configuration but 6 cm from a neighbor (equivalent to $345 \text{ nubbins m}^{-2}$; $n = 8$). Half of the replicates of each density treatment were left exposed to corallivores, while the other half was ensconced in a thin-gauge vinyl-coated 6.25 cm² mesh wire cage that excluded larger corallivorous fishes but did not impede flow and light (Schmitt et al. 2019). Following the rationale of other predator-exclusion field experiments (e.g., Thorp and Bergey 1981), we did not include a cage control (e.g., partial cage treatment) as predators in this system are attracted to structures (Schmitt and Holbrook 2007). A pair of caged and uncaged replicates of the same density treatment were deployed ~ 0.5 m apart atop a *Porites* bommie (patch reef); replicate patch reefs were spaced at least one meter apart and distributed over an area of roughly 3000 m² (see Fig. S1, Supplemental Materials).

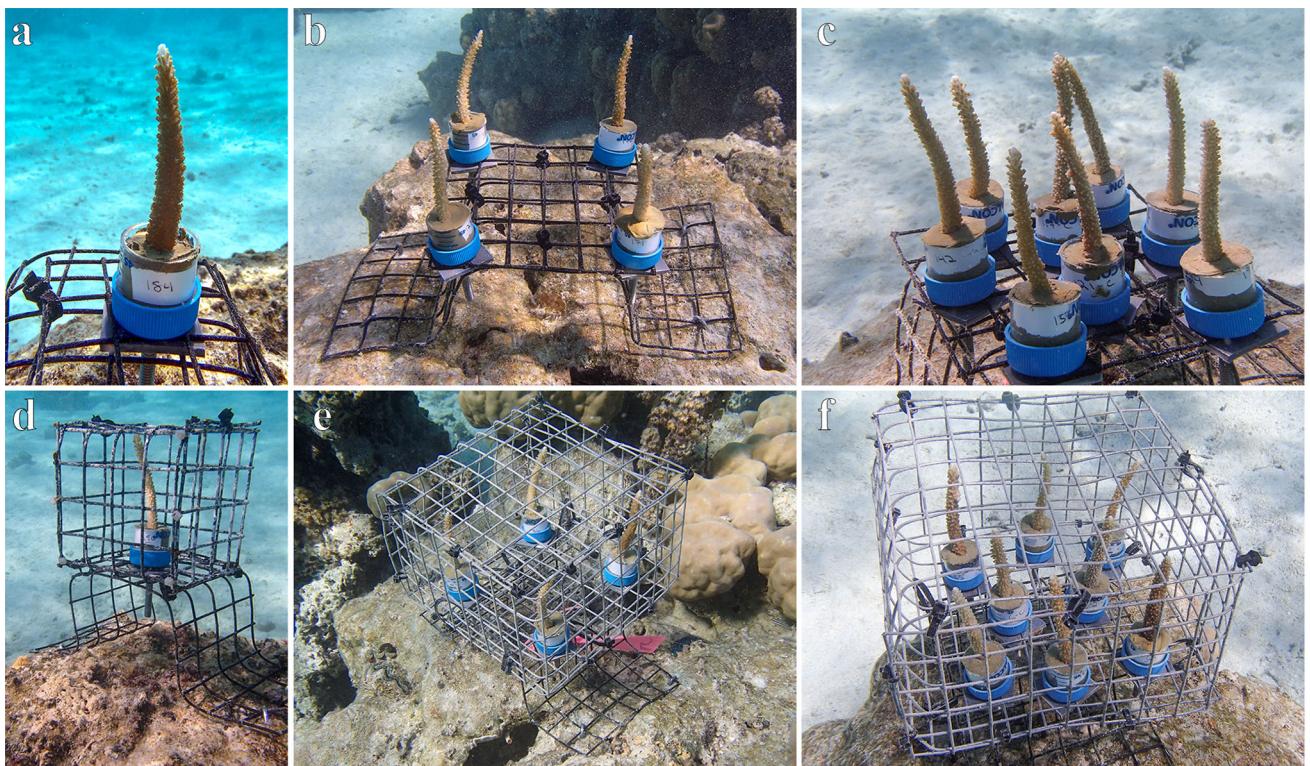


Fig. 1 Factorial experimental design crossing two levels of corallivore exposure with three levels of colony density of the staghorn coral *Acropora pulchra*. Panels **a–c** show plots exposed to corallivores, while **d–f** show plots protected from corallivores (via enclosure cages)

The spatial scale of the experiment is smaller than the home range of the major excavating corallivores in this system (e.g., *Balistapus undulatus*, *Balistoides viridescens*, *Arothron meleagris*; Johnson et al. 2011), so we assume that we distributed patches of different resource densities over a relatively uniform landscape of corallivory. For each corallivore treatment, we deployed 28 platforms collectively holding 108 nubbins (experiment total = 216 nubbins on 56 platforms).

After 30 days, we collected all nubbins and re-measured their VE, TLE, and buoyant mass in the laboratory. We revisited the plots 8 months after deployment and found that cage surfaces did not require cleaning, presumably because herbivory kept them almost completely free of macroalgae (Figure S2); only a few cages became somewhat more fouled after 12 months when surviving experimental corals were re-measured. After a year, corals protected from predators grew extensively and when present, often fused with neighbors; this meant that we could only compare the change in total volume of live coral over the year between the corallivore exposure treatments (see Supplemental Materials). The mid-lagoon experimental site was not subjected to either storm waves or high velocity current flows throughout the study (<http://mcr.lternet.edu/cgi-bin/showDataset.cgi?docid=knb-lter-mcr-30>).

