Decapod crustaceans associating with echinoids in Roatán, Honduras

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Abstract.—Echinoids comprise an integral component of coral reef ecosystems, providing trophic links, microhabitats, and refuge for a wide diversity of symbiotic organisms. We studied the association of at least eight species of decapod crustacean ectosymbionts with six species of echinoids at Roatán, Honduras, during 6–11 September 2015. Decapods associated most frequently with the echinoid *Diadema antillarum* (10.80% of individuals of this echinoid, six decapod species; $n = 799$), followed by *Eucidaris tribuloides* (1.74%, three species; $n = 746$), *Echinometra lucunter* (1.30%, six species; $n = 8349$), *Tripneustes ventricosus* (0.86%, four species; $n = 1167$), *Echinometra viridis* (0.23%, two species; $n = 862$), and *Lytechinus variegatus* (0%, no species; $n = 12$). Of 239 individual decapods observed, *Percnon gibbesi* was the most common species (48.5% of decapods, four echinoid species), followed by unidentified hermit crabs (Paguridae; 27.2%, five species), *Stenorhynchus seticornis* (11.7%, three species), *Stenopus hispidus* (6.3%, three species), *Plagusia depressa* (3.3%, three species), *Panulirus argus* (1.3%, one species), an unidentified small crab (possibly *Pitho* sp.; 1.3%, one species), and *Mithrax verrucosus* (0.4%, one species). The frequency of association varied with water depth for *P. gibbesi*, which associated more frequently with *D. antillarum* in shallow water (< 5 m), and *S. seticornis*, which associated more frequently with *D. antillarum* in deep water (> 5 m). None of the decapod species associated exclusively with echinoids or was specialized for associating with echinoids. Decapods associated with the longest-spined species, *D. antillarum*, at a rate more than six times higher than that of any other echinoid species, supporting the hypothesis that decapods seek shelter among the spines of echinoids to benefit from decreased predation.

Key words: associations, Caribbean Sea, Crustacea, Decapoda, Echinodermata, Echinoidea

■ Introduction

Sea urchins (Echinodermata: Echinoidea), hereafter referred to as echinoids, comprise an integral component of coral reef ecosystems, providing trophic links, microhabitats, and refuge for a wide diversity of symbiotic organisms (Clark, 1976; Carpenter, 1997; Glynn & Enochs, 2011). Ectosymbionts representing at least ten animal phyla have been reported to associate with echinoids, including Porifera, Cnidaria, Ctenophora, Platyhelminthes, Annel- ida, Arthropoda, Mollusca, Echinodermata, Bryozoa, and Chordata (e.g., Randall *et al.*, 1964; Strasburg, 1966; Magnus, 1967; Gooding, 1974; Bruce, 1982; Hayes *et al.*, 1998a, 2006; Coppard & Campbell, 2004; Hétérier *et al.*, 2004; Hopkins *et al.*, 2004; Hayes, 2007; Campos *et al.*, 2009; Britayev *et al.*, 2013). The ectosymbionts of echinoids may obtain several potential benefits from their hosts; for example, sessile species procure a hard substrate for attachment on the test or spines of echinoids, parasites obtain nutrition from echi-

noid hosts, filter feeders increase foraging efficiency by being elevated above the substrate, and many species seek shelter from predators among the spines (Bruce, 1976; Ross, 1983).

There is ample evidence that some ectosymbionts associate with the spines of echinoids, especially the longer-spined species, to gain protection from predators. For example, several species of fishes associate almost exclusively with long-spined echinoid species and, when threatened, retreat deeper into the echinoids' spines (Strasburg, 1966; Magnus, 1967; Tamura, 1982; Gould *et al.*, 2014). Some fish ectosymbionts match the color of echinoid hosts, some possess dark horizontal lines on their bodies which are aligned with the echinoids' spines, and some change color when departing from their echinoid hosts to forage away from them (Strasburg, 1966; Magnus, 1967; Tamura, 1982; Gould *et al.*, 2014). Experiments with echinoid models revealed that fish ectosymbionts preferred those with longer or more dense spines (Magnus, 1967; Tamura, 1982) and the fish used the models to extend their territories over soft substrates (Fricke, 1970).

