



Ecological traits of Caribbean sea anemones and symbiotic crustaceans

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ABSTRACT: In Caribbean coral reefs, many crustacean species associate with sea anemones, but only a few are anemone symbionts. We examined several ecological traits of 3 anemone species (*Bartholomea annulata*, *Condylactis gigantea*, *Lebrunia danae*) and their crustacean symbionts (6 species) on a coral reef at Puerto Morelos, Mexico. On average, *C. gigantea* was the largest and *B. annulata* the most abundant of the 3 anemone species. Season did not affect the density distribution of any species, whereas reef zone (back reef, fore reef, reef channels) significantly affected density and mean size of *B. annulata* and *C. gigantea*, but only density of *L. danae*. The probability of harboring crustaceans increased with anemone size in all species, but varied with reef zone and season in *B. annulata* only. These patterns may be due to different microhabitat requirements, reproductive strategies, or photosynthetic plasticity of dinoflagellate endosymbionts among hosts, and different flow regimes among reef zones. *Alpheus armatus* and *Ancylomenes pedersoni* were strongly associated with *B. annulata*, and *Periclimenes Rathbunae* with *L. danae*. *Thor amboinensis* and *Mithraculus cinctimanus* occurred more often in *C. gigantea*, while *P. yucatanicus* was more evenly associated with the 3 hosts. Only *Ancylomenes pedersoni* and *T. amboinensis* occurred in conspecific groups more often than expected by chance. Commensal complexes of up to 3 symbiont species occurred in all host species, with symbionts that typically used different parts of the host coexisting more frequently. These results provide a baseline to assess the potential influence of local and global anthropogenic stressors on anemone–crustacean symbioses.

KEY WORDS: Symbiosis · Coral reef · Mexico · Commensal complex · Puerto Morelos

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INTRODUCTION

Coral reefs support the highest biodiversity of all marine ecosystems, with invertebrates contributing dominantly to this condition (Reaka et al. 2008). In the complex community networks typical of coral reefs, an important ecological role is played by many invertebrates that may serve as ‘habitat providers’ (i.e. species that offer structure or substrate that other species may live in or on). Habitat providers are ubiquitous and include numerous spe-

cies of sponges, hard and soft corals, tube-dwelling polychaetes, ascidians, echinoderms, molluscs, and sea anemones. Equally diverse are the organisms that live in or on habitat providers, which include a vast array of invertebrates and fishes (review in Glynn & Enochs 2011).

Organisms that associate with habitat providers ('hosts') may obtain a variety of benefits, including physical shelter from predation, camouflage, stability, range expansion, or advantageous positioning. For example, the nematocyst-armed tentacles of sea

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anemones provide protection from predation to many crustaceans (Fautin et al. 1995, Wirtz 1997, Khan et al. 2004) that acquire immunity from the toxic compounds produced by their hosts through a process known as acclimation (Levine & Blanchard 1980, Crawford 1992, Giese et al. 1996). The general term 'crustacean associates' refers to any crustacean found in, on, or very close to an anemone, but such crustaceans can be categorized into 2 types: 'facultative associates', i.e. crustaceans that are primarily free-living but may briefly associate with anemones, and 'symbionts', i.e. crustaceans wherein the association with the host is not random or occasional, but long-term (Ross 1983, Gwaltney & Brooks 1994, Calado et al. 2002).

In the wider Caribbean region, some field studies have focused on the abundance, distribution, or population dynamics of anemones without regard to their symbionts (e.g. Sebens 1976, Barrios-Suárez et al. 2002, Herrera-Moreno & Betancourt-Fernández 2002, Nelsen 2008). Other studies have mainly focused on ecological traits of the crustacean symbionts, such as degree of host specificity (e.g. Knowlton 1980, Gwaltney & Brooks 1994), distribution patterns (e.g. Hayes & Trimm 2008, Silbiger & Childress 2008), or demography and behavior (e.g. Mahnken 1972, Sargent & Wagenbach 1975, Patton 1979, Williams & Bunkley-Williams 2000, Huebner & Chadwick 2012a). Others have contrasted ecological traits of anemones with those of their crustacean symbionts, but with emphasis on a particular host species (e.g. Herrnkind et al. 1976, Stanton 1977, Huebner & Chadwick 2012b) or one or a few selected symbiont species (e.g. Mahnken 1972, Nizinski 1989, Silbiger & Childress 2008). However, because most crustacean symbionts of Caribbean anemones are host-generalists (e.g. see Silbiger & Childress 2008), their abundance and distribution at the local scale may depend to some extent on the ecological traits of multiple host anemone species, their use of space provided by the host, and intra- and interspecific interactions with other crustacean associates.

To provide some insight into these issues, we examined several ecological traits of multiple species of host anemones and their crustacean symbionts in one of the most intensely studied Caribbean coral reef systems in Mexico, the Puerto Morelos coral reef system (PMCR) (Rodríguez-Martínez 2008). Nearly 20 yr of monitoring of environmental variables and ecological features of these coral reef and sea grass communities provides continuously updated information on environmental characteristics prevailing in different parts of the PMCR (e.g. Ruiz-Rentería

et al. 1998, Jordán-Dahlgren & Rodríguez-Martínez 2003, Coronado et al. 2007, Rodríguez-Martínez et al. 2010, van Tussenbroek 2011).

Among the 13 species of sea anemones registered in the PMCR (González-Muñoz 2009), 3 actiniarians widely known as hosts for crustaceans are particularly ubiquitous: the corkscrew anemone *Bartholomea annulata* (Family Aiptasiidae), the giant anemone *Condylactis gigantea* (Actiniidae), and the branching anemone *Lebrunia danae* (Aliciidae). In the present study, we examine several ecological traits of these 3 host anemone species, and of the full array of their crustacean symbionts. We were particularly interested in examining the density and size distribution of each host species in distinct reef environments, and the degree to which these traits varied on a seasonal basis. Our aim was to assess the relative importance of these anemone species in providing habitat for crustacean symbionts in reef zones with different environmental features.

MATERIALS AND METHODS

Study area

The PMCR (centered at 20° 51' N, 86° 53' W) is located near the town of Puerto Morelos on the NE coast of the Yucatan Peninsula (state of Quintana Roo, Mexico). It is an extended fringing reef composed of a series of reef patches differing in size and structural complexity (Fig. 1). The reef is separated from the shoreline by a narrow (~500 to 1500 m in width) and shallow (<5 m in depth) reef lagoon characterized by calcareous sand stabilized by sea grass meadows (Ruiz-Rentería et al. 1998). The PMCR has a well-developed back reef and reef crest, and a relatively flat fore reef that descends gradually to 20–25 m into an extensive sand platform (Jordán-Dahlgren 1989, Rodríguez-Martínez et al. 2010). The back reef is dominated by the scleractinians *Acropora palmata* and *Montastraea annularis*, and varies from shallow (2 to 3 m) protected flat areas, to deeper (5 to 7 m), relatively more exposed areas with higher relief. The fore reef also varies from areas of hard substrate with a relatively gentle slope, colonized by many small scleractinian colonies, gorgonians, and sponges, to high relief areas where large scleractinians dominate (Jordán-Dahlgren & Rodríguez-Martínez 2003). A detailed study on the physical oceanography of this coral reef system found that the exchange of water between the reef lagoon and the adjacent ocean is mainly driven by the circulation

