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Juvenile *Trapezia* spp. crabs can increase juvenile host coral survival by protection from predation

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ABSTRACT:Adult crabs are known to play critical roles in the survival of their adult coral hosts, but little is known of the mutualism between juvenile crabs (≤0.5 cm) and their juvenile hosts. Field and laboratory experiments both demonstrated that the presence of juvenile crabs of the genus *Trapezia* in young host *Pocillopora* corals (2 to 3 cm diameter) increased coral survival by 32% and reduced consumption by the corallivorous seastar *Acanthaster planci*. These experiments also showed that juvenile *Trapezia* were not effective at deterring predation by another common predatory seastar, *Culcita novaeguineae*. Finally, our work highlights that the defensive ability of symbiotic crabs may be genus-specific, as juvenile *Tetralia* spp. crabs, obligate symbionts of *Acropora* spp., displayed no protection against either *A. planci* or *C. novaeguineae*.

KEY WORDS: Juvenile · Trapeziid · Corals · *Acanthaster planci* · *Culcita novaeguineae* · Mutualism · Predation · Defence

INTRODUCTION

Over the last 30 yr, coral cover has drastically declined worldwide mainly due to a combination of global (i.e. increased seawater temperature and ocean acidification) and local changes (e.g. anthropogenic perturbations) (Birkeland & Lucas 1990, Fabricius et al. 2008). However, outbreaks of *Acanthaster planci*, the major coral predator of Indo-Pacific corals, are an increasingly common threat to coral reef systems (Birkeland & Lucas 1990) and can lead to mass mortality of corals and drastic modifications to reef communities (Berumen & Pratchett 2006, Pratchett et al. 2009). For example, the *A. planci* outbreak first recorded in 2006 in French Polynesia lasted approximately 4 yr and resulted in a 90% decline in the populations of adult *Acropora* and *Pocillopora*, 2 dominant coral genera in reefs surrounding the island of Moorea (Kayal et al. 2011, Trapon et al. 2011, Leray et al. 2012). During this outbreak (2008 and 2009), the smallest size classes of *Pocillopora* suffered the highest predation around Moorea (Leray et al. 2012). However, despite the depletion of preferred prey, *A. planci* were still found at higher than normal densities up until 2010 (Kayal et al. 2011, Mills 2012) as well as in 2011 (authors' pers. comm.). The resistance, recovery and resilience of coral assemblages following such devastating outbreaks of *A. planci* is reliant, in part, on the ability of juvenile corals to persist and/or repopulate the reef during and after outbreaks. Nevertheless, to date, predation dynamics for juvenile corals have received little attention.

Scleractinian corals associate with a wide diversity of organisms that contribute to their overall fitness and survival (Stella et al. 2010, 2011). Beyond the well-known endo-symbiotic zooxanthellae association (see Stat & Gates 2011 and references therein), recent works also highlight the important role of exo-symbionts for coral survival (McKeon et al. 2012, Stier et al. 2012), as well as the fragility of this mutualism under climate-induced high temperatures (Stella et al. 2014). For example, coral hosts benefit tetraliid and

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trapeziid crabs by offering spatial refuge and providing food in the form of mucus (Rinkevich et al. 1991, Patton 1994). In turn, adult crabs play a critical role in adult coral survival by removing sediment from the surface of soft coral tissue (housekeeping: Stewart et al. 2006, Stier et al. 2012), and by actively defending against the deleterious effects of vermetid snails (Stier et al. 2010) and corallivory by gastropods and seastars (Glynn 1976, Pratchett 2001, McKeon et al. 2012). However, with the exception of a recent study focusing solely on the housekeeping services of newly settled exo-symbiotic crabs to their newly recruited host corals (Stewart et al. 2013) and a study investigating the defensive abilities of juvenile *Trapezia* against *Drupella cornus* (McKeon & Moore 2014), these studies have been carried out on adult corals and adult crabs. In order to understand the limitations to the recovery of coral populations following perturbations, such as an *A. planci* outbreak, a comprehensive understanding of the coral-crab symbiosis, in terms of protection against predation, throughout the life cycle of both parties is crucial. Young pocilloporid recruits (1 to 4 cm diameter) harbour increasing numbers of trapeziid crabs with an increasing complexity of their branching morphology (Stewart et al. 2013). Therefore, the presence of effective coral guards in juvenile corals may indeed have important implications for the recovery and, therefore, resilience of coral assemblages. This study aimed to bridge this gap by focusing on the protection against predation afforded by juvenile crabs to their juvenile hosts from 2 coral genera, *Pocillopora* and *Acropora*.

