

Coral density and predation affect growth of a reef-building coral

A. A. Shantz · A. C. Stier · J. A. Idjadi

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Abstract The influence of predation on the growth of stony corals has gained increased attention, although the degree to which coral conspecific density can modify the effects of corallivores remains poorly studied. Here, a field experiment was used to quantify the independent and combined effects of coral colony density and coral predators on the skeletal growth of massive *Porites*. Predator exclusion increased coral growth by 20%. Increasing coral density increased growth by 30%. However, the effect of predators was independent of coral density. Possible alternative mechanisms for increased skeletal growth at higher colony density include changes in near-field flow, resulting in increases in photosynthetic activity, nutrient uptake, or the increased accessibility of coral mutualists.

Keywords Corallivore · Density dependence · *Porites* · Predation

Introduction

Stony coral colonies often occur in high densities, which can affect their growth, competitive ability, and survival by modifying abiotic (Thomas and Atkinson 1997; Sebens et al. 2003; Reidenbach et al. 2007) or biotic (Idjadi and Karlson 2007) conditions. For example, Vermeij and Sandin (2008) showed a positive effect of conspecific density on the mortality of recently settled *Siderastrea radians*, and evidence suggests that heterospecific aggregation in adult fungiid corals can depress growth rates (Elahi 2008). Similarly, studies of population regulation theory highlight the importance of prey density as a modifier of predator–prey interactions via processes such as predator dilution/aggregation and predator swamping (Murdoch 1994). Yet, despite the fact that corallivores are well known to affect the demography of corals (Meesters et al. 1994; Aeby and Santavy 2006; Cole et al. 2008; Pratchett et al. 2009), few studies have explored how the size of coral aggregates affects predation on stony corals.

A rare exception was a recent study in which Jayewardene et al. (2009) quantified predation rates via grazing scars on *Porites compressa* transplants placed in differing densities of existing live coral. This study found lower bite frequencies at higher coral densities, which was evidence of predator dilution. However, some coral predators (e.g., butterfly fishes) are cryptic in their foraging (e.g., removal of single polyps), and therefore, their effects are less conspicuous due to the absence of grazing scars (Rotjan and Lewis 2008). An alternative approach to quantifying the effects of corallivores is to measure net growth. This incorporates the costs of tissue damage and skeletal removal. In our study, a factorial field experiment examined the effects of coral density and corallivore exposure on the skeletal growth of massive reef-building *Porites*.

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A. A. Shantz (✉)
Northeastern University, Marine Science Institute, Nahant,
Massachusetts 01908, USA
e-mail: Ashantz@fiu.edu

A. C. Stier
Department of Biology, University of Florida, Gainesville,
Florida 32611-8525, USA

J. A. Idjadi
Department of Biology, Eastern Connecticut State University,
Willimantic, CT 06226, USA

Materials and methods

Study site and species

This study was conducted in February and March 2009, on the northern shore of Moorea, French Polynesia ($17^{\circ}30' S$, $149^{\circ}50' W$) (see electronic supplemental material, ESM, for a map of Moorea and schematic of the experimental setup). Moorea is a volcanic island with a narrow lagoon containing patch reefs, interspersed with sand, coral rubble, and pavement enclosed by a discontinuous barrier reef (Galzin and Pointier 1985). Patch reefs are dominated by stony corals, the most common of which are massive members of *Porites* spp. (a species complex composed mostly of *Porites lobata* and *P. lutea*, hereafter referred to as *Porites*; Edmunds and Lenihan 2010) and the branching/sheeting coral, *Porites rus*. A diverse suite of corallivores exist in Moorea, including fishes (Table 1) and

Table 1 Obligate and facultative corallivorous fish species observed along 25-m transect lines on reefs within 3 km of the experimental site

Obligate corallivores observed at reef sites within 3 km of the experimental array
<i>Chaetodon lunulatus</i> ^a
<i>C. ornatus</i> ^a
Facultative corallivores observed at reef sites within 3 km of the experimental array
<i>Balistapus undulatus</i> ^a
<i>Balistoides viridescens</i> ^a
<i>Calotomus carolinus</i>
<i>Canthigaster solandri</i> ^a
<i>Cetoscarus bicolor</i>
<i>Chaetodon citrinellus</i> ^a
<i>C. ephippium</i>
<i>C. lunula</i>
<i>C. reticulatus</i>
<i>C. trichrous</i> ^a
<i>C. unimaculatus</i>
<i>C. vagabundus</i> ^a
<i>Coris aygula</i>
<i>Diodon hystrix</i> ^a
<i>Forcipiger flavissimus</i>
<i>Heniochus chrysostomus</i>
<i>Pseudocheilinus hexataenia</i> ^b
<i>Rhinecanthus aculeatus</i> ^a
<i>Scarus ghobban</i>
<i>Zanclus cornutus</i>