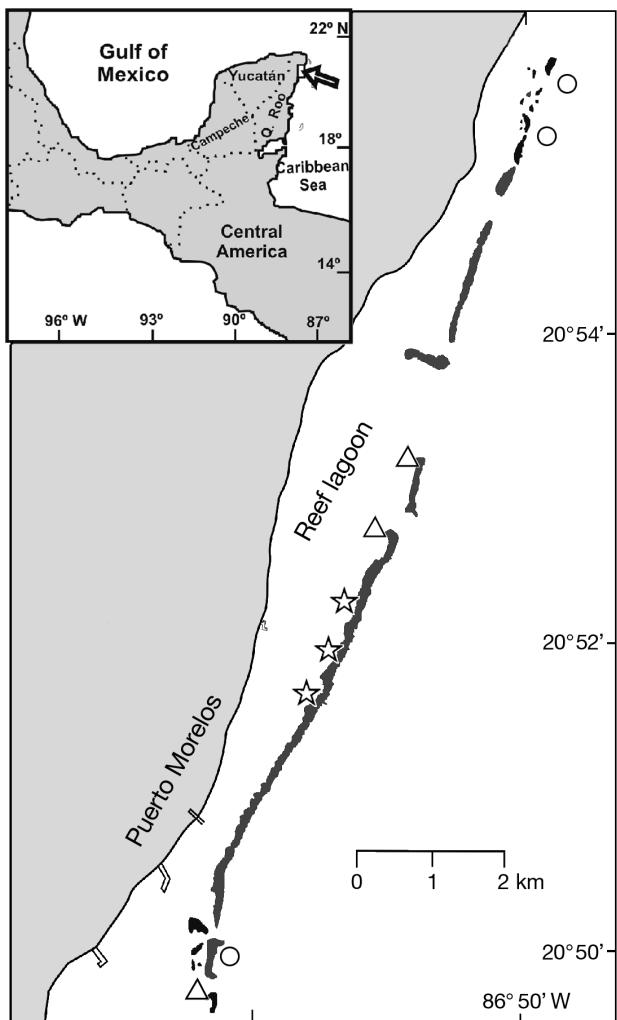


Fig. 1. The Puerto Morelos coral reef system. Black structures = coral reef patches. Symbols = location of 9 fixed sampling sites (\star : back-reef site; O: fore-reef site; Δ : reef-channel site). Inset: location of Puerto Morelos (arrow) in Mexico

induced by surface waves overtopping the reef and spilling water into the lagoon, with the water eventually leaving the lagoon through the reef channels (Coronado et al. 2007).

Sampling design

To account for the local hydrodynamic regime, and for differences in structural complexity as well as environmental gradients along and across the reef tract, we established 3 replicate fixed sites in each of 3 reef zones: back reef, fore reef, and reef channels (Fig. 1). Each site measured 50×50 m (i.e. 0.25 ha) and was delineated with flag tags. The back-reef sites (1.8 to 2.0 m depth) were located along the lee-

ward side of a large, elongated reef patch that extends for ~6 km (Fig. 1). The fore-reef sites (8.0 to 10.2 m depth) were located on the exposed side of 3 relatively well-developed reef patches. The reef channel sites (5.0 to 7.0 m depth) were located on relatively exposed, deeper areas of the back reef adjacent to 3 reef channels (Fig. 1).

Using SCUBA, we surveyed the entire area of each site for individuals of *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae* during 4 consecutive seasons starting in the spring of 2007 (spring: 12 April to 4 May; summer: 10 to 30 September; autumn: 21 November to 4 December 2007; winter: 13 February to 3 March 2008). All surveys were conducted between 10:00 and 13:00 h. Within each site, we counted all anemones, and measured the length (L) and width (W) of the tentacle crown of each individual with a metal ruler (± 0.5 cm) to estimate the tentacle crown surface area ($TCSA = \pi \times 0.5 L \times 0.5 W$; Hattori 2002). We also counted and identified *in situ* the crustaceans associated with each anemone, and recorded their positions relative to the host ('on host': on the tentacle crown; 'under host': under the tentacle crown; 'near host': on the substrate surrounding the anemone, within a radius of ~10 cm).

Statistical analyses

Variability in anemone density and size (TCSA)

We subjected the anemone density data (number of individuals 0.25 ha $^{-1}$) to a factorial repeated-measures ANOVA (RM-ANOVA). The main (fixed) factors were anemone species (AS, with 3 levels) and reef zone (RZ, with 3 levels: back-reef, reef channels, and fore-reef, and 3 replicate sites per level). Time (T, with 4 levels corresponding to the 4 seasons) was the repeated measure. The data were previously transformed to $\ln(n + 1)$ to meet the assumption of homogeneity of variances as assessed with Levene tests. In repeated-measures studies, the data may be auto-correlated (i.e. non-independent) across times. To overcome this problem, we assessed the degree to which the assumption of sphericity was violated with a Mauchly's test and, if necessary, adjusted the degrees of freedom of T and its residuals with the Huynh-Feldt correction (Howell 2002).

Because the 3 anemone species were not present on all replicate sites of each zone at all seasons (precluding the use of RM-ANOVA), the data on size (TCSA in cm 2) for each species were pooled by

reef zone and subjected to a factorial ANOVA to test the effects of AS and RZ on mean size of anemones (Underwood 1981). The data were previously transformed to $\ln(\text{TCSA})$ to increase homogeneity of variances, as assessed with Levene tests.

Distribution of crustaceans among host anemones

We used 3 logistic regression analyses (1 per anemone species) to test the effects of size (TCSA, continuous factor), time, and reef zone (categorical factors with 4 and 3 levels, respectively) on their probabilities of harboring crustaceans (Quinn & Keough 2002). The binary response variable was the absence or presence of at least 1 crustacean associate. We then used a simple linear regression to examine the relationship between TCSA and the number of crustacean associates.

To examine the distribution of crustaceans among conspecific hosts, we computed the mean number of crustaceans per anemone (and the corresponding variance), and subjected the count data to a χ^2 goodness-of-fit test to a Poisson (random) distribution. If the test was significant, we further subjected the data to a χ^2 goodness-of-fit test to a negative binomial distribution. Finally, we categorized the crustaceans into symbionts and facultative associates based on previous knowledge on the types of habitats used by each species (e.g. Chace 1972, Wagner 1990, Monroy-Velázquez 2000, Briones-Fourzán & Lozano-Álvarez 2002, Silbiger & Childress 2008), and used exclusively the symbiont species in the following analyses.

Density of crustacean symbionts, affinity for hosts, and use of space provided by host

The density of symbionts (number of individuals 0.25 ha^{-1}) was examined with a factorial RM-ANOVA. The main (fixed) factors were symbiotic crustacean species (CS, with 6 levels corresponding to the 6 symbiotic species) and RZ. T was the repeated measure. The data were previously transformed to $\ln(n + 1)$ to increase homogeneity of variances, and the degree to which the assumption of sphericity was violated was assessed with Mauchly's test.

For each symbiont species, we used separate χ^2 goodness-of-fit tests to compare the proportions of individuals distributed among the 3 host species and the 3 positions relative to the host. Seasonal variability in these traits was separately examined with a

3×4 contingency table (3 levels for the corresponding categorical factor \times 4 seasons).