Of the 3 dominant coral genera found in Moorea, *Pocillopora* and *Acropora* are the most sensitive to *A. planci* predation (Kayal et al. 2012, Leray et al. 2012). *Pocillopora* spp. are associated with exo-symbiotic *Trapezia* spp. crabs and *Acropora* spp. are associated with *Tetralia* spp. crabs (Garth 1964, Castro 1976) and as such were the focus of this study. This study used *in situ* manipulations and controlled laboratory experiments including the 2 corallivorous seastar species *A. planci* and *Culcita novaeguineae*, that are common on the reef, to investigate the protection afforded by these juvenile crabs to their respective juvenile hosts.

MATERIALS AND METHODS

Study sites

In situ manipulations were conducted on fringing reefs at 2 sites located along the north shore of Moorea, French Polynesia (17° 30′ S, 149° 50′ W) between January and May 2009. One site was located near Opunohu Bay (17° 29′ S, 149° 52′ W) and the other at the mouth of Cook's Bay (17° 29′ S, 149° 49′ W). Both sites were located in shallow water (depth of 2 to 3 m) within 20 m of shore. Corallivorous seastars occurred naturally at both sites during the study.

Biological material

Juvenile *Pocillopora* spp. and *Acropora* spp. corals (mean whole colony diameter 2.3 ± 0.4 cm and 2.7 ± 0.8 cm, respectively, Fig. 1) were collected from the reef crest and transported back to the laboratory in individual plastic bags that retained symbiotic crabs within their respective host colonies. Coral colonies were immediately transferred into outdoor aquaria (400 l circular plastic tanks; 146 cm diameter) equipped with a continuous flow of seawater. Of these small-sized coral colonies, more than half were associated exclusively with a single exo-symbiotic crab, while the rest lacked crab exo-symbionts entirely. Corals were, therefore, separated into 2 categories, hereafter designated as either 'Crab' or 'No crab', and the coral hosts' natural association with a crab or lack thereof was conserved.

Coral-associated crabs were only identified to the genus level in order to minimise handling stress (≤0.5 cm, Fig. 1). Even though crabs were only identified to the genus level, McKeon & Moore (2014) highlighted the similar defensive abilities of small (4 to 6 mm carapace width) *Trapezia* species (*T. serenei* and *T. bideutata*) against *Drupella*. Therefore, in the unlikely event that *Trapezia* species varied between predation treatments, they should not differ in their defensive abilities.

Corals were affixed to small plastic tiles with 2-part epoxy adhesive (Splash Zone Z-Spar), in order to facilitate laboratory manipulations by limiting direct handling damage to the coral. After a minimum of 2 d of acclimation in aquaria, juvenile corals were subsequently used for the different experiments. Collection efforts were limited at both *in situ* experimental sites by the low abundance of juvenile acroporiids compared to the juvenile pocilloporids. Seastars of each species collected for use in the caged experiment were of approximately equal sizes, ranging between 13 and 17 cm for *Culcita novaeguineae* and 29 and 35 cm diameter for *Acanthaster planci*. Crab behaviour during predation was not recorded because of the difficultly in observing the crabs, owing in part to their small size and in part to the large size

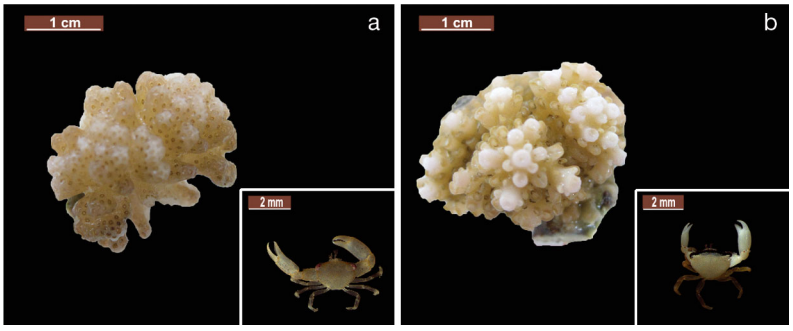

Fig. 1. Species-specific juvenile crab-coral mutualistic associations: (a) *Trapezia* spp. crab with *Pocillopora* spp. coral and (b) *Tetralia* spp. crab with *Acropora* spp. coral

of the predator covering the coral recruit and obscuring our view.