Data analysis

We treated each deployed platform (with 1, 4, or 8 nubbins) as a replicate. To obtain overall averages within density treatments, we first calculated the mean of a given metric for each replicate (medium and high densities) to obtain a single estimate for a platform, then took an average of all replicates within a density treatment to explore for treatment effects. We used a two-way ANOVA to test for interactive effects between corallivore presence/absence and coral density on coral survival. Nubbins that suffered < 95% loss of tissue and skeleton after 30 days were considered to have survived.

Within the corallivore exclusion treatment, we used planned orthogonal contrasts to first look at the effects of having neighbors (low vs. medium and high density treatments), then effects of neighbor density (medium vs. high density treatment) on coral growth. We adjusted for variation in growth due to slight differences in initial nubbin size by converting raw changes in VE, TLE, and buoyant mass to proportional changes. No coral exposed to corallivores showed measurable growth, and thus we did not use this approach for the uncaged density treatments.

Results and discussion

Our test of whether the effects of corallivores depended on coral colony density in *Acropora pulchra* revealed that, although predators had a substantial negative effect on both growth and survival of juvenile-sized coral, we found no evidence that the rate of corallivory was dependent on coral density (i.e., there was no interaction between corallivore exposure and coral density). This does not support the notion that corallivory alters the stability of coral populations in this system. After 30 days, corallivores had consumed > 95% of tissue and skeleton in 64% of exposed corals, while all corals protected from corallivores survived without any partial mortality (two-way ANOVA: $F_{1,50} = 60.0911$, $P < 0.001$; Fig. 2). Repeated observations of our experimental corals revealed the pattern of tissue and skeletal loss for the exposed nubbins was precisely that known to be caused by excavating corallivores: bites that remove a portion of the distal end, gradually reducing the length of a nubbin over time (Johnson et al. 2011; Kamath et al. 2019; Fig S3). With respect to growth, corals exposed to corallivores showed no measurable signs of skeletal growth after 30 days (Fig. 3a), while virtually all protected corals increased in VE, TLE, and mass, and had also begun to develop secondary branches after the same duration (Fig. 3b). After one year, the total volume of surviving corals that were protected from corallivores increased from 742.5 cm^3 to $55,251 \text{ cm}^3$, while that for corals exposed to corallivores decreased from 752.5 cm^3 to 381.4 cm^3 (Fig. 3c, d; Fig S4). Thus, patterns measured after 30 days held over the long term, where the volume of coral protected from predators increased by two orders of magnitude in a year, while that of exposed corals declined by half.

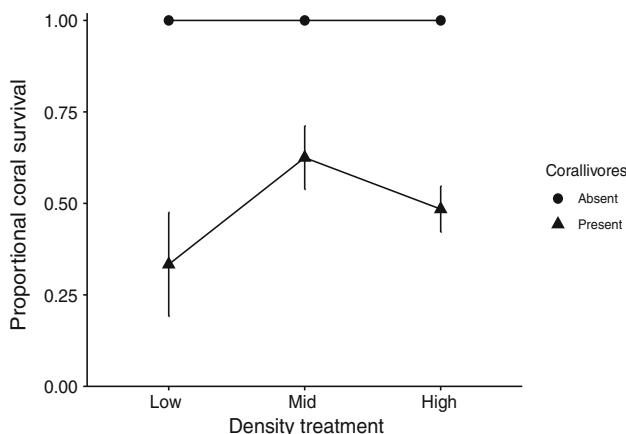


Fig. 2 Average proportional survival of coral nubbins as a function of coral density (low, medium, high) and corallivore exposure (absent or present). Survival is expressed as the mean ($\pm 1 \text{ SE}$; platforms as replicates) proportion alive after 30 days

Our findings contrast with previous studies that suggest high densities of coral colonies can dilute predator effects. For example, Jayewardene et al. (2009) showed that corallivory decreased as coral cover increased, which is indicative of predator dilution. One possible explanation for our failure to detect predator dilution is that it occurs only when corals are at extraordinarily large patch sizes. While our study focused on a range of variation in *A. pulchra* density that is most commonly found on patch reefs in Moorea, some enormous thickets of *A. pulchra* tens of meters long exist, which is a situation that might promote predator dilution, although natural staghorn patches in Moorea are protected by territorial farmerfishes that defend against both herbivorous and corallivorous fishes (Johnson et al. 2011). Here, we found that corallivores exerted strong negative effects on coral growth and survival at small colony sizes at a range of densities, corroborating other recent studies on corallivory (Lenihan et al. 2011, 2015; Roff et al. 2011; Shantz et al. 2011) and suggesting that corallivory does not become increasingly concentrated at low coral densities. We note that the mid-lagoon location of our experiment may well be characterized by a relatively high level of corallivory, and that the performance of staghorn might scale with coral density in areas where corallivory is lower.

