Determinants of the onset and strength of mutualistic interactions between branching corals and associate crabs

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ABSTRACT: In mutualisms involving a host and symbiotic resident, the nature and strength of their interactions are unlikely to be constant over time or space. The efficacy of such mutualisms can be crucial to the population dynamics of one or both partners, particularly where survival bottlenecks occur at early life stages. In laboratory and field outplant experiments, we explored determinants of the onset of mutualistic interactions between early stages of branching corals and their trapeziid crab partners. We confirmed that recently settled crabs are capable of providing housekeeping services to their young coral partners (as has been reported for older crabs and corals), and the presence of a crab in areas of high sedimentation conferred growth benefits ~3 times as strong compared with low sediment conditions. We also showed that recruitment of post-larval crabs to very young corals increases with morphological complexity of the coral, which relates to the ability of the host to provide micro-refugia for its crab symbiont, and indicates the potential for selective pressure for traits that attract and retain crabs during this high-mortality bottleneck life stage. These findings provide insight into the recruitment process and ontogenetic constraints that influence the onset of mutualistic interactions between corals and their associated symbionts.

KEY WORDS: Mutualism · Interaction strength · Crabs · Symbiosis · Coral morphology · Sediment · Ontogeny · Habitat selection

INTRODUCTION

Mutualistic interactions between species are increasingly recognized to be dynamic and context dependent (Connor 1995, Knowlton & Rohwer 2003, Thomson 2003, Hay et al. 2004). In heterogeneous or temporally varying habitats, the strength and nature of mutualisms can change in response to environmental stressors (Callaway et al. 2002). Additionally, just as the functional ecology of organisms changes through ontogeny (Werner & Gilliam 1984), so too may the nature of species associations (Miriti 2006, Yang & Rudolf 2010). The existence and strength of a mutualism may be especially critical for life stages that are particularly vulnerable and/or have great influence on population and community dynamics.

Reef-forming corals are the foundational species in coral reef communities, and their early fate plays a fundamental role in population (Caley et al. 1996) and community dynamics (Schmitt & Holbrook 2003).

The bottleneck to survival for these corals is the stage immediately following initial colonization to the reef (Hughes & Connell 1987), when these small, young recruits experience the highest rates of mortality of any reef-associated life stage (Vermeij & Sandin 2008). Individual corals in this stage are also the most vulnerable to environmental stressors (Caley et al. 1996, Leray et al. 2012), including smothering by sediment (Fabricius et al. 2003). While the formation and strength of mutualistic interactions among corals and their infaunal symbionts can have substantial dynamic and community ramifications (Thompson et al. 2006), the ontogeny of these interactions has not been thoroughly investigated.

We explored the factors that influence the onset and strength of reciprocally positive interactions between branching corals and trapeziid crabs (Abele & Patton 1976), which represent a general class of mutualisms where one partner provides shelter to the other (Holbrook & Schmitt 2004, Thompson et al. 2006) and in return receives housekeeping services (Stewart et al. 2006, Stier et al. 2012) and defense (e.g. Glynn 1976, 1983, Pratchett 2001, Stier et al. 2010, McKeon et al. 2012). Although Stewart et al. (2006) found that crab symbionts, present in nearly all small adult-stage branching corals, removed sediment from their host corals — a housekeeping service essential for the survival of colonies located where sediment load was high — the initiation and relative importance of the association between recently settled branching corals (genus *Pocillopora*) and their trapeziid crab partner *Trapezia serenei* to coral performance has not been investigated. In this study, we tested the housekeeping abilities of newly settled crabs on coral recruits in a laboratory experiment and assessed whether observed sediment removal capacities were due to the presence of the crabs or whether the crabs settle to corals that have inherently superior sediment-clearing abilities. We then assessed the efficacy and consequences of the housekeeping services crabs provide to very young corals *in situ* and examined the morphological attributes that best explained the number of crabs observed on newly recruited corals.

MATERIALS AND METHODS

Study area

Surveys and field experiments were conducted in the Vaipahu Lagoon (17° 28' 51.10'' S, 149° 49' 58.30'' W) (0.8 to 1.3 km wide, ~5 to 7 m deep) on the north shore

of Moorea, French Polynesia. Patch reefs are scattered sparsely across the sandy back-reef and densely on coral pavement near the reef crest. Dominant coral genera include massive *Porites* and *Montipora*, as well as common branching corals, including several species of *Acropora* and *Pocillopora* known to host a variety of associated mutualists such as crabs (Leray et al. 2012, Stier et al. 2012). Surveys and field outplant experiments were conducted in July and August 2006, and the laboratory sediment removal experiment was conducted in January 2012.