Coral survival in the presence/absence of juvenile *Trapezia* spp. crabs

To determine the general effectiveness of protection afforded by juvenile crabs to their hosts, we compared their defensive abilities when facing natural predators, including corallivorous fishes and seastars, using exclusion cages in the field. This study was carried out on the fringing reef of Cook's Bay. In this experiment, a total of 103 juvenile *Pocillopora* spp. corals with 'Crab' and 'No crab' were subjected to 2 levels of predator access: (1) protected from predators: 'Cage', or (2) exposed to predators: 'No cage'. Colonies of juvenile *Pocillopora* spp. corals with crabs were randomly divided into 2 treatments: 'Cage/Crab' (n = 26, mean coral diameter ± SE: 3.0 ± 0.5 cm, size range: 2.1 to 4.2 cm) and 'No cage/Crab' (n = 27, mean diameter: 3.1 ± 0.6 cm, range: 1.7 to 4.5 cm), as were those without crabs: 'Cage/No crab' (n = 21, mean diameter: 2.7 ± 0.5 cm, size: 2.0 to 4.0 cm) and 'No cage/No crab' (n = 29, mean diameter: 2.8 ± 0.5 cm, range: 1.9 to 4.3 cm). For logistical reasons, the experiment was repeated over two 18 d periods.

Cages were made using galvanized steel mesh (40 cm in diameter and 30 cm in height with a 3 cm mesh size) and were placed on top of 2 colonies of the same treatment. Although these cages did not protect the corals from all predators (i.e. those fishes and snails <3 cm), they effectively kept out both species of corallivorous seastars (*A. planci* and *C. novaeguineae*) and larger fishes. Every 2 d during the experiment, sample corals were categorized as either 'alive', where live tissue was clearly present, or 'dead', where live tissue was absent and the entire colony was white and the presence or absence of associate crabs was also verified. Care was taken to remove all newly-settled juvenile crabs from coral colonies using soft wooden skewers without touching or damaging coral tissue (observed only in 1 case). No symbiotic crabs were lost within the 'Crab' treatment.

The survival rate of *Pocillopora* spp. colonies in each treatment was estimated based on the proportion of corals that were alive every other day. A homogeneity test (Pearson's chi-squared test statistic) was used to compare survival frequencies in each treatment on the final day of each experimental run (Day 18). To test the effect of coral size on their survival, an ANOVA was performed on the logarithm of size according to treatment ('Crab/No crab', 'Cage/No cage') and survival ('alive/dead'). These analyses were performed with R 2.15.2 software and the survival package.

Protection of juvenile *Pocillopora* spp. from *Acanthaster planci* by juvenile *Trapezia* spp. crabs

To specifically test the ability of juvenile *Trapezia* spp. crabs to protect their juvenile host *Pocillopora* spp. corals against *A. planci* on the reef, we conducted an *in situ* predation experiment on the fringing reef of Opunohu Bay with 45 *Pocillopora* spp. juvenile corals ('Crab': mean coral diameter ± SE: 2.1 ± 0.6 cm, size range: 1.2 to 4.3 cm, and 'No crab': mean diameter: 1.9 ± 0.5 cm, range: 1.0 to 3.4 cm). Every evening, just before sunset after which predators and crabs generally become active, 1 juvenile *Pocillopora* spp. colony with a crab associate and one juvenile *Pocillopora* spp. colony without a crab were simultaneously placed under a galvanised steel cage (80 cm in diameter and 50 cm in height with 3 cm mesh size) equidistantly from the inner perimeter and one *A. planci* was added into the centre of the cage. *A. planci* predators had been acclimatised in cages located on bare sand at the experimental site for 2 d prior to the experiment. Each *A. planci* individual and each coral colony were used only once. Approximately 12 h after the beginning of the experiment, any signs of predation on the coral colonies

was recorded as consumed (e.g. exposed white skeleton). In the event that both sample juvenile *Pocillopora* spp. colonies in a given trial, with and without crab, were not consumed (n = 3/45), results were excluded from the statistical analyses. Results were evaluated using a chi-square test of independence (homogeneity test) on corresponding reformulated 2-by-2 contingency tables. To estimate the uncertainty in measurement, 95% confidence intervals of an exact binomial distribution were used. To test the effect of coral size on consumption, an ANOVA was performed on the logarithm of size according to treatment ('Crab/No Crab') and rank consumption.