Though the effects of corallivores on survival were independent of coral density, vertical extension was positively correlated with density for corals protected from corallivores (Fig. 4). In the absence of corallivory, the VE of corals in aggregations increased two-fold more than for solitary corals (low density vs. medium + high densities, $F_{2,103} = 5.954$, $P < 0.004$). However, the positive effect of coral neighbors did not differ between the medium and high density treatments (Fig. 4). Corals protected from corallivores also exhibited increases in mass and TLE, but these did not differ significantly by density treatment (see Supplemental Materials). Morphology and extension rates of Caribbean staghorn coral (*Acropora cervicornis*) have been found to be plastic (Kuffner et al. 2017), while calcification and skeletal growth are energetically expensive (Gattuso et al. 1999). Thus, if resource acquisition (and therefore, growth rate) is enhanced for corals in higher density aggregations, we would expect to have seen density dependent increases in skeletal mass as well as VE. Because only VE increased for corals in higher density aggregations and not mass, we posit that the increase in VE we found for corals in high density treatments was likely a plastic, competitive response to maximize resource capture (Lang and Chornesky 1990) and not a true density dependent increase in growth rate. This is corroborated by a well-known phenomenon in terrestrial plants and subtidal algal forests—the self-thinning rule—by which individuals tend to grow taller in higher density stands in order to

Fig. 3 High density platforms after being (a) exposed to or (b) protected from corallivores for 30 days. Platforms were revisited after one year, showing even stronger effects of (c) exposure to or (d) protection from corallivores (cage removed for photograph)

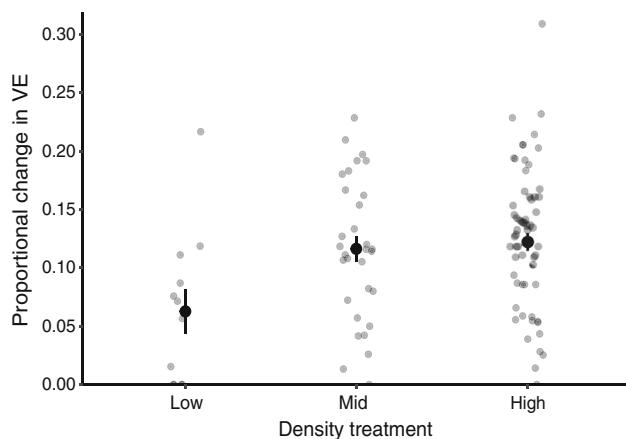


Fig. 4 Average increase in vertical extension (VE) as a function of density when protected from corallivory. Shown are the mean (± 1 SE; platforms as replicates) proportional changes in VE (large black dots) and proportional changes for each nubbin (small gray dots) after 30 days

maximize light capture, while individuals in low density aggregations are able to allocate more energy into reproduction (Weller 1989; Reed 1990). Additional research would be required to determine if this was the mechanism at play in our experiment and whether or not corals differentially allocate energy as a function of their aggregation density.

Our study shows that corallivory and coral density independently modify survival and growth of small staghorn corals. Corallivores in this system exerted substantial

mortality that was independent of coral density, which may be the common pattern when corallivory-induced mortality is intense (Lenihan et al. 2015). However, additional research on corallivore foraging behavior is necessary to fully evaluate the role of predation in shaping the dynamics of coral populations. Given the findings of both positive and negative effects of coral density on coral fundamental traits (Table S1), further exploration of the mechanisms underlying the reported effects of coral density are critical to determine whether and how variation in density influences the dynamics of coral populations. The present study deepens our understanding of the ecological processes that govern population dynamics via effects on vulnerable, juvenile-sized corals by considering explicitly the link between variation in density and their fundamental traits.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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References

- Bakun A (2006) Wasp-waist populations and marine ecosystem dynamics: Navigating the 'predator pit' topographies. *Prog Oceanogr* 68:271–288
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dyn Popul* 298:312
- Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. *Trends Ecol Evol* 14:405–410
- Davies PS (1989) Short-term growth measurements of corals using an accurate buoyant weighing technique. *Mar Biol* 101:389–395
- Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interactions and control by carbonate chemistry. *Am Zool* 39:160–183
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Jayewardene D, Donahue MJ, Birkeland C (2009) Effects of frequent fish predation on corals in Hawaii. *Coral Reefs* 28:499–506
- Johnson MK, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Fish communities on staghorn coral: effects of habitat characteristics and resident farmedfishes. *Env Bio Fish* 91:429–448
- Kamath A, Pruitt JN, Brooks AJ, Ladd MC, Cook DT, Gallagher JP, Vickers ME, Holbrook SJ, Schmitt RJ (2019) Potential feedback between coral presence and farmedfish collective behavior promotes coral recovery. *Oikos* 128:482–492
- Kuffner IK, Bartels E, Stathakopoulos A, Enochs IC, Kolodziej G, Toth LT, Manzello DP (2017) Plasticity in skeletal characteristics of nursery-raised staghorn coral, *Acropora cervicornis*. *Coral Reefs* 36:679–684
- Lang JC, Chornesky EA (1990) Competition between scleractinian reef corals: a review of mechanisms and effects. *Ecosyst World* 25:209–252
- Lenihan HS, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Influence of corallivory, competition, and habitat structure on coral community shifts. *Ecology* 92:1959–1971
- Lenihan HS, Hench JL, Holbrook SJ, Schmitt RJ, Potoski M (2015) Hydrodynamics influence coral performance through simultaneous direct and indirect effects. *Ecology* 96:1540–1549
- Murdoch WW (1994) Population regulation in theory and practice. *Ecology* 75:271–287
- Murdoch WW, Walde SJ (1989) Towards a more exact ecology. In: *Analysis of insect population dynamics*. Blackwell, Oxford, pp 113–140
- Reed DC (1990) An experimental evaluation of density dependence in a subtidal algal population. *Ecology* 71(6):2286–2296
- Roff G, Ledlie MH, Ortiz JC, Mumby PJ (2011) Spatial patterns of parrotfish corallivory in the caribbean: the importance of coral taxa, density and size. *PLoS ONE* 6:e29133
- Rotjan RD, Lewis SM (2008) Impact of coral predators on tropical reefs. *Mar Ecol Prog Ser* 367:73–91
- Schmitt RJ, Holbrook SJ (2007) The scale and cause of spatial heterogeneity in strength of temporal density dependence. *Ecology* 88:1241–1249
- Schmitt RJ, Holbrook SJ, Davis SL, Brooks AJ, Adam TC (2019) Experimental support for alternative attractors on coral reefs. *PNAS* 116:4372–4381
- Shantz AA, Stier AC, Idjadi JA (2011) Coral density and predation affect growth of a reef-building coral. *Coral Reefs* 30:363–367
- Thorp JH, Bergey EA (1981) Field experiments on the responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. *Ecology* 62:365–375
- Weller DE (1989) The interspecific size-density relationship among crowded plant stands and its implications for the-3/2 power rule of self-thinning. *Am Nat* 133(1):20–41

