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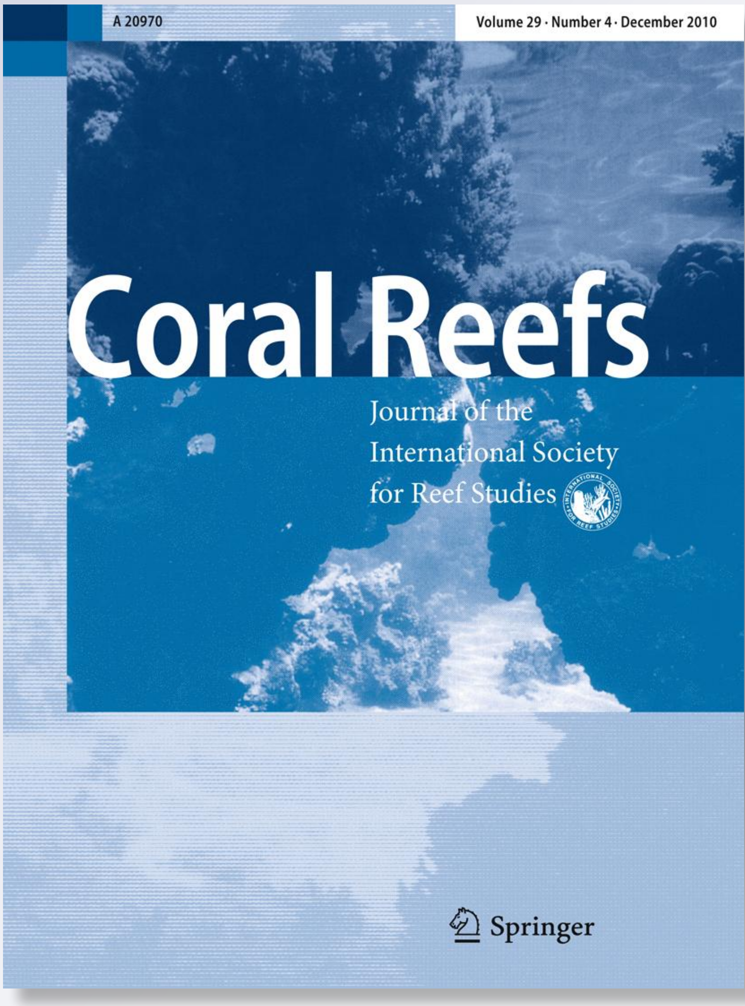

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NOTE

Guard crabs alleviate deleterious effects of vermetid snails on a branching coral

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Abstract Stony corals provide important structural habitat for microbes, invertebrates, and fishes, which in some cases has led to the evolution of beneficial interactions that may protect corals from environmental factors such as thermal stress, nutrient limitation, competitors, or predators. For example, guard crabs (*Trapezia* spp.) protect corals (*Pocillopora* sp.) from attacks by crown-of-thorn seastar and sedimentation. Here, a field experiment demonstrates that guard crabs (*Trapezia serenei*) also ameliorate the strong negative effects of the giant vermetid (*Dendropoma maximum*) on growth of *Pocillopora*. This experiment highlights the importance of this crab-coral mutualism: guard crabs facilitate the growth of corals in stressful environments (e.g., where vermetids are abundant), thereby preserving the ecological goods and services (e.g., food and shelter) that these corals may provide to other reef-associated species.

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Introduction

Understanding the ecological processes governing the persistence and demography of stony corals is among the most fundamental goals of coral reef ecology. The positive species interactions between corals and their microbial, invertebrate, and fish inhabitants are of particular importance to predicting the ability of corals to persist in a rapidly changing environment. The majority of work on mutualisms involving stony corals has focused on their relationship with endosymbiotic zooxanthellae. Yet, mutualisms involving other symbionts are not uncommon and may be of great importance in shaping the response of corals to environmental conditions. For example, Stachowicz and Hay (1999) found that competition between macroalgae and the temperate coral *Oculina arbuscula* can be mitigated by a coral-associated crab, *Mithrax forceps*, which consumes algae and prevents algal overgrowth. Several species of coral crabs (e.g., *Trapezia* and *Tetralia*) live among the branches of corals (e.g., *Pocillopora* and *Acropora*) in the tropical Pacific and have been shown to increase coral survivorship (Glynn 1983) through the alleviation of deleterious effects of sedimentation (Stewart et al. 2006) and predatory seastars (Glynn 1976; Pratchett and Vytopil 2000; Pratchett 2001). Benefits attributable to guard crabs may extend beyond defense against coral predators and sedimentation.