Influence of different symbiotic crab genera on the feeding preferences of two seastar predators

To specifically determine the influence of juvenile trapezioid crabs (*Trapezia* spp. and *Tetralia* spp.) on feeding preferences of predatory seastars, we conducted a laboratory tank-based predation experiment. *Trapezia* spp. were always paired with their *Pocillopora* spp. host and *Tetralia* spp. with their *Acropora* spp. host. Four treatments were created: 'Crab' vs. 'No crab' crossed with juvenile individuals of the coral genus, *Acropora* (n = 116; 'Crab': mean coral diameter ± SE: 2.7 ± 0.6 cm, size range: 1.5 to 4.1 cm, and 'No crab': mean coral diameter: 2.9 ± 0.7 cm, range: 1.6 to 4.9 cm) and *Pocillopora* (n = 116, 'Crab': mean coral diameter: 3.0 ± 0.7 cm, size range: 1.8 to 5.2 cm, and 'No crab': mean coral diameter: 2.8 ± 0.6 cm, size range: 1.4 to 4.5 cm). These 4 treatments were positioned randomly, equidistant from each other and from the centre at the periphery of a large circular tank (400 l, 146 cm in diameter). An open-flow system continuously supplied the experimental tanks with seawater from the lagoon. Prior to the experiment, seastars were kept in laboratory aquaria and starved for 2 d to allow ample time for acclimation to aquarium conditions. At sunset, 1 corallivorous seastar, either *A. planci* or *C. novaeguineae*, was introduced into the centre of each tank, equidistant from each coral. Seastar displacement among juvenile coral colonies was observed, and the order in which coral colonies were consumed was recorded throughout the night. These feeding experiments were replicated 32 times using *A. planci* and 26 times using *C. novaeguineae*. Individual seastars and coral colonies were used for only one trial. A feeding event was defined as the removal of all tissue from the coral skeleton by the seastar.

The feeding preferences of the predatory seastars were assessed based on the order in which they fed on coral (rank ranged from 1 to 4, 1 being the first choice, and 4 being the last choice). The frequency of feeding of a given treatment was estimated using the NCi:NC ratio, with NCi being the number of consumed corals of one treatment at the rank i, and NC being the total number of consumed corals of the same treatment in all 4 ranks. To establish whether there were differences in feeding preferences between seastar taxa for all treatments, we used a non-parametric Kruskal-Wallis rank sum test with the 8 possible treatment combinations by the 2 predator genera, 2 coral genera, and 'Crab' vs. 'No crab' conditions. A post hoc Conover-Inman test was performed to evaluate pairwise comparisons between the different combinations. To test the effect of coral size on consumption, an ANOVA was performed on the logarithm of size according to the factors: treatment and rank consumption.

RESULTS

Coral survival in the presence/absence of juvenile *Trapezia* spp. crabs

The observed distribution of living and dead colonies between the 2 coral samples placed under the same cage was not significantly different from an expected distribution for 2 colonies taken randomly from the whole sample population (Goodness of fit test, $\chi^2 = 0.93$, p = 0.63), indicating that the 2 colonies under the same cage are independent. Therefore, each colony was hereafter analysed individually.

Statistical comparisons of the results between the two 18 d periods were not significantly different (log-rank test: $\chi^2 = 4.9$, p = 0.675) and, therefore, were combined for subsequent analyses. Of the 103 juvenile *Pocillopora* spp. corals, 18 died during the first 4 d of the experiment, but mortality was not significantly different between the 4 treatments (ranging from 15 to 25%; homogeneity test: $\chi^2 = 2.95$, p = 0.4). Following Stewart et al. (2006), we thus considered this period as the acclimation phase, removed the 18 dead colonies from the analyses and used Day 4 as the start of the experiment for subsequent analyses (n = 85; 'Cage/Crab' n = 20; 'No cage/Crab' n = 22; 'Cage/No crab' n = 16, and 'No cage/No crab' n = 27). The survival rate of corals in each of the 4 treatments was not dependent on coral size (Treatment × Survival, ANOVA: df = 3, $F = 0.378$, p = 0.77).