Conspecific groups and commensal complexes

To assess the tendency of symbionts to form groups, we computed the number of conspecific symbionts that were alone or in groups of 2, 3, etc., in the same host, and compared the frequency data with a truncated Poisson (random) distribution using χ^2 (Cohen 1960). We then computed all commensal complexes (2 or more species of symbionts coexisting in the same host) for each host species, and explored how coexisting species used the space provided by the host (e.g. Stanton 1977).

RESULTS

Host anemones

Anemone density and size

The data on anemone density did not violate the assumption of independent samplings across time (Mauchly test, $W = 0.863$, $\chi^2_5 = 2.456$, $p = 0.783$; Huynh-Feldt correction = 1). Density varied significantly with AS and T, and there were interaction effects between AS \times RZ and T \times RZ (Table 1). The overall density (all means \pm SE) of *Bartholomea annulata* (23.2 ± 3.1 ind. 0.25 ha^{-1}) was almost twice as high as that of *Lebrunia danae* (13.5 ± 3.0 ind. 0.25 ha^{-1}) and over 4 times as high as that of *Condylactis gigantea* (5.3 ± 0.9 ind. 0.25 ha^{-1}). In particular, the density of

Table 1. *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae*. Repeated-measures ANOVA of anemone density ($\ln[n + 1] 0.25 \text{ ha}^{-1}$) with anemone species (AS) and reef zone (RZ; back reef, reef channels, fore reef) over time (T; spring, summer, autumn, and winter)

Effect	df	MS	F	p
Intercept	1	480.425	179.922	<0.001
AS	2	28.505	10.675	0.001
RZ	2	1.603	0.600	0.559
AS \times RZ	4	12.250	4.588	0.010
Error	18	0.504		
T	3	0.305	4.130	0.010
T \times AS	6	0.104	1.415	0.226
T \times RZ	6	0.247	3.343	0.007
T \times AS \times RZ	12	0.041	0.550	0.871
Error	54	0.014		

B. annulata was highest in the reef channels (35.9 ± 1.2 ind. 0.25 ha^{-1} , averaged across seasons; Fig. 2a), while densities of *C. gigantea* (1.2 ± 0.2 ind. 0.25 ha^{-1}) and *L. danae* (1.3 ± 0.1 ind. 0.25 ha^{-1}) were lowest in the reef channels and on the back reef, respectively (Fig. 2b,c). The density distribution of each species by reef zone remained rather stable over time ($T \times AS \times RZ$; Table 1). However, within each reef zone during any season, there was considerable variation in density among replicate sites, especially for *C. gigantea* on the fore reef (where this species was generally rare in 2 of the 3 sites) and *L. danae* on the back reef (Fig. 3), indicating a rather patchy distribution.

The overall range in TCSA was 3.1 to 380.1 cm^2 for *Bartholomea annulata*, 2.4 to 276.5 cm^2 for *Lebrunia danae*, and 7.1 to 452.4 cm^2 for *Condylactis gigantea*. Mean TCSA (averaged across seasons) varied signif-

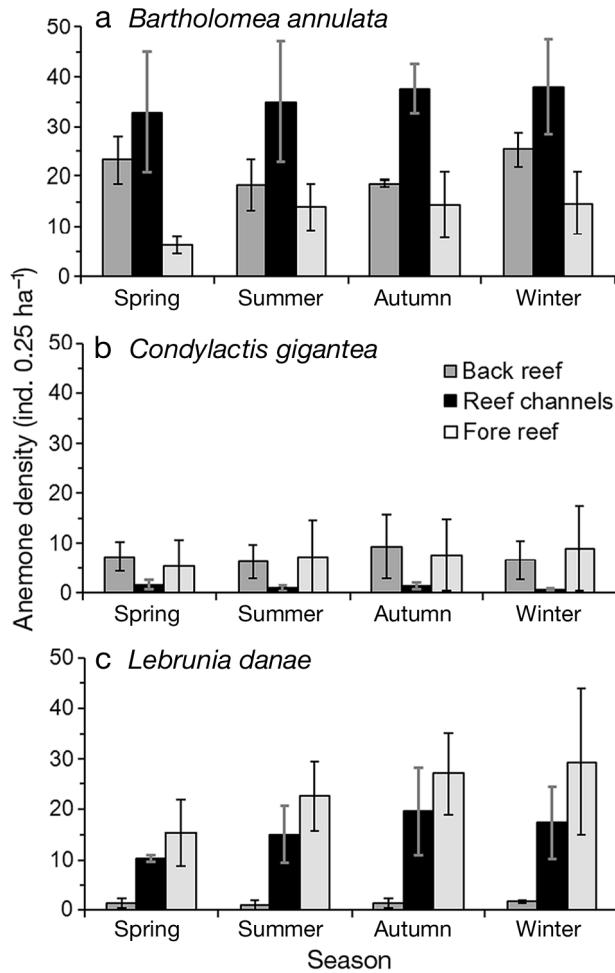


Fig. 2. *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae*. Density (mean \pm SE) of (a) *B. annulata*, (b) *C. gigantea*, and (c) *L. danae* in 3 reef zones (back reef, reef channels, fore reef, 3 replicate sites per zone) at 4 seasons (spring, summer, and autumn 2007, and winter 2008)

icantly among species ($F_{2,27} = 31.581$, $p < 0.001$) and reef zones ($F_{2,27} = 20.330$, $p < 0.001$), with a significant interaction effect between these 2 variables ($F_{4,27} = 8.714$, $p < 0.001$). The TCSA (all means \pm SE) of *C. gigantea* ($109.2 \pm 17.4 \text{ cm}^2$) was twice as large as those of *L. danae* ($56.9 \pm 4.1 \text{ cm}^2$) or *B. annulata* ($50.6 \pm 4.1 \text{ cm}^2$). However, the TCSA of *B. annulata* was significantly larger on the fore reef ($66.1 \pm 4.1 \text{ cm}^2$) than in the reef channels ($46.3 \pm 4.8 \text{ cm}^2$) or on the back reef ($39.2 \pm 3.3 \text{ cm}^2$) (Fig. 4), and the TCSA of *C. gigantea* decreased significantly from the fore reef ($173.0 \pm 27.6 \text{ cm}^2$) to the back reef ($105.0 \pm 5.0 \text{ cm}^2$) to the reef channels ($49.5 \pm 2.7 \text{ cm}^2$; Fig. 4), whereas the TCSA of *L. danae* did not vary significantly with reef zone (Fig. 4).