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1 **Supplemental materials**

2 **Supplemental methods**

3 **Literature review**

4 We obtained and summarized studies examining the effects of density dependence on
5 scleractinian corals, observationally or experimentally, by conducting an exhaustive electronic search on
6 Google Scholar and Web of Science under the queries "coral density dependence" and "coral disease."
7 Of the approximately 350 search results produced, we found 27 relevant studies that directly observed
8 or tested for the effects of density dependence in hard corals. These studies span 1996-2020 and are
9 published in 14 different journals: *Coral Reefs*, *Bulletin of Marine Science*, *PLOS Biology*, *Royal Society of*
10 *Open Science*, *Restoration Ecology*, *Oecologia*, *Ecology*, *Elsevier*, *Frontiers in Marine Science*, *Frontiers in*
11 *Ecology*, *Marine Ecology Progress Series*, *Diseases of Aquatic Organisms*, *Ecological Monographs*, and
12 Anziam J.

13

14 **Natural Staghorn coral density**

15 To inform the experimental coral densities used in our study, we took density estimates of the
16 standing stock of *A. pulchra* in the lagoons of Moorea. At the patches from which we collected our
17 experimental corals, we counted the number of branch tips and measured maximum and minimum
18 distances between them (for branches extending at least 50mm from the basal branch) in 50 randomly
19 placed quadrats the size of the platforms used in our experiment. Measurements were taken within 4
20 large thickets of *A. pulchra*. We used the mean number of branch tips from these quadrats (7.94 ± 2.94
21 tips) as the number of corals for our high density treatment (8 nubbins) to reflect the average density
22 from a well-established thicket. We used the mean inter-branch distance (8.36 ± 1.29 cm) to inform the

23 spacing of corals in the high-density treatment. In practice, the spacing of the corals in the high-density
24 treatment was slightly less than this (~6cm) due to mechanical restrictions of the materials we had
25 available in the field. We then selected our medium density treatment to be roughly half of the high-
26 density treatment. Finally, we selected our low density treatment as a single nubbin on an experimental
27 platform, as this is the lowest density possible in the units of coral nubbins.

28

29 **Coral volume estimation**

30 We revisited our experimental plots after one year, but due to the extent of growth and fusion
31 in the caged corals, we were unable to make the same measurements as in the initial 30-day
32 experiment. We instead estimated the change in total volume of live after one year for corals exposed
33 to or protected from corallivores. We estimated the volume of a single coral nubbin (from the initial
34 deployment) by multiplying each nubbin's vertical extension by a width and length of 1 cm (an
35 estimation of the thickness of a staghorn coral branch), then summed all nubbin volumes within the
36 corallivore inclusion/exclusion treatments. To obtain volume measurements after a year had passed, we
37 measured the height, width, and length of each protected and unprotected nubbin *in situ* when it was
38 possible to discern divisions between nubbins. When this was not possible, we measured the height,
39 width, and length of the "coral cube" to estimate the volume of coral on the platform. We then summed
40 the volumes of all nubbins and coral cubes within each corallivore exposure treatment to estimate the
41 total change in volume of live coral.