The survival of juvenile *Pocillopora* spp. colonies that hosted juvenile crabs was significantly higher than colonies lacking associate crabs (Fig. 2). The survival of corals hosting crabs remained constant after 8 d, whether corals were protected by a cage or not (85 and 73% survival rate respectively). On the other hand, coral colonies devoid of crabs exhibited relatively constant rates of mortality over time, 13 and 6% of the colonies were lost between Days 10–12 and 16–18, respectively, for caged colonies, and for uncaged colonies, 22 and 7% of colonies were lost between Days 6–10 and 14–16, respectively (Fig. 2). Although corals experiencing the simultaneous protection of a crab and a cage had higher survival than those with a crab but without a cage, this was not significantly different (χ^2 = 0.937, p = 0.167; Δ% = 12%, Table 1). Furthermore, after 18 d, there was no difference in mortality either between caged colonies with and without crabs (Table 1) or between 'Cage/No crab' and 'No cage/Crab' colonies (Table 1). On the other hand, when neither a cage nor a crab protected the coral host, it had a significantly lower survival rate than all other treatments (Fig. 2, Table 1).

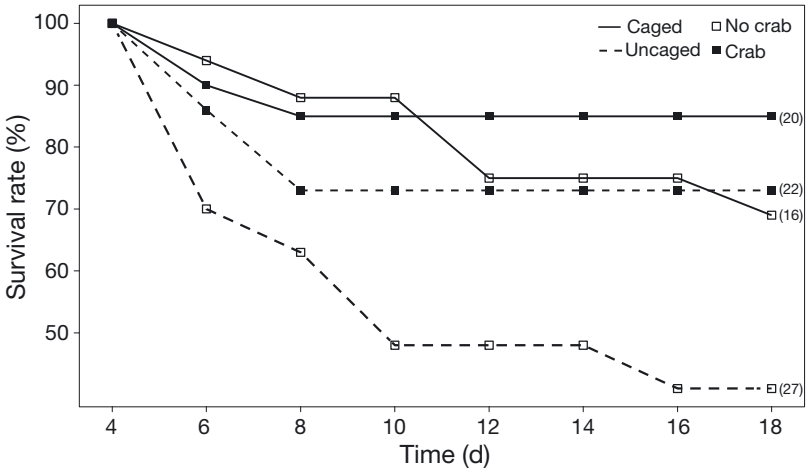

Fig. 2. Survival rates of juvenile *Pocillopora* spp. corals as a function of the presence or absence of a cage and the presence or absence of associate symbiotic crabs (n = 85 on Day 4). Caged (continuous line), uncaged (dashed line), crab (filled square) and no crab (empty square). Parentheses: sample sizes

Table 1. Comparative statistical analyses of percent survival of juvenile *Pocillopora* spp. corals on the reef exposed to different treatments (with or without a cage and with or without a crab). Statistical analyses excluded juvenile corals that died during the initial 4 d acclimation period and compared results among different treatments (n = 85 coral colonies). The relative gain or loss in percent (values of the difference between 'line treatment' and 'column treatment'; Δ% = line %-column %) is indicated in the column (Δ%) and tested using Pearson's chi-squared test statistic (*p-values < 0.05)

	Cage/No crab		No cage/Crab		No cage/No crab	
	Δ%	p (χ^2)	Δ%	p (χ^2)	Δ%	p (χ^2)
Cage/Crab	+16	0.122 (1.358)	+12	0.167 (0.937)	+44	0.001* (9.345)
Cage/No crab			−4	0.395 (0.071)	+28	0.038* (3.154)
No cage/Crab					+32	0.013* (5.013)

Protection of juvenile *Pocillopora* spp. from *Acanthaster planci* by juvenile *Trapezia* spp. crabs

Taking into account the 42 controlled feeding trials, a significant difference in alive/consumed corals according to presence or absence of juvenile trapeziid crabs was observed (χ^2 = 5.97, p = 0.014), independent of coral size (seastar consumption × exo-symbiont presence, ANOVA: df = 3, F = 1.149, p = 0.33). Corals lacking crabs were consumed preferentially (standardized residual = +2.44, p < 0.05). Of these 42 trials, 25 (60%) ended with the consumption of both juvenile corals, with and without crabs, whereas 17 (40%) ended with the consumption of only one specific juvenile coral ('Crab', n = 4; 'No crab', n = 13).