Test of the housekeeping services

We conducted a laboratory experiment to determine whether very young crabs (weeks to months post settlement) showed the ability to clear sediment from very young coral recruits (~1 yr post recruitment) similar to older crabs on juvenile corals (as reported in Stewart et al. 2006). We collected small (1 to 3 cm diameter) pocilloporid corals from the back-reef and then brought these corals into the laboratory to evaluate them for the presence or absence of crabs. We selected 20 corals that were initially occupied by crabs and 20 corals that were initially not occupied by crabs, and from these 2 sets of corals created 4 treatment groups: (1) 'No crab/never' — corals that initially did not have associate crabs in the field and were subsequently kept crab free for the duration of the experiment; (2) 'No crab/removed' — corals that had crabs when collected initially, but then had these crabs gently removed and subsequently kept crab free for the duration of the experiment; (3) 'Crab/added' — corals that initially did not possess associate crabs in the field, but had crabs added; and (4) 'Crab/always' — corals that initially possessed associate crabs in the field and were left with their original associate crabs. These treatments allowed us to determine whether the observed sediment removal capacity was due to the presence of the crab, and to examine the alternative possibility that crabs are attracted to corals that have an inherently better capacity to clean themselves.

Corals were maintained in an outdoor tank with seawater re-circulating slowly enough to prevent disruption of any sediment that was added to the corals. Sediment was collected from the same area of the back-reef as the corals, returned to the laboratory, sieved into size classes, cleaned and rinsed with fresh water, and then dried for 48 h in a drying oven at 60°C. One standardized scoop of sediment, composed of an average of 370 grains (± 107 SD), was

poured onto each coral, covering the entire surface of the corals with a layer of sediment at least 1 grain thick, and the coral was immediately photographed. Grain size of added sediment was 0.25 to 0.5 mm, and a scoop averaged 0.06 ± 0.001 g dry mass (mean ± SE). This produced standardized rates of sedimentation of 20 to 76 mg cm^{-2} per 24 h, which was well within the range we measured *in situ*, and comparable to the sediment size and load applied to larger (5 to 10 cm) corals in Stewart et al. (2006). Corals were left in ambient light overnight to allow natural diurnal activity of the crab and its host coral. After 24 h had elapsed, a second photo was taken of each coral. We then quantified the number of sediment grains on each coral before and after the 24 h period using the image analysis software package Image J (version 1.42). The relative contribution of crab activity to sediment removal was quantified by the percentage of the sediment initially deposited on the crab and coral treatments remaining after 24 h. This percentage was then compared across the 4 treatments using a 2-way ANOVA with crab (Crab/No crab) and state (Original/Altered) — representing originally having or not having a crab, and extraction or addition of crab, respectively — as the factors. Data were arcsine-transformed before analysis to meet assumptions of normality.

Quantifying prevalence of coral–crab mutualism across host size, morphology, and environmental gradients

To explore the relationship between variation in environmental conditions (e.g. sedimentation rate), coral host size, and morphology on the presence of trapeziid crabs within young pocilloporid colonies, we conducted surveys using 3 band transects (5 m wide × 10 m long) at 12 sites across the Vaipahu Lagoon parallel to the reef crest. In each transect, we enumerated every recruit (1 to 4 cm diameter) pocilloporid coral to quantify density (no. per m^2). For each colony discovered, we noted the number of branches, measured size dimensions with calipers, and counted trapeziid crabs housed within the young coral; there were 7 to 28 corals identified at each site. We calculated coral colony size (volume) as half ellipsoids using the longest colony diameter, the greatest diameter perpendicular to the longest diameter, and colony height as parameter estimates. Branches were defined as skeletal formations that were at minimum a 30° angle from the vertical and extending at least 0.5 cm beyond the base of the colony.

To relate occupancy to environmental condition, we deployed 8 replicate sediment collectors flush to the substrate haphazardly across each survey site concurrently for 2 wk. Sediment collectors were 24 cm^2 in area and 1 cm in height, and were constructed from pieces of sponge-like mats that were fastened to nails in the reef pavement. The traps collected fine sediment (<0.5 mm) that settled, whether through lateral translocation, resuspension, or precipitation from the water column. Traps were collected and rinsed with 0.5 l of fresh water before sediments were vacuum filtered onto pre-weighed filter paper (pore size: 100 μm). To measure sediment load per trap, the sediment-loaded filter paper was dried at 60°C for 12 h and reweighed.