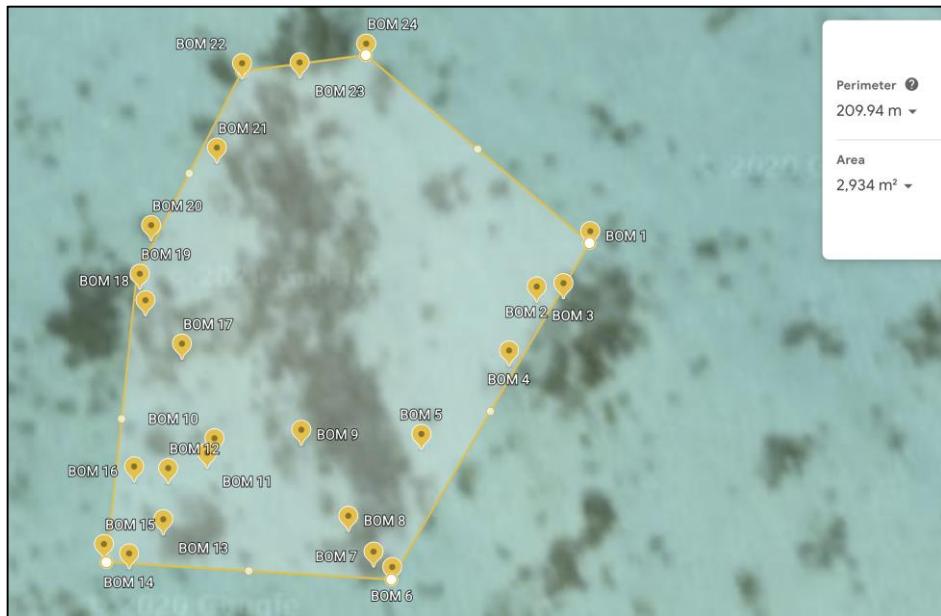
42 **Supplemental results**

43 **Coral growth**

44 Corals protected from corallivores increased both in mass (Fig S3) and TLE (Fig S4) during the 30-
45 day study period; however, one-way ANOVAs revealed that these increases did not vary significantly by
46 density treatment (mass: $F_{2,103} = 1.115, P = 0.332$; TLE: $F_{2,103} = 0.989, P = 0.375$). Corals increased
47 proportionally in mass by an average of 8.8 (± 0.9)% in the low density treatment, 8.0 (± 0.8)% in the
48 medium density treatment, and 7.3 (± 0.4)% in the high density treatment. As for TLE, corals increased
49 proportionally by an average of 30 (± 5.6)% in the low density treatment, 24.6 (± 3.3)% in the medium
50 density treatment, and 26.2 (± 2.2)% in the high density treatment.