The population size distribution of each anemone species in increments of 25 cm^2 TCSA revealed that,

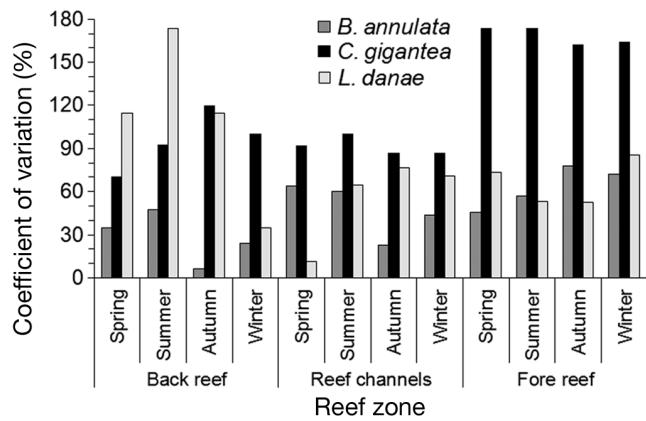


Fig. 3. *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae*. Coefficient of variation (%) of anemone density among replicate sites for each reef zone and season

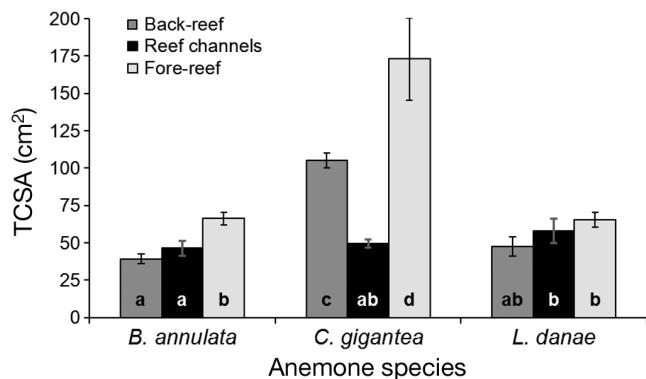


Fig. 4. *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae*. Size (tentacle crown surface area, TCSA, mean \pm SE) measured in the back reef, reef channels, and fore reef zones (3 replicate sites per zone). Similar letters in columns denote statistically similar means

for *Bartholomea annulata*, the mode increased from the back reef ($\leq 25 \text{ cm}^2$) to the reef channels (25 to 50 cm^2) to the fore reef (50 to 75 cm^2 ; Fig. 5a). *Lebrunia danae* exhibited a single mode in the size class 25 to 50 cm^2 in all 3 reef zones, albeit more markedly in the back reef (Fig. 5b). In contrast, *Condylactis gigantea* exhibited a multimodal size distribution in all 3 reef zones (Fig. 5c).

Distribution of crustaceans among host anemones

Across the study period, crustaceans were present in 72.8 % of individuals of *Bartholomea annulata* ($n = 835$), 70.7 % of *Condylactis gigantea* ($n = 191$), and 27.2 % of *Lebrunia danae* ($n = 486$). In *B. annulata*, the probability of harboring crustaceans increased significantly with TCSA, and was also affected by

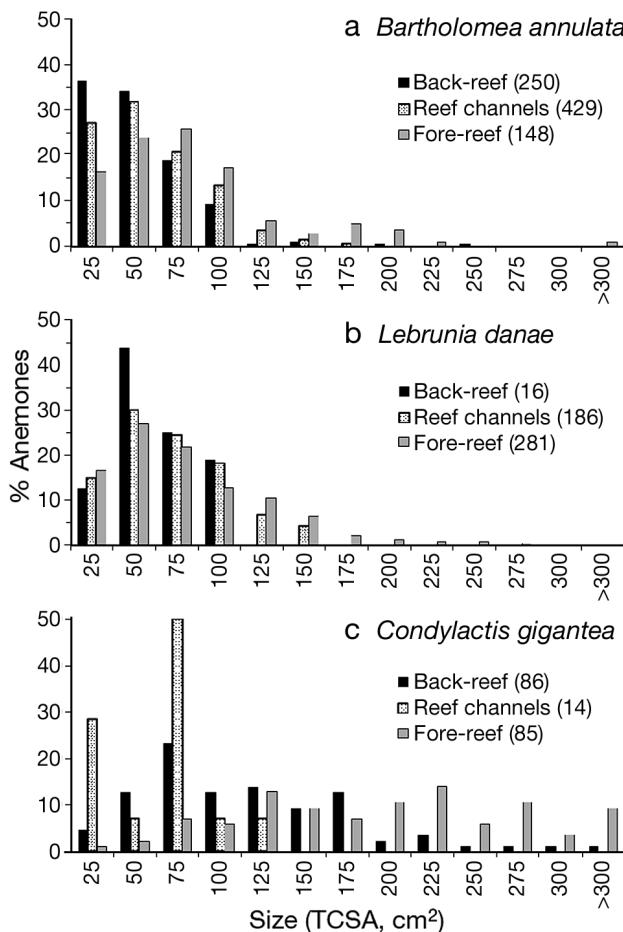


Fig. 5. *Bartholomea annulata*, *Lebrunia danae*, and *Condylactis gigantea*. Size distribution (tentacle crown surface area, TCSA) of individuals of (a) *B. annulata*, (b) *L. danae*, and (c) *C. gigantea* in the back reef, reef channels, and fore reef zones. Numbers on the x-axis: end points of intervals. Numbers in (): sample size

reef zone and season (Table 2). In particular, the probability was significantly lower in the reef channels (Table 2). By contrast, the only factor significantly (positively) affecting the probability of finding crustaceans in *C. gigantea* and *L. danae* was TCSA (Table 2).

Per individual anemone, *Bartholomea annulata* and *Condylactis gigantea* harbored from 0 to 7 individual crustaceans, and *Lebrunia danae* from 0 to 5. In all 3 host species, there was a significant (all p -values < 0.001) but rather weak relationship between number of crustaceans and TCSA (*B. annulata*: $r^2 = 0.115$, $n = 825$; *C. gigantea*: $r^2 = 0.173$, $n = 187$; *L. danae*: $r^2 = 0.055$, $n = 484$). The distribution of crustaceans among conspecific hosts differed significantly from random in all cases (Table 3). In *B. annulata*, the count data were dominated by solitary crustaceans (i.e. 1 per host) and the mean was greater than the variance, indicating under-dispersion (Table 3). By contrast, in *C. gigantea* and *L. danae*, the variance was greater than the mean, indicating over-dispersion, and the negative binomial distribution fitted the distribution of crustaceans well (Table 3).

Diversity of crustacean associates

In total, we found 1371 individual crustaceans on these anemones, of which 1283 (93.8 %) belonged to 6 species of symbionts: the alpheid shrimp *Alpheus armatus*, the palaemonid shrimps *Ancylomenes pedersoni* (previously known as *Periclimenes pedersoni*; Okuno & Bruce 2010), *Periclimenes yucatanicus* and *P. Rathbunae*, the hippolytid shrimp *Thor amboinensis*, and the majid crab *Mithraculus cinctimanus* (Table 4). The rest (86 individuals, 6.2 % of the total) belonged to 9 species of facultative associates (the shrimps *Stenopus hispidus*, *Brachycarpus biunguiculatus*, and *Cinetorhynchus rigens*, and the crabs *Stenorhynchus seticornis*, *Mithraculus sculptus*, *Mithraculus forceps*, *Mithrax pilosus*, *Mithrax* sp., and *Macrocoeloma trispinosum*; Table 4).