^a Species that were also observed within cages at experimental array

^b Species was not known to consume coral at the time of the study

Species were considered corallivores based on Rotjan and Lewis (2008), Berumen and Rotjan (2010)

invertebrates (Rotjan and Lewis 2008). Surveys were conducted in the lagoon east of Cook's pass at an average depth of 3 m. This study focused on the net growth of small colonies (2–3 cm diameter) of *Porites*, an effective colonist and generally weak interference competitor for space in direct interactions with most other genera of corals (Idjadi and Karlson 2007).

Experimental design

In January 2009, a field experiment was conducted to quantify the effects of predator exposure (cage and partial-cage) and coral density (low and high) on the growth of *Porites*. Because local structure can augment fish populations (Jennings et al. 1996; Syms and Jones 2000), potentially impacting predation rates, the experiment was set up in an open sand-plain, parallel to the reef, at least 30 m from the nearest structure.

Thirty-two (32) concrete blocks, each measuring $0.5 \times 0.25 \times 0.25$ m (length \times width \times height), were placed at 10-m increments along the plain to create experimental reefs. Sixteen reefs were fully caged to exclude corallivores (circumference = 1.5 m, height = 1 m, mesh size = 2.54 cm). The remaining 16 reefs served as cage controls, possessing a full top and up-current side, with all remaining sides extending only 5 cm above the concrete blocks in order to allow access by corallivores.

To obtain a better understanding of the subset of corallivores present in the experimental region, divers conducted surveys at four different lagoon sites within 3 km of the experimental array in February 2010. At each site, divers swam five 25-m transects and noted the presence of any corallivores within 4 m of the transect (Table 1), as well as bite scars on live coral. Corallivorous fish were considered as any species listed as a consumer of live coral (see Rotjan and Lewis 2008).

In studies of density dependence, the most relevant metric for determining densities is the local neighborhood of a focal individual, rather than the mean abundance in a quadrat (Lloyd 1967). This metric, termed mean crowding (m^*), is calculated as follows:

$$m^* = m + \frac{m}{k}, \quad (1)$$

where m and k are the maximum likelihood estimates of a mean and shape parameter of a negative binomial distribution (Lloyd 1967).

The m^* of *Porites* nubbins near the study site was estimated as 9.52 ± 1.93 (mean \pm 0.1 SE; range: 0–12), based on data from 30 randomly assigned 1-m² quadrates placed along six 30-m transect lines. This natural variation in *Porites* density was used to assign appropriate low- and

high-density treatments which contained two and eight coral colonies, respectively.

Coral collection, measurement, and predator surveys

One hundred and sixty (160) nubbins (2–3 cm in diameter) of *Porites* were collected from the pavement near the reef crest and affixed to small plastic bases using Z-spar marine epoxy (Splash Zone CompoundTM). Colonies were weighed using the buoyant weight technique (Davies 1989), returned to the field, and affixed several centimeters apart from each other to experimental reefs via cable ties at one of the two density treatments. An analysis of variance confirmed that the average nubbin size was equal among treatment groups ($F_{2,28} = 0.126, P = 0.882$).

Approximately every 4 days, a single observer swam the length of the experimental array, pausing ~5 m from each cage, to note any corallivorous species (Table 1) and their abundance within the cages (Fig. 1). The diver then approached each cage to check for cryptic fishes and checked for the evidence of skeletal removal on the experimental corals. Cages were scrubbed twice weekly to reduce fouling, and after 23 days, corals were collected and transported back to the laboratory, where a final buoyant weight was obtained. The foil technique (Marsh 1970) was used to estimate the surface area of each colony to standardize the growth rates (g per cm^2 per day).