51 **Supplemental figures**

52 **Figure S1.**



53

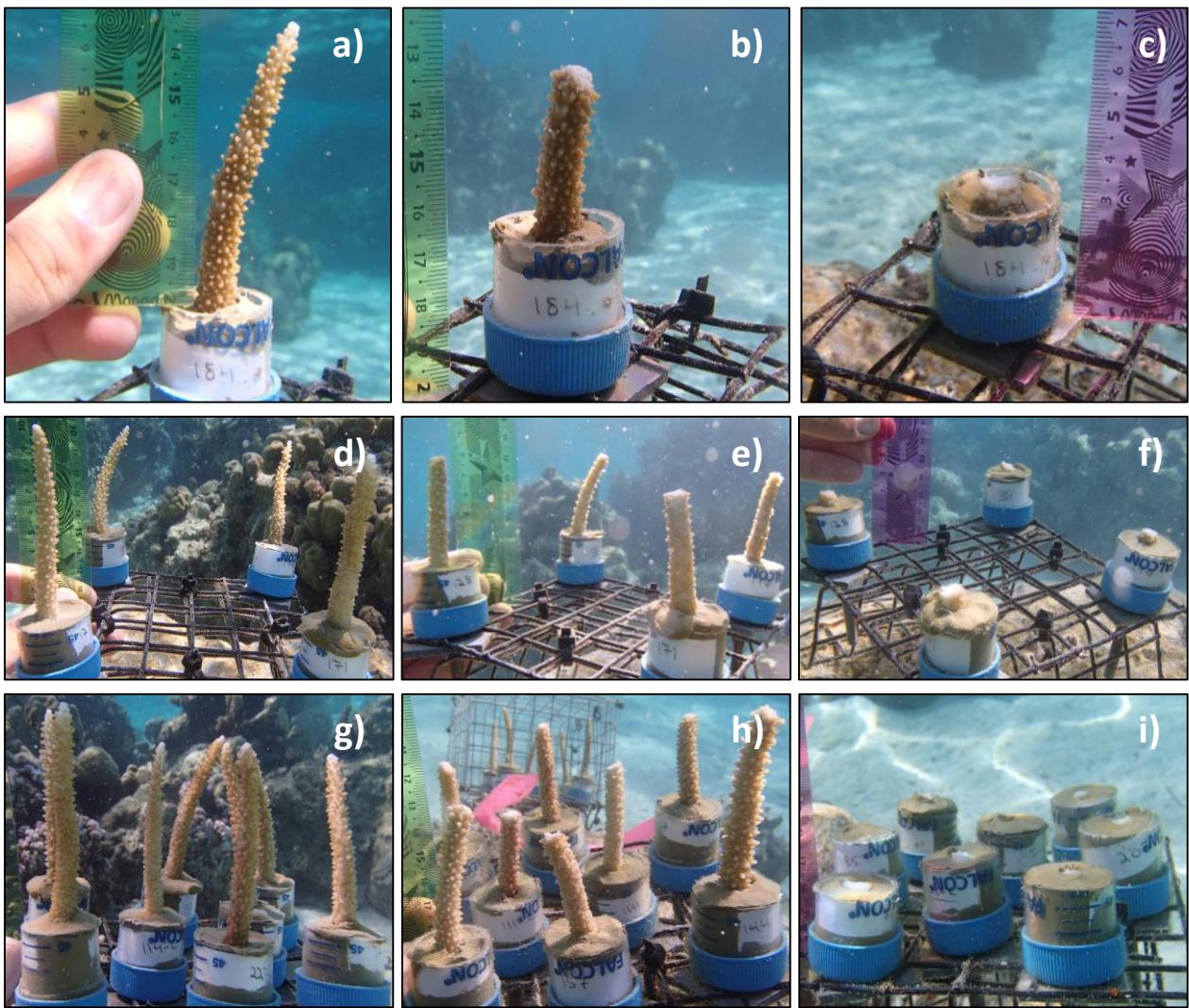
54 **Figure S2.**



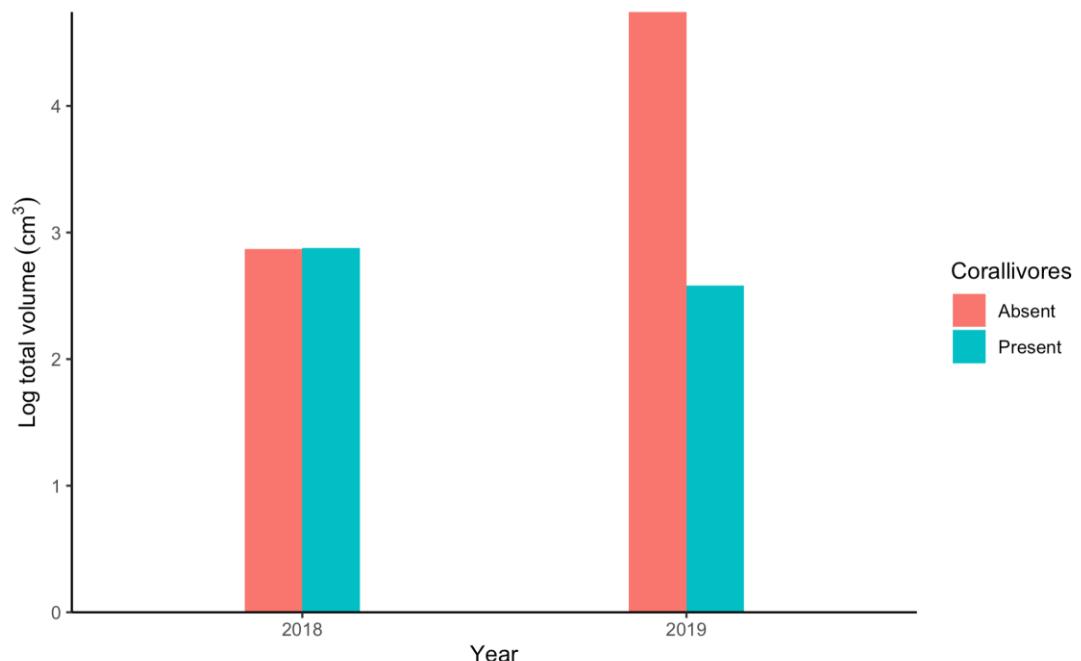
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56 **Figure S3.**

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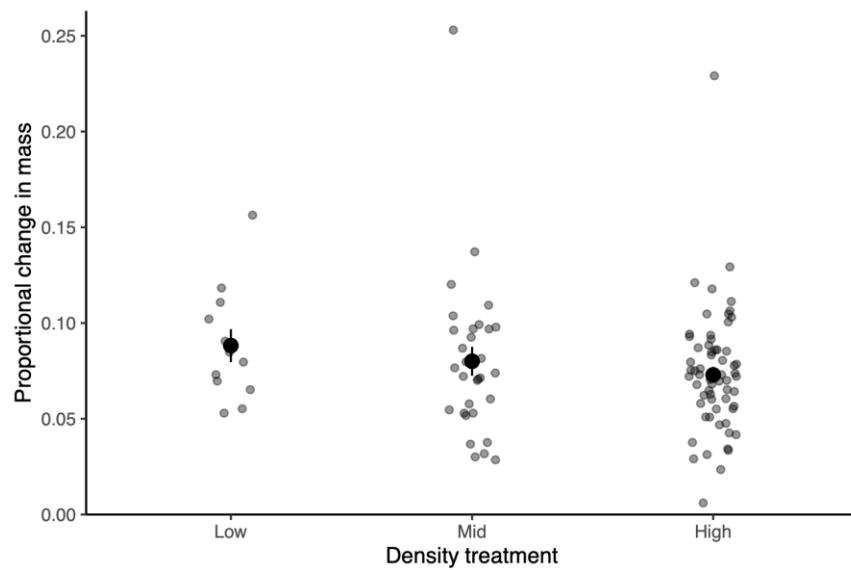


58 **Figure S4.**



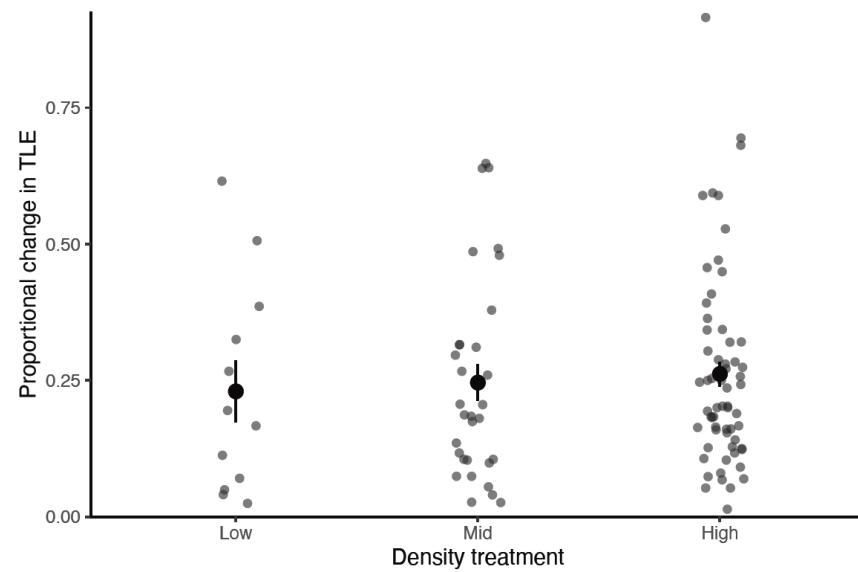
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60 **Figure S5.**



61

62 **Figure S6.**



63

64 **Supplemental figure captions**

65 **Fig S1.** Satellite image of experimental array. Experimental platforms were deployed to replicate reefs
66 within an area of 2,934 m² on the north shore lagoon of Moorea, French Polynesia. The reef area in the
67 center of the displayed image was avoided due to a high density of territorial damselfishes which ward
68 off corallivorous fishes.

