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NOTE

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

Kai L. Kopecky[1] · Dana T. Cook[1] · Russell J. Schmitt[1,2] · Adrian C. Stier[1,2]

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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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✉ Kai L. Kopecky
kaikopecky@ucsb.edu

Dana T. Cook
danacook@ucsb.edu

Russell J. Schmitt
russellschmitt@ucsb.edu

Adrian C. Stier
astier@ucsb.edu

[1] Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA

[2] Marine Science Institute, University of California, Santa Barbara, CA 93106, USA

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 farmerfishes 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 ($\sim 350\ \mathrm{m}^{-2}$) 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 ~ 172 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 nubbins m^{-2}; $n = 8$). Half of the replicates of each density treatment were left exposed to corallivores, while the other half was enshrouded in a thin-gauge vinyl-coated 6.25 cm^2 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 m^2 (see Fig. S1, Supplemental Materials).

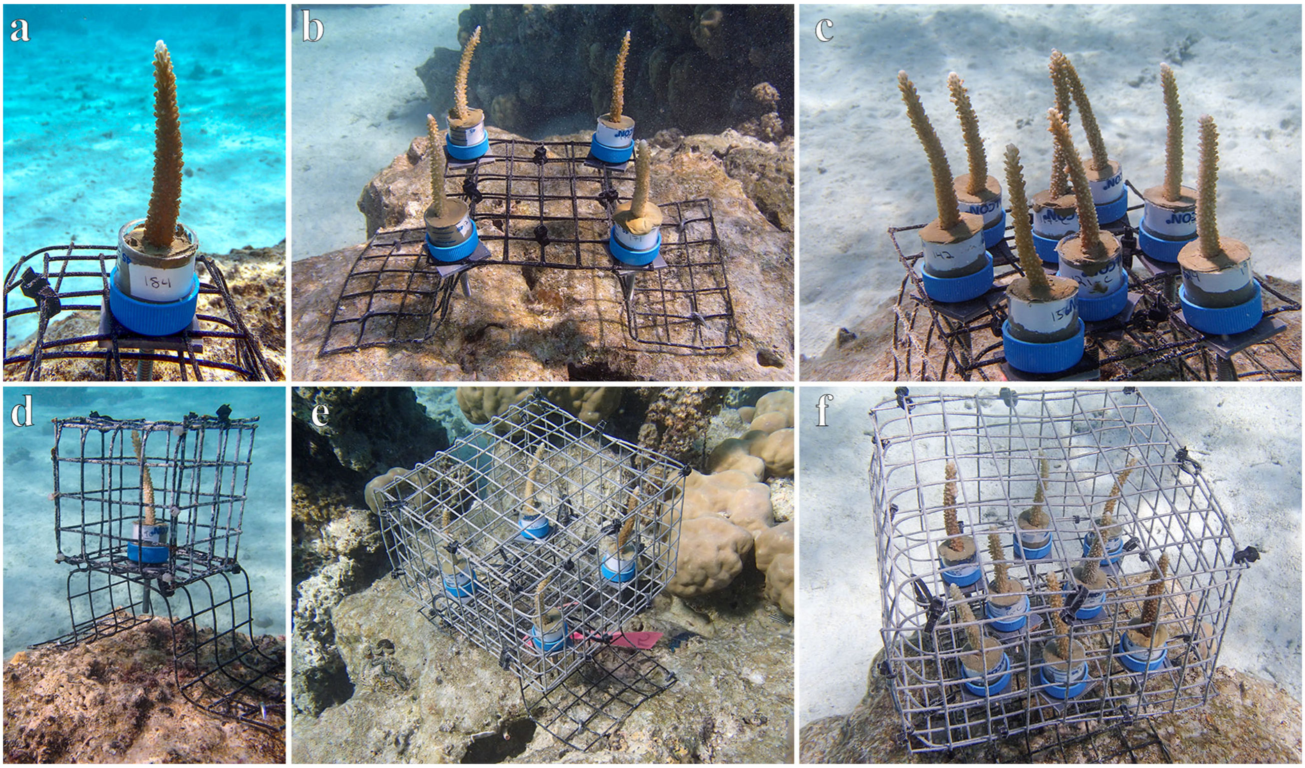


Fig. 1 Factorial experimental design crossing two levels of corallivore exposure with three levels of colony density of the staghorn coral *Acropora pulchra*. Panels **a**–**c** show plots exposed to corallivores, while **d**–**f** show plots protected from corallivores (via exclosure cages)

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 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.