Crustacean symbionts

Density and distribution of crustacean symbionts

Data on the density of crustacean symbionts did not violate the assumption of independent samplings across time (Mauchly test, $\chi^2_5 = 10.267$, $p = 0.067$; Huynh-Feldt correction = 1). Density varied significantly with CS and T, and there was a significant in-

Table 2. *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae*. Estimates of separate logistic regression analyses testing effects of size (tentacle crown surface area, TCSA in cm²), reef zone (back reef, reef channels, and fore reef; reference level: fore reef), and season (reference level: winter) on the probability of finding at least 1 crustacean associate on each species of host anemone

Effect	Estimate ± SE	Wald statistic	df	p	Odds ratio (95 % CI)
<i>B. annulata</i>					
Size	0.026 ± 0.004	48.689	1	<0.001	1.03 (1.03–1.05)
Zone: Back reef	0.189 ± 0.142	1.775	1	0.183	1.21 (0.91–1.59)
Reef channels	-0.383 ± 0.124	9.556	1	0.002	0.68 (0.53–0.87)
Season: Spring	0.071 ± 0.206	0.118	1	0.731	1.07 (0.72–1.61)
Summer	0.435 ± 0.197	4.862	1	0.027	1.54 (1.05–2.27)
Autumn	-0.358 ± 0.162	4.861	1	0.027	0.70 (0.51–0.96)
<i>C. gigantea</i>					
Size	0.011 ± 0.004	9.386	1	0.002	1.01 (1.00–1.02)
Zone: Back reef	-0.059 ± 0.294	0.040	1	0.841	0.94 (0.53–1.68)
Reef channels	-0.759 ± 0.456	2.767	1	0.096	0.47 (0.19–1.14)
Season: Spring	0.428 ± 0.437	0.958	1	0.328	1.53 (0.65–3.61)
Summer	0.132 ± 0.488	0.073	1	0.786	1.14 (0.44–2.97)
Autumn	-0.549 ± 0.406	1.823	1	0.177	0.58 (0.26–1.28)
<i>L. danae</i>					
Size	0.010 ± 0.003	12.867	1	<0.001	1.01 (1.00–1.02)
Zone: Back reef	0.252 ± 0.386	0.426	1	0.514	1.29 (0.60–2.74)
Reef channels	0.012 ± 0.229	0.003	1	0.958	1.01 (0.65–1.59)
Season: Spring	-0.276 ± 0.371	0.551	1	0.458	0.76 (0.37–1.57)
Summer	0.538 ± 0.366	2.160	1	0.142	1.71 (0.84–3.51)
Autumn	0.239 ± 0.327	0.534	1	0.465	1.27 (0.67–2.41)

Table 3. *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae*. Statistics and goodness-of-fit tests for types of distributions of crustaceans among individuals of each host anemone species

	Host anemone species		
	<i>B. annulata</i>	<i>C. gigantea</i>	<i>L. danae</i>
Total N	835	191	486
N with crustaceans (%)	608 (72.8)	135 (70.7)	132 (27.2)
Mean no. of crustaceans	1.04	1.70	0.37
Variance	0.83	3.26	0.52
Variance/Mean	0.798	1.918	1.475
Goodness of fit to Poisson distribution	$\chi^2_4 = 80.10$, p < 0.001	$\chi^2_4 = 49.46$, p < 0.001	$\chi^2_2 = 16.92$, p < 0.001
Type of distribution	Underdispersed	Overdispersed	Overdispersed
Goodness of fit to negative binomial distr.		$\chi^2_6 = 8.69$, p = 0.192	$\chi^2_3 = 1.795$, p = 0.578

teraction effect between these 2 variables (Table 5). On average, *Alpheus armatus* was much more abundant than the other 5 symbionts. All interaction effects with RZ were non-significant (Table 5), indicating that the relative density of each symbiont by reef zone remained rather stable over time. Thus, by reef zone, the highest densities corresponded to *Alpheus armatus* on the back reef and in reef channels, while the lowest densities corresponded to the 3 palaemonids

(*Ancylomenes pedersoni*, *Periclimenes yucatanicus*, and *P. rathbunae*) on the back reef, and to *P. yucatanicus* in the reef channels (Fig. 6a).

Degree of affinity for host and use of space provided by host

Alpheus armatus and *Ancylomenes pedersoni* exhibited a high affinity for *Bartholomea annulata* (Fig. 6b), but the former showed a strong tendency to occur under the host, whereas the latter was more often found on or near the host (Fig. 6c). *Periclimenes rathbunae* showed a high affinity for *Lebrunia danae* (Fig. 6b) and tended to occur on or under the host (Fig. 6c). *Thor amboinensis* and *Mithraculus cinctimanus* were mostly associated with *Condylactis gigantea*, but many were also found with *L. danae* or *B. annulata* (Fig. 6b). These 2 symbionts, in particular *M. cinctimanus*, occurred more often under the host (Fig. 6c). *P. yucatanicus* exhibited a rather low degree of host affinity, with 41% individuals associated with *C. gigantea*, 39% with *L. danae*, and 20% with *B. annulata* (Fig. 6b), and showed a similar pattern of host space use as in *Ancylomenes pedersoni*, with most individuals occurring on or near the host (Fig. 6c).

Season did not affect the degree of host affinity for any symbiont (contingency table analyses, range in p-values: 0.109 to 0.918), or the pattern of host space use for *Mithraculus cinctimanus* ($\chi^2_6 = 8.874$, p = 0.181), *Periclimenes rathbunae* ($\chi^2_6 = 8.656$, p = 0.194), or *P. yucatanicus* ($\chi^2_6 = 11.659$, p = 0.07). However, there was significant seasonal variation in host space use by *Alpheus armatus* ($\chi^2_6 = 40.190$, p < 0.001), *Ancylomenes pedersoni* ($\chi^2_6 = 18.726$, p = 0.005), and *Thor amboinensis* ($\chi^2_6 = 25.397$, p < 0.001). In *Alpheus armatus*, this variability reflected changes in the proportions of individuals located under or near the host, and in *Ancylomenes pedersoni* and *T. amboinensis*, it reflected changes in the proportions of individuals located near or on the host.

Table 4. *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae*. Crustacean species and numbers of individuals observed to associate with 3 sea anemone host species. Symbiotic species establish long-term associations with hosts, while facultative associates are primarily free-living but may associate with anemones for brief periods (Ross 1983, Gwaltney & Brooks 1994)

Crustacean species	Host anemone species			Total
	<i>B. annulata</i>	<i>C. gigantea</i>	<i>L. danae</i>	
Symbionts				
<i>Alpheus armatus</i>	598	2	3	603
<i>Thor amboinensis</i>	15	167	59	241
<i>Ancylomenes pedersoni</i>	158	3	5	166
<i>Mithraculus cinctimanus</i>	48	84	29	161
<i>Periclimenes yucatanicus</i>	14	22	25	61
<i>Periclimenes rathbunae</i>	2	6	45	53
Subtotal	835	284	166	1285
Facultative associates				
<i>Stenorhynchus seticornis</i>	26	19	0	45
<i>Mithrax</i> sp.	1	6	6	13
<i>Mithraculus sculptus</i>	1	5	1	7
<i>Stenopus hispidus</i>	3	2	0	5
<i>Mithrax pilosus</i>	2	1	1	4
<i>Mithraculus forceps</i>	1	2	0	3
<i>Macrocoeloma trispinosum</i>	2	1	0	3
<i>Brachycarpus biunguiculatus</i>	2	1	0	3
<i>Cinetorhynchus rigens</i>	1	1	1	3
Subtotal	39	38	9	86
Total	874	322	175	1371

Table 5. Repeated-measures ANOVA of crustacean symbiont density ($\ln[n + 1] \cdot 0.25 \text{ ha}^{-1}$) with crustacean species (CS; 6 levels corresponding to 6 species of crustacean symbionts) and reef zone (RZ; back reef, reef channels, fore reef) over time (T; spring, summer, autumn, winter)

Effect	df	MS	F	p
Intercept	1	357.702	161.030	<0.001
CS	5	21.887	9.853	<0.001
RZ	2	2.718	1.224	0.306
CS × RZ	10	2.704	1.217	0.313
Error	36	0.504		
T	3	1.695	6.193	0.001
T × CS	15	0.537	1.960	0.025
T × RZ	6	0.418	1.527	0.176
T × CS × RZ	30	0.242	0.884	0.641
Error	108	0.274		

Conspecific groups and commensal complexes

Alpheus armatus, *Periclimenes yucatanicus*, *P. rathbunae*, and *Mithraculus cinctimanus* were consistently found alone or in pairs on the same host (Table 6). In contrast, groups of >2 conspecifics on the same host occurred more often than expected by chance for *Thor amboinensis* (up to 6 ind., $\chi^2_3 = 22.646$, $p < 0.001$) and *Ancylomenes pedersoni* (up to 4 ind., $\chi^2_1 = 7.495$, $p = 0.006$).