Data analysis

One replicate of the high-density caged treatment was lost during the experiment, leaving an unbalanced nested design. Therefore, each concrete reef was considered a

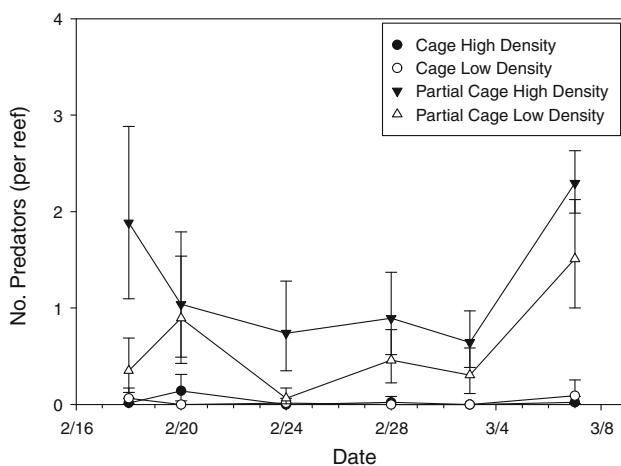


Fig. 1 Average abundance of corallivores (number individuals per reef) in each of the density (2 and 8) and predator exclusion (Caged and Partial-Cage) treatments during repeated censuses throughout the duration of the study. Points and error bars represent back-transformed means $\pm 1 \text{ SE}$

replicate, and the growth response variable was generated from the average growth of colonies within a concrete reef. Normality and variance homogeneity were assessed visually through quantile–quantile plots, Shapiro–Wilk normality test, and Levene's test. Data did not deviate significantly from a normal distribution (Shapiro–Wilk normality test, $W = 0.957, P = 0.241$), and variances were not significantly heterogeneous (Levene's test $F_{3,27} = 0.348, P = 0.791$). A two-factor ANOVA was used to test for the effects of predator exposure, density, and their interaction on average growth of experimental colonies.

Though occasionally small corallivorous fishes entered the exclusion cages, the average corallivore abundance inside each exclusion treatment did not statistically differ from zero (Fig. 1), suggesting cages effectively excluded corallivorous fishes. A mixed-effects model was used to conduct a repeated-measures analysis to test the effects of density (fixed categorical factor), time (fixed continuous covariate), reef (random intercept), and reef by time interaction (random slope term) on predator abundance. F tests were used to assess the main effects and interaction, followed by a t -test to test the hypothesis that predator abundance differed between density treatments.

Results and discussion

Coral density and predator exposure significantly affected coral growth, but there was no interaction between these factors ($F_{1,27} = 0.76, P = 0.399$). Exclusion of corallivorous fishes led to a 20% increase in *Porites* growth ($F_{1,27} = 11.71, P = 0.001$). Examination of corals throughout the experiment, as well as comparisons of before and after photographs, revealed no grazing scars or skeletal removal of the experimental corals, suggesting that any differences in growth attributed to corallivores were most likely due to the metabolic cost of tissue repair. Corals at high density grew 30% more than those in low-density treatments, suggesting a net benefit to corals at higher density ($F_{1,27} = 4.63, P = 0.041$, Fig. 2). Ijdadi and Karlsson (2007) showed decreased growth in *Porites* in aggregations, but their study focused on direct competitive interactions, whereas in this study, nubbins were placed several centimeters apart, thereby eliminating overgrowth as a possible mechanism of competition.

Although grazing was never directly observed, there was a significant effect of coral colony density on predator abundance ($F_{1,14} = 6.90, P = 0.019$, Fig. 1), which did not change through time ($F_{1,79} = 0.76, P = 0.383$, Fig. 1). Predator abundance increased significantly in high-density treatments relative to low-density treatments ($t_{14} = -2.50, P = 0.026$, Fig. 1) but did not vary substantially among