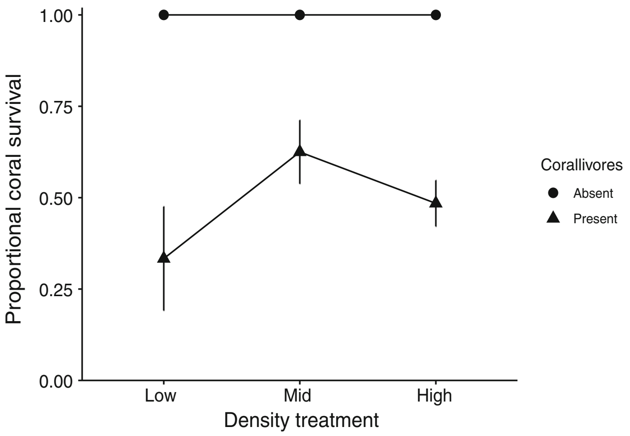
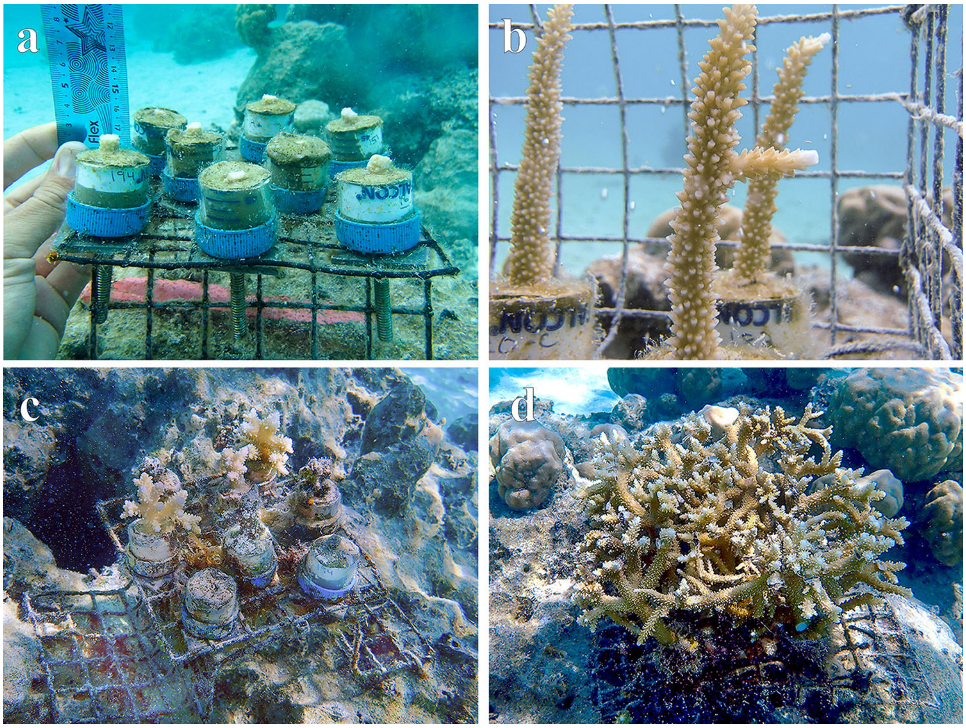


Fig. 2 Average proportional survival of coral nubbins as a function of coral density (low, medium, high) and corallivore exposure (absent or present). Survival is expressed as the mean (± 1 SE; platforms as replicates) proportion alive after 30 days

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)



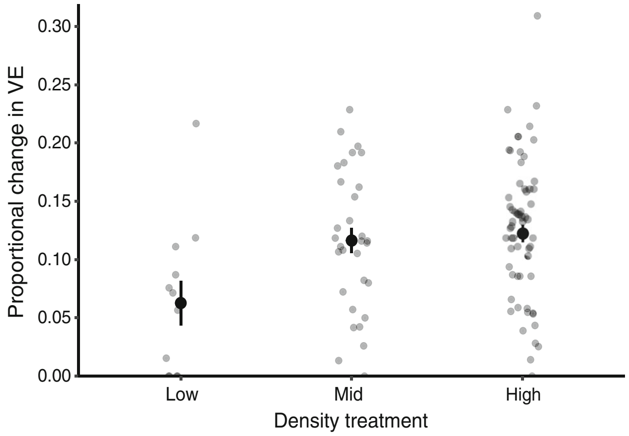


Fig. 4 Average increase in vertical extension (VE) as a function of density when protected from corallivory. Shown are the mean (± 1 SE; platforms as replicates) proportional changes in VE (large black dots) and proportional changes for each nubbin (small gray dots) after 30 days

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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