Similar evidence indicates that ectosymbiont decapod crustaceans (Arthropoda: Malacostraca: Decapoda), hereafter referred to as decapods, also benefit from protection by associating with the spines of echinoids. Several species of shrimp that associate exclusively with echinoids are cryptically colored, align their bodies with the echinoids' spines, and are quickly preyed upon when removed from echinoids (Lewis, 1956; Chace, 1969; Fricke & Hentschel, 1971; Bruce, 1976, 1982; Patton *et al.*, 1985). In an overnight experiment providing a choice between five potential host species of echinoids, the palaemonid shrimp *Tuleariocaris neglecta* Chace, 1969 associated exclusively with the diadematid echinoid *Diadema antillarum* (Philippi, 1845), which had the longest spines (Castro, 1974). In similar 12-min and 12-hr experiments providing a choice between three potential host species of echinoids,

the inachid crab *Stenorhynchus seticornis* (Herbst, 1788) associated most frequently with the longest-spined species, *D. antillarum* (Joseph *et al.*, 1998). However, along the coast of Tobago, *S. seticornis* did not prefer *D. antillarum* hosts with longer spines, occurring in denser populations, occurring nearer to each other, or occurring in deeper water (Hayes *et al.*, 1998a). Ory *et al.* (2013) demonstrated that the rhynchocinetid shrimp *Rhynchocinetes brucei* Okuno, 1994 associated more frequently with the diadematid echinoid *Diadema setosum* (Leske, 1778) than the anemone *Entacmaea quadricolor* (Leuckart in Rüppell & Leuckart, 1828), and preferred to associate with the echinoid when given a choice between the two hosts, suggesting that the sharp-spined echinoid offered greater protection than the soft-tentacled anemone.

In the Caribbean Sea, a variety of decapods associate with echinoids (Hendler *et al.*, 1995). However, the frequency of decapods associating with echinoids has been studied in only two species: the echinometrid echinoid *Echinometra lucunter* (Linnaeus, 1758) in Colombia (Schoppe & Werding, 1996; Monroy López & Solano, 2006) and *D. antillarum* in the Virgin Islands, Grenadines, Grenada, Barbados, and Tobago (Hayes *et al.*, 1998a, 2006; Hayes, 2007). In this study we provide data on the frequency of decapods associating with six species of echinoids on the island of Roatán, in the western Caribbean Sea, to test the hypothesis that decapods associate most frequently with the longest-spined species of echinoid, which is consistent with the hypothesis that ectosymbionts seek shelter among the spines of echinoids to benefit from decreased predation. We also compare variation in decapod-echinoid associations at different water depths and with other regions of the Caribbean.

■ Study Area and Methods

Study area

Roatán, one of the Bay Islands of Honduras, is situated on the Bonacca Ridge, a crest on the south edge of the deep Cayman (or Bartlett) Trough in the western Caribbean Sea. It is a small island, about 47 km long and 4 km wide, located 47 km north of the Honduran mainland between 16°25.9′ and 16°16.0′ north, and between 86°36.2′ and 86°11.4′ west. Roatán is comprised of predominantly igneous and metamorphic rocks. Uplifted fossilized reefs form limestone outcrops along the shore, which alternate with sandy beaches and mangroves. The island is surrounded by a mosaic of fringing and barrier reefs, with patch reefs in shallow lagoons. The geology of Roatán is described by McBirney & Bass (1967) and Lallemant & Gordon (1999). The marine environment is described by Wells (1988) and Keck (undated).

Methods

From 6–11 September 2015, we surveyed the association of decapods with echinoids at four sites in Roatán (Fig. 1). Snorkeling equipment was used to survey echinoids in water <5 m deep at West Bay, West End, Paya Bay, and Parrot Tree. Scuba gear was used to survey echinoids in water 5–20 m deep at three dive sites at West End. All sites contained an abundance of hard substrates including limestone rocks, dead corals, and living corals. We carefully inspected each echinoid for decapods. Because many echinoids were partially hidden within a rock or coral crevice, some small decapods may have been overlooked. We did not inspect echinoids that were mostly hidden within a crevice. An association was considered to occur when a decapod was encountered within 2.5 cm of the spines of an echinoid (Hayes, 2007). Each decapod observed (tiny species may have been overlooked) was identified in the field or photographed and subsequently identified based on Keith (1985) and Humann & DeLoach (2002). However, we did not attempt to identify hermit crabs to species because they were hidden inside small gastropod shells, requiring their collection and subsequent removal, which was prohibited by the West Bay-West End Marine Reserve (where we obtained most of our data). The number of individuals of each species associating with
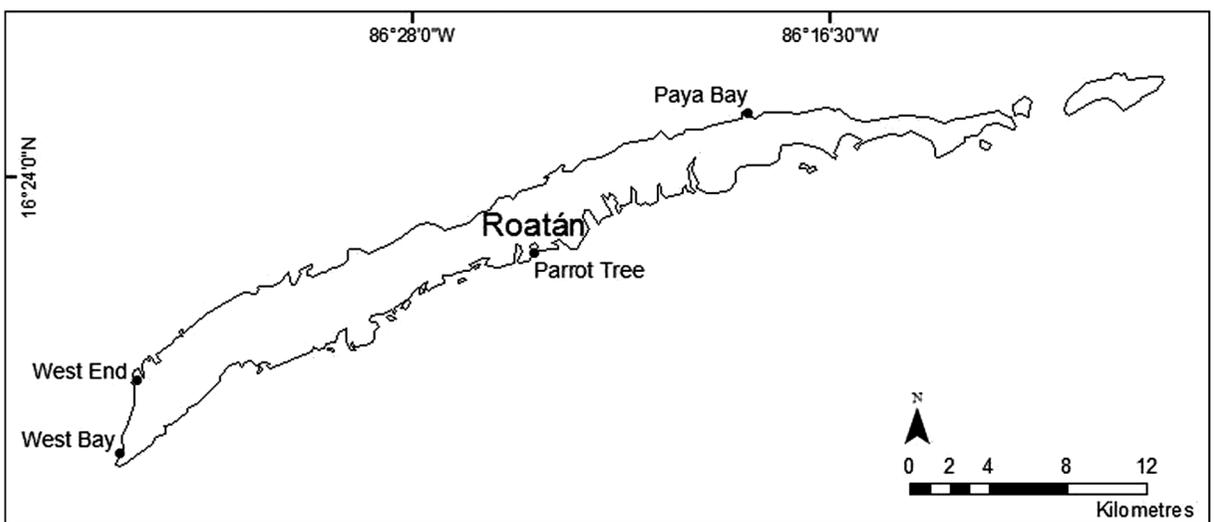