The vermetid snail, *Dendropoma maximum* is sessile and extrudes a mucous net for feeding. Previous observational studies suggest vermetids can have negative effects on coral growth and morphology (Smalley 1984; Colgan

1985; Zvuloni et al. 2008), and recent experiments show that vermetids reduce the growth and survival of some coral species by as much as 80% (Shima et al. 2010). Effects of vermetids are particularly deleterious for the branching coral, *Pocillopora cf. verrucosa*, which commonly co-occurrs with vermetids atop massive *Porites* reefs, and provides critical habitat for many fishes and invertebrates, including several species of guard crabs (obligate symbiotic crabs that live in the interstitial spaces of the coral) (Glynn 1976). One such guard crab, *Trapezia serenei*, lives among the branches of pocilloporid corals, and it is known to protect corals (e.g., Stewart et al. 2006). However, the role of guard crabs with respect to vermetid-coral interactions remains unknown. Importantly, past experiments on vermetid-*Pocillopora* interactions (Shima et al. 2010) were done on small coral fragments that lacked guard crabs. The deleterious effects of vermetids are likely induced by contact with the mucous net (Shima et al. 2010), suggesting that guard crabs might reduce the observed effects of vermetids on corals by cleaning the corals of vermetid mucus (as they do sediments). Using a field experiment that manipulated presence/absence of vermetid snails (primarily *Dendropoma maximum*) and guard crabs (*Trapezia serenei*), this study tested whether guard crabs ameliorate the negative effects of vermetids on *Pocillopora* growth.

Materials and methods

A field experiment was conducted to explore the separate and joint effects of vermetids and guard crabs on the growth rate of small colonies of *Pocillopora*. Twenty patch reefs (mean size 15.55 m^2, SD = 4.07), comprised predominately of massive *Porites* sp. and containing abundant vermetids were selected in the northern lagoon of Moorea, French Polynesia (17°30′ S, 149°50′ W). On 10 of the 20 patch reefs, all vermetids were removed from their shell by placing a hooked wire between the wall of the shell and snail and extracting the snail; on the remaining reefs, vermetids were not manipulated. Forty colonies of *Pocillopora* (each approximately 10 cm in diameter) that lacked vermetids but contained at least one pair of guard crabs were collected from the reef flat near the Richard B. Gump research station in Moorea. In half of the coral colonies ($n = 20$), wooden skewers were used to remove all exosymbionts, while in the remaining colonies ($n = 20$) exosymbionts were removed selectively, leaving only a pair of *T. serenei*. Irrespective of treatment, all 40 experimental *Pocillopora* colonies were similarly handled to equalize potential handling effects. The starting size (i.e., skeletal mass) of each experimental *Pocillopora* colony was estimated using a buoyant weight technique (Davies 1989).

Two *Pocillopora* colonies (one with *Trapezia* and one without) were transplanted onto each of 20 *Porites* patch reefs ($n = 10$ with vermetids removed, $n = 10$ with vermetids present). All *Pocillopora* colonies were positioned on *Porites* reefs within the neighborhood (<2 cm) of the mucous net of at least one vermetid (mean ± 1 SD number of vermetids with ≥5 mm aperture diameter per 500 cm^2 centered on *Pocillopora* colony: 5.02 ± 3.05) or within similar distances to an empty vermetid shell (for the vermetid removal treatment). Colonies of *Pocillopora* were attached to the patch reefs within PVC collars (10 cm in diameter and 2 cm in height) that were affixed to the reef using A-788 splash zone epoxy (Z-spar). Each collar was transected by three stainless steel bolts (evenly spaced around the circumference) and tightened to secure the coral in place. The experiment was maintained for 40 days, and all corals were checked weekly to evaluate potential immigration and emigration of guard crabs. All corals with guard crabs retained their crabs, and all corals in the treatment without crabs remained crab-free for the duration of the study. After 40 days, corals were returned to the laboratory and final skeletal mass was measured (Davies 1989).

Data analysis

Because corals are modular organisms, *Pocillopora* growth was estimated assuming an exponential model: $G = [(\ln(M_f/M_i))/t]$, where M_f is the final skeletal mass, M_i is the initial skeletal mass, and t is the duration of the study (days). The paired nature of the experimental design (*Pocillopora* colonies with- and without guard crabs were paired on individual *Porites* reefs) violates the assumption of independence for classical ANOVA. Therefore, the effects of guard crabs on coral growth were evaluated as the difference in growth of corals of paired colonies on each of the twenty reefs, with- and without guard crabs, calculated as: $\delta G = G_{crab} - G_{no\ crab}$. The *t*-tests were used to test three specific *a priori* (and orthogonal) hypotheses:

1. The beneficial effect of guard crabs is greater in the presence vs. absence of vermetids. Rephrased in the context of a statistical null hypothesis: $H_{0,V-,V+} : \delta G_{V-} = \delta G_{V+}$.
2. Guard crabs do not affect the growth of *Pocillopora* in the absence of vermetids ($H_{0,v-} : \delta G_{V-} = 0$).
3. Guard crabs increase coral growth in the presence of vermetids ($H_{0,v+} : \delta G_{V+} = 0$).