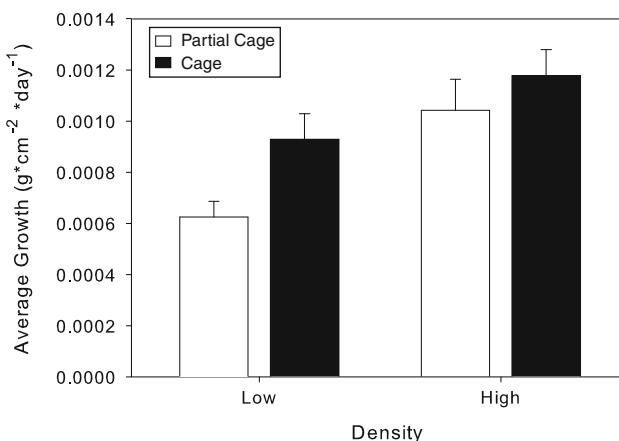


Fig. 2 Average growth ($\text{g cm}^{-2} \text{ day}^{-1}$) of *Porites* sp. nubbins in each of the density (2 and 8) and predator exclusion (Caged and Partial-Cage) treatments. Error bars represent 1 SE

reefs (random reef intercept $\text{SD} = 2.842 \times 10^{-5}$) or among reefs through time (random slope $\text{SD} = 7.66 \times 10^{-11}$). This aggregative response may have been offset by disproportionate increases in coral density and predator abundance: predator abundance increased by 98%, whereas coral density increased by 300% (suggesting predator dilution, although nothing is known about the residence time). While placement of experimental reefs >30 m from the nearest reef structure helped ensure that the observed differences in predator abundance were not due to habitat differences near the treatments, such a distance most likely resulted in an under-representation of corallivores. Therefore, the actual impact of these animals on reef systems could be greater than that noted in this study.

Previous studies have suggested that predator dilution can result in decreased predation rates on corals (Jayewardene et al. 2009). However, if predator dilution was responsible for the greater growth measured in the high-density treatment, then the dilution effect should have been evident in the partial-cage treatments and absent in caged treatments. The lack of a significant interaction between density and predation treatments suggests that predators were not responsible for the positive effect of coral density on skeletal growth. There are two plausible alternative explanations for the positive effect of coral density on skeletal growth. First, corals may have grown faster at high densities by augmenting the local physical environment. Higher coral densities most likely altered the near-field-flow-surrounding colonies, which increases turbulence, mass transfer of nutrients and dissolved gases (Thomas and Atkinson 1997), and photosynthetic efficiency (Finelli et al. 2006). Second, high densities of corals increase the abundance of coral-associated organisms, which themselves often benefit corals. For example, corals provide

habitat to bacteria and invertebrates that can increase disease resistance, reduce fouling (Koh 1997; Rosenberg et al. 2007), or protect corals from predation (e.g., arthropods from the genera *Trapezia* and *Alpheus*; Glynn 1976). Additionally, associated fauna increase availability of nutrients that limit growth (Bracken et al. 2007). For example, Roopin et al. (2008) showed increased abundance of fishes, like those noted at high-density treatments, which produce more nitrogenous waste, which is readily assimilated by cnidarians.

Finally, the hypothesis that predators mediate a positive effect of density might be correct, but the ability to detect an interaction between predation and coral density treatments may have been limited by statistical power. High-density treatments increased growth by 40% in the presence of predators and only 20% in their absence, and while this difference was not significant, it is in the expected direction of a predator dilution effect. Additionally, cages may not have excluded all predators. For example, the six-line wrasse, *Pseudocheilinus hexataenia*, was observed occasionally within experimental reefs but has only recently been identified as a corallivore (Berumen and Rotjan 2010) and thus was not counted as a corallivorous species in this study. Similarly, although not observed, cages could not prevent access by many of the small invertebrate corallivores present in Moorea (Rotjan and Lewis 2008). As a result, responses by predators with access may have contributed to the observed growth differences, thus mirroring the effects of predators in the partial-cage treatments. While the obvious impacts of large corallivores have garnered much of the attention of corallivore studies, this example highlights the need for greater understanding of how unobserved and unknown corallivores may impact coral health and growth rates.

Little is known about the functional response of corallivores or the scale over which they respond to differences in prey density. Similarly, the relative importance of corallivory, compared to other ecological processes (e.g., competition, parasitism, or mutualisms), on coral growth remains poorly studied. However, the impact of corallivory remains germane; heavily grazed corals face increased susceptibility to disease (Aeby and Santavy 2006), and reduction in growth and fecundity due to the energetic cost of tissue repair (Meesters et al. 1994) and, in many species, smaller corals intrinsically display reduced fecundity and an increased probability of mortality (Hughes 1984). Because coral growth changes with size (Vollmer and Edmunds 2000), future studies of coral density–corallivore interactions should examine how the effects of predators may change with colony size and should identify alternative mechanisms responsible for the benefits of living in conspecific aggregations.

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