Multiple logistic regression analysis was used to jointly examine the relationship between crab occupancy and several predictor variables, including the number of branches per host (N = 263 colonies across all sites), host coral volume, and mean site sedimentation rate. We tested for multi-collinearity among the predictors or the independent variables before analysis. The strongest covariance measured was between host volume and the number of branches per coral, with a correlation coefficient of 0.49; all other pair-wise comparisons were less and also non-significant. Best model fits were selected using minimum Akaike's information criterion to determine relative contribution of explanatory variables to the full model.

Host performance across environmental conditions

We explored spatial variation in context-dependent benefits of crab partners to growth and survival of hosts by outplanting recruit corals (2 to 4 cm diameter) to reef areas, where we measured differences in average sedimentation rates. Corals were collected from the back-reef at Viapahu Lagoon and were assigned randomly to Crab and No crab treatments; this required removal of crabs from half of the hosts (randomly selected) as all corals collected had partners. Corals (N = 30 corals per crab treatment) were then affixed to numbered PVC plates and buoyant weighed as in Stewart et al. (2006). Corals in each crab category were paired, and pairs were assigned at random to 2 areas of the back-reef characterized as low sedimentation sites and 2 additional areas characterized as high sedimentation sites. Sediment load at all sites was quantified for 48 h intervals over the course of the experiment using the same collectors and methods as in Stewart et al. (2006). Corals

were checked every 48 h to determine the prevalence of crabs, qualitatively assess sediment load, and quantify mortality (% live tissue lost per colony by visual assessment). A coral was considered to be 'smothered' by sediments if the load was visually similar to those applied in our laboratory experiment (a layer of sediments covering the entire surface of the coral at least 1 layer thick). Because post-larval crabs settled from the plankton onto experimental corals during the assay, the arrival and any movements between corals of newly settled megalopes were noted and new settlers on corals in the No crab treatments were gently removed. After 18 d, coral pairs were collected, returned to the laboratory and reweighed. Additionally, a final visual estimate of partial mortality (% live tissue lost) was conducted in the laboratory. Change in buoyant weight for each colony was standardized to initial size, (mass$_{t18}$ − mass$_{t0}$)/mass$_{t0}$/18, to yield growth units of mg mg^{-1} d^{-1}. The effect size, defined as the difference in standardized growth rates between paired corals with and without crabs, was used as the response variable to compare the relative effectiveness of mutualistic partnerships across study sites.

A 1-way nested ANOVA (main effect: site, with reef areas nested within site) on the effect size was used to compare the relative influence of crab occupancy across sedimentation regimes. The same nested and factorial approach was used for the smothering data, but in this case, we used a generalized linear model with a binomial distribution and the logit link function to analyze the bivariate data (smothered = 1 or clear = 0). All statistics were conducted using the software package JMP (SAS version 9.0.0).

RESULTS

Test of housekeeping services

Laboratory observations revealed that very small crabs are fully capable of removing sediment from their host corals. Small corals hosting a crab achieved a much greater reduction in sediment load (~98%), than corals that lacked a crab (~68%) (Fig. 1). Crabs increased the removal of sediments ($F_{1,35}$ = 71.3, p < 0.001), but there was no difference due to original state of the corals ($F_{1,35}$ = 0.95, p = 0.34). Importantly, in the case of the No crab treatments, there was no difference in the sediment removal rates between corals that had or lacked crabs at the initial time of collection. Similarly, there was no difference in the
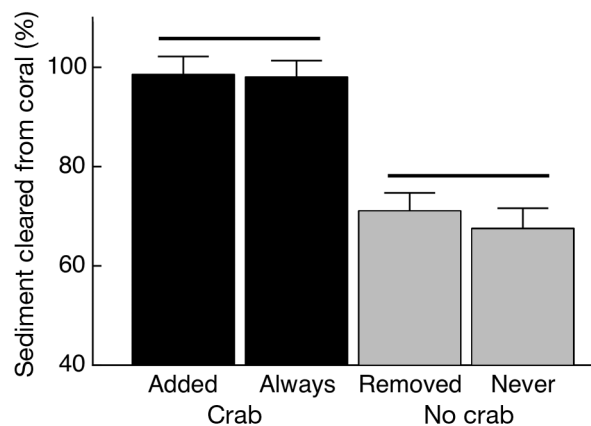