Results and discussion

The effect of *Trapezia* on coral growth was significantly greater in the presence of vermetids than in the absence

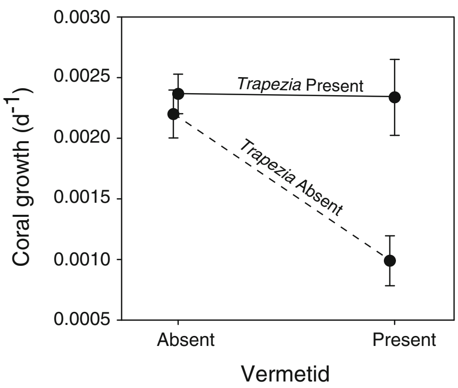

Fig. 1 Effects of vermetid snails (*Dendropoma maximum*) and guard crabs (*Trapezia serenei*) on the daily growth of *Pocillopora cf. verrucosa* (means ± 1 SE) during a 40-day field experiment. *Pocillopora* growth was estimated from an exponential growth model: $G = [(\ln (M_f/M_i))/t]$, where M_f is the final skeletal mass, M_i is the initial skeletal mass, and t is the duration of the study (i.e., 40 days). Shown are the mean ±95% confidence interval ($n = 10$ for each treatment)

(Fig. 1: $t_{18,V-,V+} = 2.22$, $P = 0.039$). There was no effect of guard crabs on *Pocillopora* growth in the absence of vermetids ($t_{9,V-} = 0.670$, $P = 0.52$); however, in the presence of vermetids, guard crabs increased *Pocillopora* growth by 100% ($t_{9,V+} = 2.86$, $P = 0.019$). Phrased differently, the effect of vermetids depended upon the presence or absence of guard crabs. In the absence of a pair of guard crabs, vermetids reduced the daily growth rates of *Pocillopora* by 50% (Fig. 1), which was a similar magnitude as observed by Shima et al. (2010). However, in the presence of guard crabs, vermetids had no demonstrable effect on coral growth, suggesting that guard crabs completely ameliorated the deleterious effects of vermetids.

It is unlikely that guard crabs in the experiment attacked vermetids directly. Surveys quantifying vermetid densities (a 500 cm^2 quadrat centered on each *Pocillopora* colony) at the beginning and end of the experiment found equivalent densities of vermetids, providing no evidence that crabs were killing snails. Additionally, observers conducting weekly censuses of *Pocillopora* found no evidence that guard crabs were leaving their coral colonies to interact with the snails. Instead, it is speculated that guard crabs mitigated the deleterious effects of vermetids on corals by (1) consuming vermetid mucus, (2) inadvertently dislodging mucus during their movements, and/or (3) actively removing mucus via 'housekeeping' behaviors: e.g., as has been previously demonstrated in response to sedimentation (Stewart et al. 2006).

Pocillopora is a dominant genus of stony coral throughout much of the eastern Pacific, and in this region it provides critical habitat to fishes and invertebrates (Schmitt and Holbrook 2000; Shima 2001; Shima et al. 2008). Moreover, vermetid populations may be increasing in Moorea (reviewed in Shima et al. 2010). Because vermetids have differential effects on coral species, they may also drive shifts in coral composition (Shima et al. 2010). However, the first study that identified negative effects of vermetids on *Pocillopora* (Shima et al. 2010) used small coral fragments that did not support adult guard crabs. Because guard crabs can effectively mitigate the effects of vermetids, crabs may protect *Pocillopora* and their associated fishes and invertebrates in ways not included in the projection of coral dynamics modeled by Shima et al. (2010).

These effects of guard crabs on the corals' other fish and invertebrate inhabitants will, however, likely be complex. For example, recent work suggests that another guard crab species (*Trapezia rufopunctata*) can increase mortality rates of recently settled fishes by increasing competition for predator-free space (Schmitt et al. 2009). This reduction in fish abundance may feedback to the corals because fish increase coral growth, possibly via oxygenation or nitrogen excretion (Holbrook et al. 2008). Such multispecies interactions among the underappreciated reef invertebrate community may be highly important to the resilience of reef ecosystems and the goods and services they provide.

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