69

70 **Fig S2.** Photos showing minimal fouling on experimental cage structures roughly 8 months after
71 initiation of the experiment (photos taken April 1st and 2nd of 2019).

72

73 **Fig S3.** Photos depicting progressive consumption of our experimental corals in a low (panels a-c),
74 medium (panels d-f), and high (panels g-i) density treatment exposed to corallivores. Removal of coral
75 skeleton and tissue began at the distal ends of each nubbin and progressed toward the artificial bases.
76 The consumption shown above occurred during the 30-day experimental period.

77

78 **Fig S4.** Estimated log total volume (cm³) of live coral present at the initiation of the experiment and one
79 year after when protected from (red bars) or exposed to corallivores (green bars).

80

81 **Fig S5.** Proportional increases in dry mass (converted from buoyant mass) as a function of density
82 treatment. Treatment means are displayed as large black dots (\pm 1 SE), while small grey dots are
83 proportional changes for individual nubbins.

84

85 **Fig S6.** Proportional increases in total linear extension (TLE) as a function of density treatment.

86 Treatment means are displayed as large black dots (± 1 SE), while small grey dots are proportional

87 changes for individual nubbins.

88 **Table S1.** Table compiling results from 27 studies, spanning 1996-2020 and published in 14 journals that observed or tested for density
 89 dependent effects in scleractinian corals. ‘Focal life stage(s)’ refers to the life stage that is the recipient of the density dependent effect (e.g.,
 90 effect of *adult density* on *recruit survival* would be listed as “Recruit”). “Pattern” refers to distributional observations (e.g., disease prevalence),
 91 “process” refers to an ecological process or vital rate (e.g., settlement or growth), and “mechanism” refers to a driver of density-dependent
 92 effects (e.g., corallivory). ‘Focal taxa’ refers to the primary study taxa examined.

Focal life stage(s)	Pattern, process, or mechanism described	Effect of density	Focal taxa	Geographic region	Study
Adult	Genotypic diversity	Negative	<i>Acropora palmata</i>	Caribbean/western Atlantic	Baums et al. 2006
Recruit	Recruitment	Positive	<i>Acropora spp.</i>		
Recruit	Recruitment	Negative	<i>Pocillopora spp.</i>	Mo’orea, French Polynesia	Bramanti & Edmunds 2016
Adult	Disease prevalence	Positive	<i>Orbicella annularis</i> <i>Siderastrea radians</i>	Jamaica	Bruckner et al. 1997
Not specified	Disease prevalence	Positive	Great Barrier Reef spp.	Great Barrier Reef	Bruno et al. 2007
Adult	Corallivory	Positive	See study	Florida Keys	Burkepile et al. 2012
Adult	Disease prevalence	Positive	<i>Porites spp.</i> <i>Montipora spp.</i>	Hawaiian archipelago	Caldwell et al. 2016
Juvenile	Distribution	None	See study	Florida Reef Tract	Chiappone & Sullivan 1996
Larvae	Settlement	Positive			
Larvae	Survivorship	None			
Recruit	Post-settlement survivorship	Positive	<i>Acropora millepora</i>	Western Australia	Doropoulos et al. 2017
Larvae	Settlement	Positive	<i>Acropora digitifera</i> <i>Acropora millepora</i> <i>Goniastrea retiformis</i>	Western Australia	Doropoulos et al. 2018
Adult	Genotypic diversity	Positive	<i>Acropora cervicornis</i>	Florida; Dominican Republic	Drury et al. 2019
Recruit, juvenile, adult	Recruitment, distribution	Negative	<i>Pocillopora spp.</i>	Mo’orea, French Polynesia	Edmunds et al. 2018
Juvenile, adult	Distribution	Positive	Central Pacific spp.	Palmyra atoll	Edwards et al. 2017

Adult	Growth	Negative	<i>Acropora cervicornis</i>	St Croix, US Virgin Islands	Griffin et al. 2015
Adult	Disease prevalence	Positive	<i>Acropora clathrata</i> <i>Acropora cytherea</i> <i>Acropora hyacinthus</i>	Indian Ocean (Cocos and Christmas islands)	Hobbs & Frisch 2010
Recruit	Recruitment	None	Acroporidae	Great Barrier Reef	Hughes et al. 2000
Adult	Growth, mortality	Positive	<i>Acropora cervicornis</i>	Florida; US Virgin Islands	Huntington et al. 2017
Adult	Growth, survivorship	Positive	<i>Porites rus</i> <i>Porites lobata</i>	Mo'orea, French Polynesia	Idjadi & Karlson 2007
Adult	Corallivory	Negative	<i>Porites compressa</i>	Main Hawai'ian islands	Jayewardene et al. 2009
Adult	Disease prevalence	None	<i>Orbicella faveolata</i> <i>Montastraea cavernosa</i>	Florida Keys	Kuta & Richardson 1996
			<i>Colpophyllia natans</i> <i>Diploria clivosa</i> <i>Diploria strigosa</i> <i>Diploria labyrinthiformis</i>		
Adult	Growth	Negative			
	Survivorship	Negative	<i>Acropora cervicornis</i>	Florida Keys	Ladd et al. 2016
	Habitat production	Positive			
Juvenile	Survivorship	Negative	<i>Orbicella faveolata</i>	Caribbean	Marhaver et al. 2013
Not specified	Disease prevalence	Positive	Western Australian spp.	Western Australia	Onton et al. 2011
Not specified	Disease prevalence	Positive	<i>Porites attenuata</i>	Philippines	Raymundo et al. 2003
Not specified	Corallivory	Positive	<i>Orbicella faveolata</i>	Bahamas	Roff et al. 2011
			<i>Orbicella annularis</i> <i>Porites atreoides</i>		
Adult	Growth	Positive	<i>Porites lobata</i>	Mo'orea, French Polynesia	Shantz et al. 2011
	Corallivory	Positive	<i>Porites lutea</i>		
Recruit	Recruitment, depth	See study	Acroporidae	Western Australia	Turner et al. 2018
			Pocilloporidae Poritidae		
Settled planulae	Settlement	Positive	<i>Siderastrea radians</i>	Florida Keys	Vermeij & Sandin 2008
Recruit	Survivorship	Negative			