Fig. 1. Percent of experimentally deposited sediment (0.25 to 0.5 mm grain size) removed in 24 h from the tissue of juvenile pocilloporid corals (1 to 3 cm) in the presence (Crab) or absence (No crab) of a crab partner. To test whether the origin of the crab was of relevance, Crab treatments included coral recruits that had crabs at the time of collection (Always; n = 12) and corals that lacked a crab partner at collection but to which we added a crab for the experiment (Added; n = 10), as well as No crab treatments. These included corals that had crabs when collected but that were removed for the experiment (Removed; n = 8) and corals that lacked crabs when collected and remained so for the duration of the experiment (Never; n = 10). Data are mean ± SE. There was no interaction between Crab and State when compared with a 2-way ANOVA; horizontal lines indicate treatments that were not significantly different from each other when compared using Tukey post-hoc multiple comparisons

additional amount of sediment removed in the Crab treatments between corals that always had a crab and those that previously had lacked the partner (Fig. 1). Thus, there was no significant interaction of crab occupancy before or during the experiment ($F_{1,35}$ = 0.89, p = 0.35).

Quantifying prevalence of coral–crab mutualism across host size, morphology, and environmental gradients

Regression model selection using corrected Akaike's information criterion favored a reduced, single parameter model (Table 1). This best fit model indicated that pocilloporid coral recruits (1 to 4 cm diameter) acquired and/or retained a crab settler as colonies developed branches (Fig. 2A), but that sedimentation regime and coral volume did not appear to influence coral occupancy by crabs. The probability that a colony hosted a crab was related to the increasing complexity of its branching morphology (Fig. 2A), and most coral recruits had 1 to 4 branches at the time they were surveyed (Fig. 2B). The proportion of

Table 1. Multiple logistic regression predicting the likelihood of a coral recruit hosting a trapeziid crab, jointly dependent on mean site sedimentation regime (g m^{-2} d^{-1}), coral host volume (cm^3), and coral host 'branching' (no. of branches). Final model selected and presented in Fig. 2 uses only the intercept and 'branching', as selected by using minimum corrected Akaike's information criterion (AICc). Odds ratio indicates the relative change in odds, per unit increase in the regressor, of a coral colony hosting a crab partner

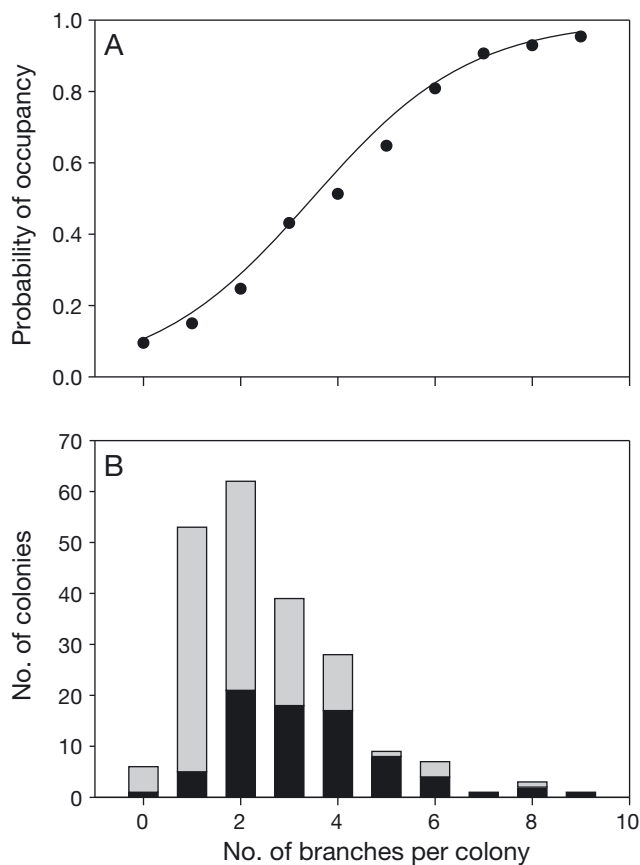| Source	β	SE	Odds ratio	Wald χ^2	df	p	AICc
Intercept	2.471	0.497		24.660	1	<0.0001	278.2
Branching	−0.525	0.151	1.69	12.008	1	0.001	243.6
Coral volume	−0.039	0.044	1.04	0.760	1	0.380	260.9
Sedimentation	−0.012	0.013	1.01	0.977	1	0.320	281.0
Branching and volume							245.1
Branching and sedimentation							244.9
Volume and sedimentation							261.1
Full model							246.2