Up to 3 species of symbionts coexisted on 98 individuals of *Bartholomea annulata* (16% of all *B. annulata* that harbored crustaceans), 42 of *Condylactis gigantea* (31%), and 20 of *Lebrunia danae* (15%) (Fig. 7). *L. danae* harbored 11 different commensal complexes, but none were particularly frequent. *B. annulata* harbored 8 different commensal complexes, of which the most frequent (86%) was constituted by *Alpheus armatus* and *Ancylomenes pedersoni*, the 2 symbionts with the highest affinity for this host (Fig. 7a). Coexisting individuals of *Alpheus armatus* and *Ancylomenes pedersoni* were invariably in different places relative to the host (under and on the host, respectively, or under and near the host). Six commensal complexes occurred in *C. gigantea*, with the most frequent (62%) also consisting of the 2 symbiotic species with the greatest affinity for this host: *Thor amboinensis* and *Mithraculus cinctimanus*

(Fig. 7b). However, in this case, the 2 symbionts were often under the host at the same time.

DISCUSSION

Host anemones

The anemones *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae* occur on coral reefs throughout the Caribbean region, but their relative abundance varies widely with geographic area and local habitat features (e.g. Panamá: Sebens 1976; Colombia: Barrios-Suárez et al. 2002; Hispaniola: Herrera-Moreno & Betancourt-Fernández 2002). In the PMCR, *B. annulata* is the most abundant and *C. gigantea* the least abundant of these 3 anemone species, but the density distribution of each species by reef zone remains rather stable over time, suggesting that these sessile organisms quickly acclimate to local microhabitats. However, reef zone differently affects the density and size of *B. annulata* and *C. gigantea*, and the density but not the size of *L. danae*. These contrasting results may reflect interspecific differences in susceptibility to local environmental features (e.g. the flow regime, which may vary in effects on feeding efficiency with anemone size),

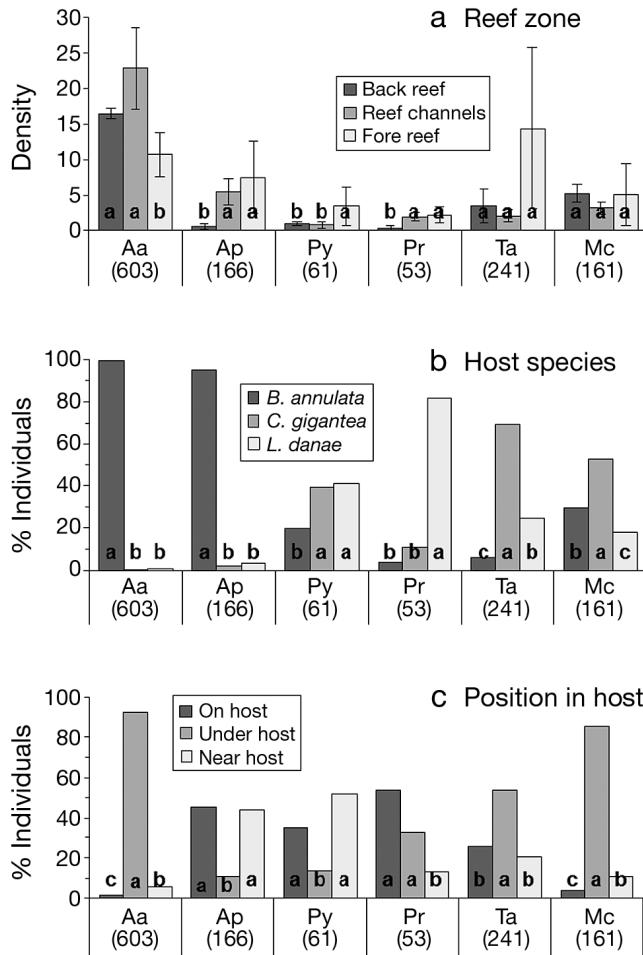


Fig. 6. *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae*. (a) Density (ind. 0.25 ha⁻¹, mean ± SE) of crustacean symbionts by reef zone, (b) percentages of individuals of each species distributed among 3 species of host anemones, and (c) 3 positions on hosts. Similar letters in columns for each species denote statistically similar groups. Numbers in () on x-axes denote sample sizes. Aa: *Alpheus armatus*; Ap: *Ancylomenes pedersoni*; Py: *Periclimenes yucatanicus*; Pr: *P. rathbunae*; Ta: *Thor amboinensis*; Mc: *Mithraculus cinctimanus*

microhabitat requirements, reproductive strategy, and photosynthetic efficiency of dinoflagellate endosymbionts borne by these cnidarians.

Because anemones depend on water flow to bring them food, but risk being dislodged or broken by drag forces (Koehl 1977), their dimensions in a given flow habitat involve a trade-off between maximizing food availability and minimizing flow forces and physical stress (Anthony 1997). Although anemones can reduce drag by retracting, and many are capable of polyp shrinkage, maximum feeding efficiencies are attained by small anemones at high flow regimes, and by large anemones at slow flow regimes

Table 6. Group sizes of conspecific crustacean symbionts co-occurring on the same host anemone individuals

Crustacean species	Group size					
	1	2	3	4	5	6
<i>Alpheus armatus</i>	429	87	—	—	—	—
<i>Thor amboinensis</i>	80	27	15	6	4	3
<i>Ancylomenes pedersoni</i>	100	17	8	2	—	—
<i>Mithraculus cinctimanus</i>	149	6	—	—	—	—
<i>Periclimenes yucatanicus</i>	43	9	—	—	—	—
<i>Periclimenes rathbunae</i>	47	3	—	—	—	—