References

- Baums IB, Miller MW, Hellberg ME (2006) Geographic variation in clonal structure in a reef-building caribbean coral, *Acropora palmata*. *Ecol Monogr* 76:503–519
- Bramanti L, Edmunds PJ (2016) Density-associated recruitment mediates coral population dynamics on a coral reef. *Coral Reefs* 35:543–553
- Bruckner AW, Bruckner RJ, Williams Jr EH (1997) Spread of a black-band disease epizootic through the coral reef system in St. Ann's Bay, Jamaica. *Bull Mar Sci* 61:919–28
- Bruno JF, Selig ER, Casey KS, Page CA, Willis BL, Harvell CD, Sweatman H, Melendy AM (2007) Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biol* 5:e124
- Burkepile, DE (2012). Context-dependent corallivory by parrotfishes in a Caribbean reef ecosystem. *Coral Reefs* 31:111–120
- Caldwell J, Heron S, Eakin C, Donahue M (2016) Satellite SST-based coral disease outbreak predictions for the Hawaiian archipelago. *Remote Sens* 8:93
- Chiappone M, Sullivan KM (1996) Distribution, abundance and species composition of juvenile scleractinian corals in the Florida reef tract. *Bull Mar Sci* 58:555–69
- Doropoulos C, Evensen NR, Gómez-Lemos LA, Babcock RC (2017) Density-dependent coral recruitment displays divergent responses during distinct early life-history stages. *R Soc Open Sci* 4:170082
- Doropoulos C, Gómez-Lemos, LA, Babcock RC (2018) Exploring variable patterns of density-dependent larval settlement among corals with distinct and shared functional traits. *Coral Reefs* 37:25–29

Drury C, Greer JB, Baums I, Gintert B, Lirman D (2019) Clonal diversity impacts coral cover in *Acropora cervicornis* thickets: Potential relationships between density, growth, and polymorphisms. *Ecol Evol*. 9:4518-31

Edmunds PJ, Nelson HR, Bramanti L (2018) Density-dependence mediates coral assemblage structure. *Ecology* 99:2605–2613

Edwards CB, Eynaud Y, Williams GJ, Pedersen NE, Zgliczynski BJ, Gleason ACR, Smith JE, Sandin SA (2017) Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef. *Coral Reefs* 36:1291–1305

Griffin JN, Schrack EC, Lewis KA, Baums IB, Soomdat N, Silliman BR (2015) Density-dependent effects on initial growth of a branching coral under restoration: Density affects coral restoration. *Restor Ecol* 23:197–200

Hobbs J, Frisch A (2010) Coral disease in the Indian ocean: Taxonomic susceptibility, spatial distribution and the role of host density on the prevalence of white syndrome. *Dis Aquat Organ* 89:1–8

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: The link between benthic adults, fecundity, and larval recruits. *Ecology* 81:2241–2249

Huntington BE, Miller MW, Pausch R, Richter L (2017) Facilitation in Caribbean coral reefs: High densities of staghorn coral foster greater coral condition and reef fish composition. *Oecologia* 184:247–257

Idjadi JA, Karlson RH (2007) Spatial arrangement of competitors influences coexistence of reef-building corals. *Ecology* 88:2449–2454

Kuta KG, Richardson LL (1996) Abundance and distribution of black band disease on coral reefs in the northern Florida Keys. *Coral reefs* 15:219-23

Ladd MC, Shantz AA, Nedimyer K, Burkepile DE (2016) Density dependence drives habitat production and survivorship of *Acropora cervicornis* used for restoration on a Caribbean coral reef. *Front Mar Sci* 12:261

Marhaver KL, Vermeij MJA, Rohwer F, Sandin SA (2013) Janzen-Connell effects in a broadcast-spawning Caribbean coral: Distance-dependent survival of larvae and settlers. *Ecology* 94:146–160

Onton K, Page C, Wilson S, Neale S, Armstrong S (2011) Distribution and drivers of coral disease at Ningaloo reef, Indian Ocean. *Mar Ecol Prog Ser* 433:75–84

Raymundo L (2003) Porites ulcerative white spot disease: Description, prevalence, and host range of a new coral disease affecting Indo-Pacific reefs. *Dis Aquat Organ* 56:95–104

Roff G, Ledlie MH, Ortiz JC, Mumby PJ (2011) Spatial patterns of parrotfish corallivory in the Caribbean: The importance of coral taxa, density and size. *PLoS ONE* 6:e29133

Shantz AA, Stier AC, Idjadi JA (2011) Coral density and predation affect growth of a reef-building coral. *Coral Reefs* 30:363–367

Turner JA, Thomson DP, Cresswell AK, Trapon M, Babcock RC (2018) Depth-related patterns in coral recruitment across a shallow to mesophotic gradient. *Coral Reefs*. 37:711-22

Vermeij MJA, Sandin SA (2008) Density-dependent settlement and mortality structure the earliest life phases of a coral population. *Ecology* 89:1994–2004.