Fig. 2. (A) Expected joint probabilities of corals hosting a crab partner (●) as a function of the volume of a colony, the mean sedimentation rate at a site, and the number of branches per colony from the full model multiple logistic regression. The fitted curve is based on the parameters estimated from the simple logistic regression using only number of branches as an explanatory variable (logit coefficient = −2.124 + (0.612 × branches)); this parsimonious model was selected based on smallest corrected Akaike's information criterion. (B) Frequency distribution of numbers of branches. Grey bars are coral hosts that lacked crabs; black bars are corals with a crab partner

hosts housing a partner increased with colony complexity until corals had 5 branches, by which stage ~95% were occupied by a trapeziid crab (Fig. 2A,B).

Host performance across environmental conditions

Field assessments of settlement of crab megalopes to small, outplanted corals indicated that crabs were abundant and that they arrived throughout the 18 d portion of the lunar cycle centered around the full moon. On average, the number of crabs that settled was similar for coral outplants at both types of site (low sedimentation: 1.7 ± 0.36 (mean ± SD) crab megalopes per unoccupied coral per week; high sedimentation: 1.8 ± 0.006 crab megalopes per unoccupied coral per week). There was no discernible difference between the 2 sub-sites at each site.

Our field assays indicated there were spatial patterns in the growth and mortality of outplanted recruit corals that corresponded with differences in sediment loads and odds of becoming smothered at our study localities (Figs. 3 & 4). Overall, the proportion of corals becoming smothered was higher where the sedimentation rate was higher (Fig. 3), with corals that lacked crabs having about a 5-fold higher probability of becoming covered by sediments. The presence of a housekeeping crab dramatically reduced the probability that a coral recruit would be smothered (Table 2), with the proportionate reduction being similar regardless of the sedimentation rate (Fig. 3). These patterns in odds of smothering and effects of crabs on lowering those odds were reflected in patterns of partial mortality of corals. Overall, partial mortality was 28 ± 5% (mean ±SE) when a coral lacked a crab, whereas it was <4 ± 2% when a crab was present; higher sedimentation sites
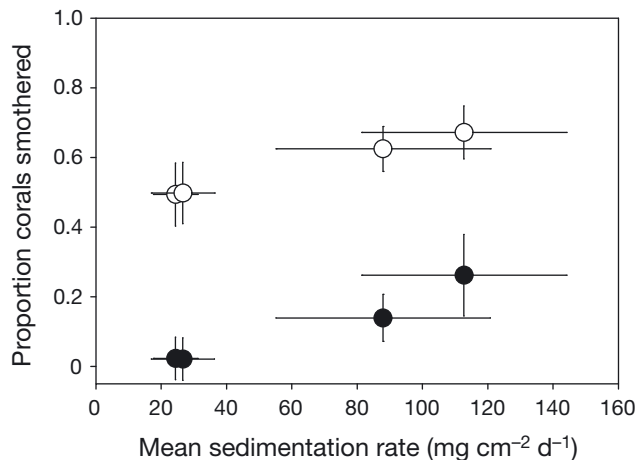
Fig. 3. Per capita probability of encountering a heavy sediment load (proportion of colonies experiencing smothering, defined in 'Materials and methods') of coral recruits (1 to 4 cm) that had (●) and lacked (○) crab partners at sub-sites of 2 reefs that were characterized by low and high sediment loads. Data are mean ± SE
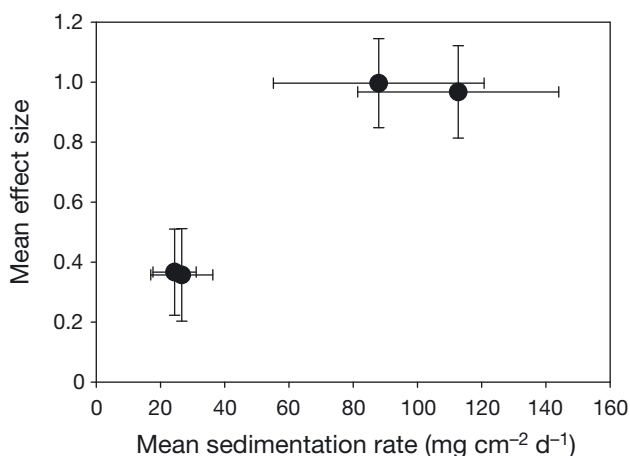