Protection afforded by symbiotic crabs against two echinoderm predators

The Kruskal-Wallis test on the rank sum of consumption indicated significant differences between predatory coral feeding preferences (W = 20.241, p = 0.009). The feeding preference of *A. planci* was significantly altered (pairwise comparison post-hoc tests p ≤ 0.002; Table 2) by the presence of juvenile *Trapezia* crabs in *Pocillopora* spp. corals (Fig. 3a), independent of juvenile coral size (rank consumption × treatment, ANOVA: df = 9, F = 1.633, p = 0.11). *Pocillopora* spp. corals with associate *Trapezia* crabs were consistently the last of the 4 treatments to be consumed (Table 2), whereas there was no significant effect on consumption order for the other 3 treatments (Fig. 3a).

Conversely, *Culcita novaeguineae* did not exhibit a feeding preference when crabs were present. Neither *Trapezia* nor *Tetralia* crabs produced any deterrent effect on the feeding choice of the seastar *C. novaeguineae* on their respective host corals (Fig. 3b). However, in the absence of exo-symbionts, consumption by this corallivorous predator showed a significant preference for coral genus: *Pocillopora* over *Acropora* (p = 0.045, Table 2). No significant effect of coral size on consumption *C. novaeguineae* was observed (rank consumption × treatment, ANOVA: df = 9, $F = 1.733$, p = 0.09).

Table 2. Comparative statistical analyses of the order in which juvenile *Pocillopora* spp. and *Acropora* spp. corals were consumed by the predators *Acanthaster planci* (n = 32) and *Culcita novaeguineae* (n = 26) in the presence ('Crab') or absence ('No crab') of associate juvenile *Trapezioid* crabs associated with *Pocillopora* or *Acropora*. p-values indicate results (*p-value < 0.05) of the post hoc Conover Inman test

Predator Coral genus	Exo-symbiont	*Acropora* No crab	*Acropora* Crab	*Pocillopora* No crab	*Pocillopora* Crab
A. planci					
Acropora	No Crab				
	Crab	0.734			
Pocillopora	No crab	0.650	0.910		
	Crab	0.002*	0.001*	<0.001*	
C. novaeguinea					
Acropora	No crab				
	Crab	0.315			
Pocillopora	No crab	0.045*	0.315		
	Crab	0.315	1	0.315	

DISCUSSION

Our *in situ* experiments demonstrated that juvenile *Trapezia* spp. crabs had a beneficial effect on juvenile *Pocillopora* spp. corals, either in terms of survival or deterring predation, when exposed to large reef predators, and particularly in the presence of the seastar *Acanthaster planci*. Furthermore, our controlled caged experiments demonstrated that juvenile *Trapezia* spp. crabs were able to deter predation on juvenile corals by the seastar *A. planci*, until coral prey was limited, when their host was ultimately eaten. Finally, this study indicated that the 2 seastars *A. planci* and *Culcita novaeguineae* have different feeding behaviours when symbiotic crabs protect corals. These experiments established that juvenile trapezioid crabs benefit juvenile *Pocillopora* corals, which play an important role in coral community structure, and thus are major players in coral reef ecosystems. Our results suggest that the absence of juvenile trapeziid crabs in juvenile coral colonies will pose severe limitations for the recovery of coral population following outbreaks of *A. planci*.

The *in situ* cage experiment highlighted the importance of juvenile trapeziid crabs in host coral survival. In this experiment, uncaged corals were likely subjected to attacks by various predators observed at