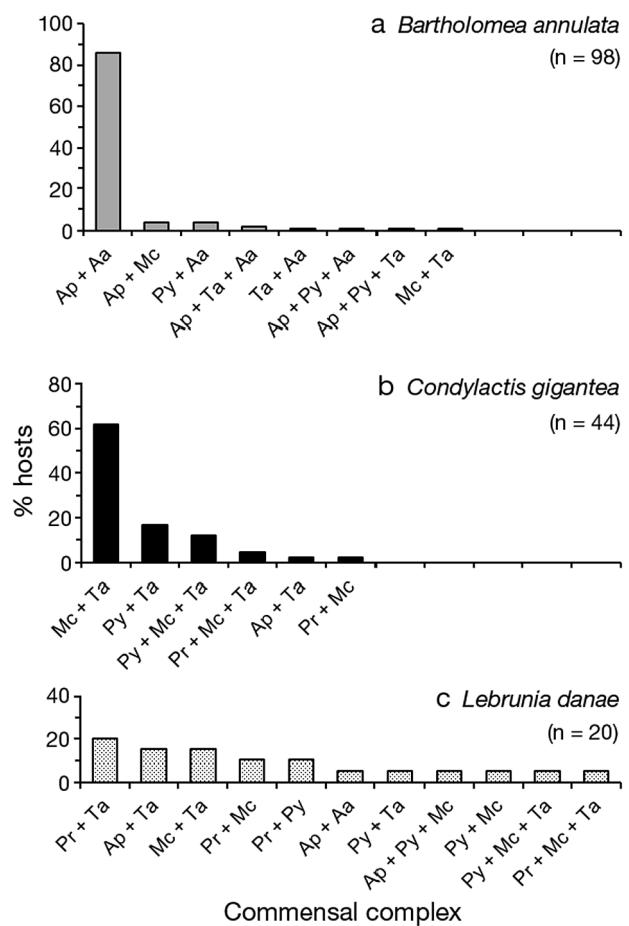


Fig. 7. *Bartholomea annulata*, *Condylactis gigantea*, and *Lebrunia danae*. Diversity and percent frequency of commensal complexes in hosts harboring >1 symbiont species: (a) *B. annulata*, (b) *C. gigantea*, and (c) *L. danae*. Abbreviations for symbiotic crustacean species as in Fig. 6

(Anthony 1997, Titus 2011). In the PMCR, water enters the reef lagoon via waves breaking on the coral reef and exits the lagoon through large reef channels. This circulation regime ensures good flushing (average turnover time: 2.25 h; Coronado et al. 2007), but results in high levels of water motion

and sediment re-suspension in the shallow back reef (Ruiz-Rentería et al. 1998), and in a high flow regime through the reef channels (average current velocity: 20 cm s^{-1}) compared to the fore reef (2 to 3 cm s^{-1} ; Coronado et al. 2007), potentially explaining the generally smaller size of anemones on the back reef and in reef channels relative to the fore reef.

The dinoflagellate genus *Symbiodinium* comprises several types within 8 subgeneric clades or lineages (A to H), and the types borne by a particular host species may vary with geographical location (Venn et al. 2008). In the PMCR, a variety of cnidarian hosts living at depths of 0 to 15 m, including *Bartholomea annulata* and *Lebrunia danae*, bear exclusively *Symbiodinium* type C1, suggesting that this type has a relatively high degree of photosynthetic plasticity (LaJeunesse 2002). However, *B. annulata* strongly tends to occupy crevices in sand pockets (e.g. Sebens 1976, Barrios-Suárez et al. 2002), a type of microhabitat that is more common in the back reef and reef channels than in the fore reef (Ruiz-Rentería et al. 1998). Moreover, individuals of *B. annulata* spawn twice a year but also undergo pedal laceration, a type of clonal replication that helps to maintain habitat space and stable population sizes (Jennison 1981, Titus 2011). In the laboratory, small *B. annulata* ($<28 \text{ cm}^2$ TCSA) replicate by pedal laceration more often than larger conspecifics (Titus 2011), while in the field, *B. annulata* replicate more frequently on near-shore reefs exposed to more suspended particulate matter than on offshore reefs with less sedimentation and more light penetration (Nelsen 2008). In conjunction, these features of *B. annulata* may underlie its greater density, but smaller mean size, in the reef channels and back reef relative to the fore reef. We found no information on the reproductive strategy of *L. danae*, but a congeneric species, *L. coralligens*, releases larvae that are negatively phototropic, show aggregated settlement behavior, and settle most frequently around the bases of the adults, with settlement and metamorphosis occurring within 24 h (Lewis 1984). If *L. danae* shows similar reproductive and settlement strategies as *L. coralligens*, these features might account for the similar size distribution and mean size of *L. danae* in all 3 reef zones. However, *L. danae* occupies crevices in hard substrates and rarely occurs at depths $<5 \text{ m}$ (Herrnkind et al. 1976, Sebens 1976, Herrera-Moreno & Betancourt-Fernández 2002), explaining its greater densities in the fore reef and reef channels relative to the back reef.

In the PMCR, *Symbiodinium* clade-A types are more constrained to hosts living within 0 to 5 m depth

below the water surface, suggesting photoacclimation to high irradiance, and *Condylactis gigantea* bears a mixture of types A4a, C1, and A3 (LaJeunesse 2002). This may explain the rather patchy distribution of *C. gigantea* and its generally lower densities in reef channels. On the other hand, because this species reproduces only sexually with individuals spawning once per year but over a prolonged reproductive period (Jennison 1981), the multimodal size distribution of *C. gigantea* in all 3 reef zones likely reflects different pulses in larval recruitment.

Crustacean associates occurred in a far higher proportion of individuals of *Bartholomea annulata* (72.8%) and *Condylactis gigantea* (70.7%) than they did in *Lebrunia danae* (27.2%). Stanton (1977) also found crustaceans in only 26% of *L. danae* in his study area in the Bahamas. Although both the probability of harboring at least 1 crustacean and the number of crustaceans per individual anemone increased with size in all 3 host species, individuals of *C. gigantea* harbored, on average, 1.6 and 4.5 times as many crustaceans as did individuals of *B. annulata* and *L. danae*, respectively. This result cannot be entirely ascribed to the comparatively larger size of *C. gigantea*, because the mean sizes of *L. danae* and *B. annulata* were similar. However, as *C. gigantea* and *B. annulata* bear most of their dinoflagellate endosymbionts within their feeding tentacles, these anemones tend to remain continuously expanded so as to maximize light capture during the day and prey capture during the night (Sebens & DeRiener 1977), potentially providing relatively stable habitats for their crustacean associates. By contrast, *L. danae*, in addition to having larger nematocysts and producing more potent toxic compounds than other sea anemones (Herrnkind et al. 1976, Sánchez-Rodríguez & Cruz-Vázquez 2006), contains most of its endosymbionts within auxiliary structures ('pseudotentacles') that are incapable of feeding behavior. Thus, during the day, the pseudotentacles are expanded and the feeding tentacles contracted, while the opposite occurs at night (Sebens & DeRiener 1977, Stanton 1977). In conjunction, these features of *L. danae* may provide a less stable or less suitable habitat for crustacean associates.

Crustacean symbionts

The vast majority (93.8%) of the crustacean associates of these anemones belonged to 6 species of symbionts. Although the 6 symbiont species occurred in all 3 host species, some exhibited a high

degree of affinity for a host species. A variety of commensal complexes were found in the 3 host species, reflecting differences in intra- and interspecific behavioral interactions and microhabitat requirements among symbionts (Herrnkind et al. 1976, Mercado & Capriles 1982, Wirtz 1997). Interestingly, the highest diversity of commensal complexes occurred in *Lebrunia danae*, the host with the lowest proportion of individuals harboring crustaceans, and the lowest diversity occurred in *Condylactis gigantea*, the host with the largest mean size and a high proportion of individuals harboring crustaceans.