Fig. 4. Mean (±SE) effect size of the housekeeping mutualism, comparing paired coral colonies with and without a crab partner, on skeletal growth. Effect size is defined as the difference between growth rates from paired outplanted colonies hosting and missing partner crabs. Growth was determined as the daily change in buoyant weight normalized by initial colony size

had higher rates of partial mortality (without crabs: mean = 42%; with crabs: mean = 7%) than sites with low rates of sedimentation (without crabs: mean = 28%; with crabs: mean = 0.5%).

With respect to skeletal growth, the effect of a crab partner was also substantially greater in areas of high sedimentation (Fig. 4). All colonies exhibited positive growth (grand mean 2.1 mg mg^{-1} d^{-1}), but corals with a crab partner always grew significantly

Table 2. Results of generalized linear model for proportion of young coral hosts becoming smothered in the presence or absence of a crab partner (Crab) across 2 sub-sites (Sub-site) nested within sites that differed in sediment regime (Sediment). The data are binomial ('smothered' or 'clear'), so the logit link function was used for this factorial analysis

Source	df	χ^2	p
Crab	1	35.291	<0.0001
Sediment	1	9.259	0.002
Crab × Sediment	1	3.041	0.0812
Sub-site (Sediment)	2	1.463	0.481

more than neighboring corals that lacked the housekeeper ($F_{1,54}$ = 7.91, p = 0.007). Thus, the mean effect size, or the difference in growth rates between paired corals with and without a crab partner, is consistently positive (Fig. 4). For example, the mean (±SE) standardized growth rates of corals without a crab partner (1.3 ± 0.1 mg mg^{-1} d^{-1}) were approximately half the growth rates of corals hosting a crab (2.3 ± 0.1 mg mg^{-1} d^{-1}) across sub-sites exposed to high sedimentation, yielding a mean effect size of ~1.0 (Fig. 4). However, the relative magnitude of the growth benefit provided by crabs differed with sedimentation regime, as evidenced by a smaller effect size across low sedimentation regimes (Fig. 4); this effect was independent of sub-site ($F_{2,54}$ = 0.69, p = 0.51). The presence of a crab in areas of higher sedimentation conferred benefits ~3 times as strong compared with low sedimentation sites (Fig. 4).

DISCUSSION

In the case of stony corals, younger life stages are typically more vulnerable than older conspecifics to environmental stresses and natural enemies (Hughes & Connell 1987, Vermeij & Sandin 2008). As foundational taxa on tropical reefs provide essential habitat for numerous other species, interactions that affect early survival of new coral colonists or transition rates to less vulnerable life stages can have tremendous effects on subsequent population dynamics (Hughes & Connell 1987, Caley et al. 1996) and result in important community-level consequences (Schmitt & Holbrook 2000, 2003). We found that recruitment of larval crabs can occur shortly after a young coral colony becomes established, and that even at this very early developmental stage, the presence of a crab greatly enhances growth and condition of the young coral. The resultant positive effects may be as, if not more, important at this young

bottleneck stage of coral life history as the interaction observed in older, larger partners (Stewart et al. 2006, Stier et al. 2012).