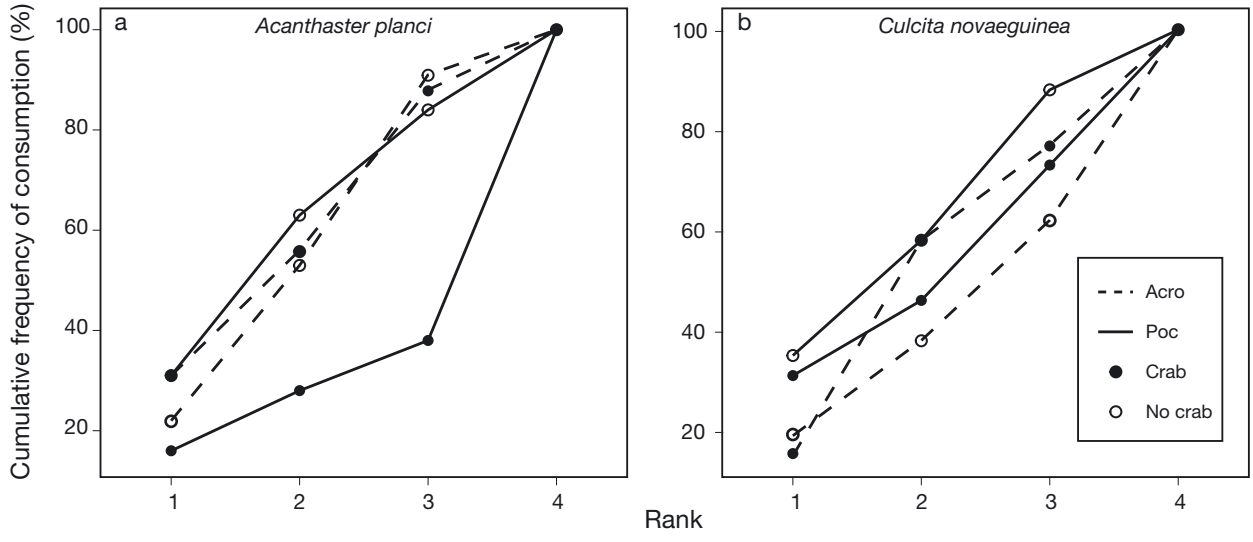

Fig. 3. Cumulative frequency of coral consumption by predatory seastars (a) *Acanthaster planci* (n = 32) and (b) *Culcita novaeguineae* (n = 26) on *Acropora* (dashed line), *Pocillopora* (continuous line), Crab (filled circle) and No crab (empty circle) in a laboratory feeding choice experiment

the site, including seastars and corallivorous fishes such as parrotfishes (Randall 1974, Rotjan & Lewis 2006) and butterflyfishes (Sano 1989, Pratchett 2005), whereas caged corals were protected from predators larger than 3 cm. However, despite being protected from predators, there was still a 16% difference in survival between caged corals with and without *Trapezia* spp. crab associates. This survival difference could be attributed to the sediment clearing abilities of both newly settled and older crabs (Stewart et al. 2006, 2013), as sedimentation is known to be an important cause of coral mortality (Fabricius 2005, Weber et al. 2012). Furthermore, the episodic decreases in survival of corals without crab associates (Fig. 2), could demonstrate sporadic sedimentation and/or predation processes, with each episodic decrease reflecting one or both of these sporadic events.

After 2 wk, uncaged corals with crabs had a higher survival rate than those without crabs: 32% more corals were alive. This difference in coral survival was greater than that between caged corals with and without crabs (16%) suggesting that beyond their housekeeping and other coral-benefiting activities, juvenile *Trapezia* spp. crabs can also protect their host corals from some, if not all, predatory attacks. This hypothesis was reinforced by our results in which the protective capacity of juvenile trapeziid crabs reduced coral consumption by *A. planci* (i.e. *in vivo* and *in vitro* feeding preference experiments): juvenile *Pocillopora* spp. corals without juvenile *Trapezia* spp. crab were consumed first. Thus, even at their juvenile life stage, trapeziid crabs were able to protect their juvenile coral host to some extent against *A. planci*.