The most abundant symbiont by far was *Alpheus armatus*. This alpheid shrimp is generally considered an obligate symbiont of *Bartholomea annulata* (Knowlton 1980, Knowlton & Keller 1983), although field (Herrnkind et al. 1976) and laboratory studies (Knowlton & Keller 1985) suggest that it may also use other hosts, at least briefly. In our study, 99% of the *A. armatus* ($n = 603$) associated with *B. annulata*, but 3 ind. associated with *Lebrunia danae* and 2 with *Condylactis gigantea*. These shrimps live in the same cavity as their host and are highly territorial, especially the juveniles, whereas the adults may share their host only with a conspecific of the opposite sex (Limbaugh et al. 1961, Knowlton 1980, Knowlton & Keller 1983). Indeed, 90% of the *A. armatus* that we observed were under the host, and 71% were dwelling alone, and the rest in pairs. The high degree of affinity of *A. armatus* for *B. annulata*, and its tendency to dwell alone, resulted in a similar density distribution by reef zone of these 2 species.

Ancylomenes pedersoni also exhibited a high degree of affinity for *Bartholomea annulata*, yet these 2 species differed in their density distribution by reef zone. This result reflects the tendency of *Ancylomenes pedersoni* to form groups and its ability to acclimate to different hosts in the absence of *B. annulata* (e.g. Silbiger & Childress 2008, Mascaró et al. 2012), as well as the lower probability of finding crustacean associates in *B. annulata* in the reef channels (where this anemone exhibited the highest densities). The high frequency of coexistence of *Ancylomenes pedersoni* and *Alpheus armatus* in *B. annulata* appears related to the inverse pattern of host space use exhibited by these 2 symbionts. *Periclimenes rathbunae* exhibited a strong affinity for *Lebrunia danae*, and because these shrimps occurred alone or in pairs in the same host, the density distribution by reef zone was similar for these 2 species. In other locations, *P. rathbunae* is strongly associated

with the sun anemone *Stichodactyla helianthus* (Hayes & Trimm 2008, Silbiger & Childress 2008), a species that was absent from our study sites because, in the PMCR, it occurs only on the reef crest at depths of 0.5 to 1.5 m (González-Muñoz 2009). *P. yucatanicus* occurred in similar percentages on *Condylactis gigantea* and *L. danae*, and to a lesser extent on *B. annulata*. In Florida, *P. yucatanicus* was strongly associated with *C. gigantea* and only occurred on *B. annulata* when *C. gigantea* was scarce (Silbiger & Childress 2008).

Ancylomenes pedersoni and *Periclimenes yucatanicus* both potentially serve as cleaner shrimps (Limbaugh et al. 1961, Bunkley-Williams & Williams 1998), although the former performs this activity more effectively than the latter (McCammon et al. 2010). It has been suggested that anemones harboring multiple *A. pedersoni* might be more easily identified as 'cleaning stations' by reef fishes, and that this might explain the tendency of *A. pedersoni* to occur in groups on the same host (Limbaugh et al. 1961, Herrnkind et al. 1976, Huebner & Chadwick 2012a). However, Huebner & Chadwick (2012b) found that the size of the anemone *Bartholomea annulata* rather than the number of associated *A. pedersoni* acts as a primary attractant to client fishes. Also, social interactions may influence group size and the distribution of conspecific cleaner shrimps among hosts (Limbaugh et al. 1961, Mahnken 1972, Wicksten 1995). This may also occur in *P. rathbunae*, a non-cleaner shrimp, which has been found alone or in pairs on the same host in some locations (e.g. Mahnken 1972, the present study), and in groups of up to 11 ind. on the same host in other locations (e.g. Mercado & Capriles 1982, Hayes & Trimm 2008).

Although heterospecific palaemonids can coexist on the same host (Mahnken 1972, Stanton 1977, Williams & Bunkley-Williams 2000), we observed coexistence of *Ancylomenes pedersoni* and *Periclimenes yucatanicus* on only 2 *Bartholomea annulata* and 1 *Lebrunia danae*, and coexistence of *P. rathbunae* and *P. yucatanicus* on only 2 *L. danae*. In all cases, heterospecific shrimps were on different parts of the host, suggesting some degree of interspecific competition for microhabitat, in particular between *A. pedersoni* and *P. yucatanicus*, given their similar pattern of host space use. We did not observe coexistence of *A. pedersoni* and *P. rathbunae*, but this was possibly due to the high affinity for different hosts exhibited by these 2 palaemonids.

Thor amboinensis was the second most abundant symbiont in our study sites, and these small hippolytid shrimps associated mostly with *Condylactis*

gigantea (70% of all shrimps on this host), with up to 6 individuals co-occurring in a single host. In general, *T. amboinensis* occurs in groups more often than expected by chance alone (Wirtz 1997, Baeza & Piantoni 2010, the present study), potentially reflecting the small size and limited defensive capability of these shrimps, which may preclude solitary individuals from monopolizing the host (Thiel & Baeza 2001). *T. amboinensis* occurred in many different commensal complexes on all 3 host species, and coexisted, often side by side, with each of the other 5 symbionts, as observed also in Puerto Rico (Mercado & Capriles 1982).

Over 50% of the small commensal crabs *Mithraculus cinctimanus* associated with *Condylactis gigantea*, and the rest with either of the other 2 hosts. Patton (1979) remarked that these majid crabs are usually solitary on hosts, and only occasionally occur in pairs, as we found in the present study. Most crabs were located under the host, a similar pattern as that of *M. commensalis* crabs associated with *Lebrunia danae* in the Bahamas (Herrnkind et al. 1976). However, according to Patton (1979), *M. commensalis* (first described by Manning 1970) is actually the juvenile phase of *M. cinctimanus*, and according to Wagner (1990), only the juveniles are symbiotic with anemones, whereas the adults are free-living. In our study, *M. cinctimanus* coexisted with all other symbionts except *Alpheus armatus*, possibly because these 2 symbionts exhibited a very similar pattern of host space use, and the highly territorial and aggressive alpheid can easily displace the smaller crab from a host (Knowlton 1980).

In summary, we found substantial variability in several ecological features of 3 species of host anemones and 6 species of their crustacean symbionts in the PMCR. These findings are relevant, because even though the PMCR was declared a national park in 1998, effectively protecting these animals from being extracted for the aquarium trade (Instituto Nacional de Ecología 2000), it is very close to a shore with one of the highest rates of touristic and urban development in Mexico (Rodríguez-Martínez 2008). Time-series ecological data from local sea grass and reef communities have detected gradual changes over time that may reflect an increase in pollution caused by the rapid rise in urban and tourist development along the coast and inland from Puerto Morelos, coupled with poor water-management practices (Rodríguez-Martínez et al. 2010, van Tussenbroek 2011). Coastal development also tends to increase water turbidity, especially in shallow reef lagoons and back-reef areas (Fourqurean & Robblee 1999,

Sullivan-Sealy 2004), potentially altering the distribution and abundance of anemones by affecting their mean size and rate of clonal replication, and photosynthetic efficiency of their endosymbionts (Sullivan-Sealy 2004, Nelsen 2008). This might further impact their crustacean symbionts, in particular those that exhibit a high affinity for a given host species (e.g. *Alpheus armatus*), and those that serve as cleaning shrimps, which depend on large hosts to attract fish clients, with potential cascading effects on the coral reef system (Mahnken 1972, Huebner & Chadwick 2012b). Therefore, the present study provides baseline information to further assess the potential influences of local (e.g. coastal development and pollution) and global (e.g. climate change) anthropogenic stressors on anemone–crustacean symbioses.

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