Sedimentation is often a major source of mortality to stony corals worldwide (Rogers 1990), and small, young colonies are the most susceptible to smothering by sediments (Fabricius 2005). While corals have the ability to slough off much of the sediment deposited on their tissues (Rogers 1990), we previously reported the influential role that trapeziid crabs play in removing especially harmful particles from adult branching corals (Stewart et al. 2006). Here we report findings that show that newly settled crabs are capable of clearing sediment off young, newly recruited coral hosts. We were surprised at how efficiently newly settled crabs were able to clear sediment off host corals. Regardless of whether the crab was one that was originally on the coral when it was collected (Always) or was added to a coral (Added), these small crabs were as efficient as older crabs in clearing sediment that was experimentally deposited on their host corals. Newly recruited corals with post-settlement crabs in this study cleared 1.5 times more sediment than corals alone, comparable to rates reported in Stewart et al.(2006) of 1.4 to 2.0 times for older corals (10 to 15 cm maximum diameter) and crabs of the same species for the same size sediment at similar loads. Stier et al. (2012) used similar methods (but larger sediment size) to examine sediment-clearing abilities of crabs (and multispecies pairs of mutualists) on larger adult *Pocillopora* colonies (45 to 160 cm maximum diameter), and found corals with the larger crabs to be 3.5 times as effective as corals that lacked crabs. However, the percent of sediment cleared from corals with associate crabs after experimental deposition in these similar experiments was only ~35% in adult colonies (Stier et al. 2012), relative to ~62% for young adult colonies (Stewart et al. 2006), and ~100% for newly recruited colonies and their post-larval crabs in the present study. This suggests that the efficacy of crabs in clearing sediment from hosts is highest at the smallest and youngest stages that are most at risk of mortality. Leray et al. (2012) report that the recent outbreak of *Acanthaster plancii* (crown of thorns) sea stars in Moorea from 2006 to 2009 resulted in almost complete mortality of small (up to 300 cm^2) *Pocillopora* corals at their sites on the north and west coasts of Moorea. Subsequent recovery of branching corals in Moorea may be, in part, a result of the ability of new coral recruits to attract and retain symbiotic crabs, particularly in higher sediment areas of the reef.

Mutualisms, by definition, benefit the host organism, and therefore it is logical that the ability of a host to attract a mutualistic partner is an evolutionary driver (Noë & Hammerstein 1994). Indeed, pollinator-mediated selection affects floral morphology (Galen 1989), and selection on the genes that affect pollinator preference drive floral evolution (Schemske & Bradshaw 1999). This selection may also be context dependent, as the relative roles and selective pressure on visual cues and shape and scent of flowers vary over space and time (Ibanez et al. 2010). With respect to the coral–crab system, newly settled corals are rapidly colonized by trapeziid crabs that settle from the plankton once the coral colonies have achieved a minimum degree of structural complexity. Many crustaceans have been shown to use visual and chemical cues when settling from the plankton (Pawlik 1992, Forward et al. 2001, Hadfield & Paul 2001, Koehl & Hadfield 2004, Lecchini et al. 2010). Given the increased host survival afforded by the partner crab and the potential for crabs to actively choose among suitable corals in an area to which they have settled, newly recruited corals may experience selective pressure for traits that attract and retain crabs during their transition from the plankton to the reef environment. Our results suggest that morphological traits of corals play a key role in attracting a crab symbiont during the settlement phase. Increased structural complexity, or branchiness, increased the chance that a coral would attract a crab; thus, corals might be expected to experience selective pressure to grow faster and develop branches as soon as possible after they settle to the reef. During our study, settlement of zoeal-stage crabs to a coral colony was a weekly (or more frequent) event, suggesting that host morphological complexity — not the potential supply of the crab partner — is the larger constraint on the onset of the mutualism. Thus, this mutualism may play an indirect role in selection of morphological phenotypes across environmental gradients, and the rate and size development of branches in small corals may be influenced by the habitat-dependent importance of obtaining a settling crab. Of course, housekeeping services are not the only benefit trapeziid crabs and similar invertebrates provide to their hosts: these sheltering symbionts can enhance protection from predators (Pratchett 2001, McKeon et al. 2012), defend against space competitors (Stier et al. 2010), and potentially increase nutrient flux in a manner similar to resident fishes (see Meyer & Schultz 1985, Holbrook et al. 2008, 2011). The relative importance of these additional benefits may also vary with host ontogeny and local environmental conditions.

Since both partners of this mutualism colonize reefs via larval dispersal and settlement, early onset of the interaction following colonization could have far-reaching effects if the housekeeping benefit to very young corals was sufficiently strong. While the reduction in the proportion of corals that were smothered was similar across areas of varying sediment load, the percentage of tissue lost per colony as a consequence of smothering was always greater at sites with higher sedimentation rates, but negligible at low sedimentation sites when a coral hosted a crab. Accordingly, the effect on growth of corals with a crab was ~3-fold greater in high sediment relative to low sediment sites, suggesting that the importance of this mutualism is a function of both life stage and the intensity of this physical stressor. Understanding the dynamics of mutualistic interactions can lend insight into the structure and dynamics of natural systems. Our ability to forecast responses of systems to perturbations will require understanding of how the nature and strength of species interactions are modified by ontogeny and environmental heterogeneity.

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