How do trapeziid crabs defend their hosts? An understanding of the defensive abilities of crabs was limited in this study, in part because of the small size of juvenile corals and crabs, and in part because of the relatively large size of predators obscuring our view, such that direct observations of seastar–crab interactions were not possible. However, it is clear that a defensive mechanism is operating. Adult *Trapezia* spp. are thought to detect danger using both visual (Glynn 1980) and chemical cues in the environment emitted from the predator (Whittaker & Feeny 1971, Kittredge et al. 1974), after which they move to the periphery of the coral host and vigorously pinch and clip off tube feet or spines with their pincers (Glynn 1980, McKeon et al. 2012). Juvenile *Trapezia* individuals (irrespective of species) may behave in a similar manner to adults, even if physical defence seems unlikely due to their small size (e.g. McKeon & Moore 2014). In addition, movement to the periphery of their host might stimulate chemical production by the coral (Brauer et al. 1970) that repels the predator (Glynn & Krupp 1986, Pratchett 2001). Furthermore, symbiotic crabs may themselves also release anti-predatory chemicals found in crustaceans (e.g. toxins, feeding repellents) (Derby & Sorensen 2008), in a similar manner to other marine and terrestrial organisms (Machado et al. 2005, Pohnert et al. 2007). Finally, trapeziid crabs could also produce snapping sounds with their chelae that are perceived by *A. planci* and deter their attack in a similar way to snapping shrimps (Glynn 1976). These possibilities, which are not necessarily mutually exclusive, may account for the protective capability of juvenile *Trapezia* spp. crabs, potentially by mimicking the presence of adult guarding crabs.

In contrast, while adult *Trapezia* spp. crabs are able to protect their coral host against *C. novaeguineae* (McKeon et al. 2012, McKeon & Moore 2014), in our experiments, juvenile *Trapezia* spp. did not. *C. novaeguineae* has a more rigid body and harder exterior compared to *A. planci*, and as such could be unaffected by juvenile trapeziid crab attacks. Moreover, juvenile *Tetralia* spp. associated with juvenile *Acropora* spp. corals did not have any deterrent effect on either *A. planci* or *C. novaeguineae*. A previous study on adult crabs suggests that morphological differences between the 2 trapezioid genera may account for their different abilities to physically repel predators, with *Trapezia* having a larger carapace and larger chelipeds than *Tetralia* (Glynn 1987). The smaller appendages of juvenile *Tetralia* spp., compared to the same-sized juvenile *Trapezia* spp, may also be insufficient to produce sounds loud enough to deter predators.

Regardless of the defence mechanisms employed by juvenile *Trapezia* spp. crabs, none of them deterred *C. novaeguineae*. The different reactions of *A. planci* and *C. novaeguineae* to the presence of *Trapezia* spp. in potential prey corals may suggest an adaptive character discriminating these seastars, crabs and corals during evolution. This is important in coral reef ecosystems because of the different life histories of each of the 3 main players. The population dynamics of *A. planci* tends to be comprised of boom-and-bust outbreaks (Moran 1986) resulting in large-scale devastation of corals during outbreak periods, whereas those of *C. novaeguineae* are stable (Goreau et al. 1972). Therefore, selection may have been stronger on the defensive behaviours of crabs against *A. planci* than on *C. novaeguineae*. Furthermore, *Acropora* spp. have faster growth rates than

Pocillopora spp. corals (Harriott 1999, Baird & Hughes 2000) and hence selection on behaviour to defend against predation in the slower growing *Pocillopora* spp. may have been stronger. Finally, how do we reconcile the difference in protective abilities between the juvenile crabs? The colonization of trapeziid and tetraliid crabs occurred on 2 independent occasions without any common ancestry, despite the monophyletic origin of obligate association of crabs with branching corals (Lai et al. 2009). However, *Acropora* spp. corals may have been colonized by tetraliids later than the colonization of *Pocillopora* spp. by trapeziids, and as such the former may not yet have developed protective abilities at the juvenile stage. Alternatively, our results may suggest that in the absence of associated juvenile trapeziid crabs, juvenile *Pocillopora* spp. host corals would be the coral species more frequently preyed upon. This result, coupled with their slower growth rates, would result in greater selection on the association of juvenile *Pocillopora* spp. corals with symbiotic crabs and less selection on Tetraliidae to protect juvenile *Acropora* spp.

In conclusion, our data reported new aspects of juvenile crab defence with implications for the survival of juvenile *Pocillopora* spp. corals (<5 cm in diameter; Harrison & Wallace 1990). The important role of this symbiotic relationship was highlighted by the high proportion of juvenile trapeziid crab-associated juvenile corals found under natural conditions on the reef (>50%). As small vulnerable juvenile recruits represent a bottleneck in coral survival (Hughes & Connell 1987), especially following *A. planci* outbreaks, the protective ability of small *Trapezia* spp. crabs may play an important role in reef resilience and reef community dynamics.

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