Fig. 1.   Map of Roatán, Honduras, indicating four study sites for decapods associating with echinoids.

each echinoid was recorded on underwater writing slates.

Statistical analyses

The percent frequency of echinoid hosts occupied by decapods and the mean number of decapods per echinoid host were calculated for each decapod species and for all decapods combined. Two-sample chi-square tests (χ^2 statistic; Zar, 2009) and Fisher exact probability tests (P statistic; Zar, 2009) were calculated to compare the frequencies of association among the echinoids and decapods, at two depth categories (<5 m, >5 m), and between geographic regions. To avoid an expected frequency of <1 in our chi-square analyses, we excluded the data for one rare species of echinoid in which no decapod associates were observed. Yates's corrected chi-square values were used for 2×2 contingency tables.

Taxonomy

We follow the taxonomy of Hendler *et al.* (1995) for echinoids and Felder *et al.* (2009) for decapod crustaceans.

■ Results

Echinoid morphology and habitat use

We identified six species of echinoids which differed in their morphology and habitat use (Hendler *et al.*, 1995; Humann & DeLoach, 2002). The diadematid echinoid *Diadema antillarum* has long and extremely thin spines up to about 200 mm long. We found it in rock and coral crevices with juveniles occurring more frequently in shallow water and larger adults occurring more frequently in deeper water (up to 15 m). The cidarid echinoid *Eucidaris tribuloides* (Lamarck, 1816) has medium-length spines that are thick and blunt, up to about 50 mm long. We encountered it in rock and coral crevices of water <5 m deep. The toxopneustid echinoid *Lytechinus variegatus* (Lamarck, 1816) has short spines up to about 20 mm long. We encountered it on relatively flat rocks or dead corals in water <5 m deep. The toxopneustid echinoid *Tripneustes ventricosus* (Lamarck, 1816) has short spines up to about 20 mm long. We found it on relatively flat rocks or dead corals, sometimes at the edge of seagrass beds, in water <5 m deep. The echinometrid echinoid *Echinometra lucunter* has medium-length spines up to about 30 mm long. We encountered high densities in holes that it bores in limestone along the shore, mostly in very shallow water <1 m deep, but some occurred up to 3 m deep and some were in living corals. The echinometrid echinoid *Echinometra viridis* A. Agassiz, 1863 has medium-length spines up to about 40 mm long. We encountered the highest densities in crevices of the agrariciid coral *Agaricia tenuifolia* Dana, 1848 from 2–10 m deep, but some were in limestone crevices <1 m deep.

Differences in association among echinoid species

The frequency of decapods associating with echinoids (Table 1) differed among the five species of echinoids ($\chi^2 = 378.47$, df = 4, p < 0.001; we excluded a sixth species, which was rare, to meet the assumptions of a chi-square test). Decapods associated with 10.80% of the longest-spined echinoid, *D. antillarum* (six species, 0.120 decapods per echinoid; n = 799), which was more than six times higher than any other echinoid species and accounted for 91.5% of the overall chi-square value. Decapods associated with 1.74% of *E. tribuloides* (three species, 0.017 decapods per echinoid; n = 746), which had the second longest spines, followed by 1.30% of *E. lucunter* (six species, 0.014 decapods per echinoid; n = 8349), 0.86% of *T. ventricosus* (four species, 0.009 decapods per echinoid; n = 1167), 0.23% of *E. viridis* (two species, 0.002 decapods per echinoid; n = 862), and 0% of the rarest species, *L. variegatus* (n = 12).

Table 1.   Percent of echinoids occupied by decapods (mean number of decapods per echinoid) at Roatán, Honduras. Echinoids by column (n = number of echinoids observed): Da = *Diadema antillarum*; El = *Echinometra lucunter*; Ev = *Echinometra viridis*; Et = *Eucidaris tribuloides*; Lv = *Lytechinus variegatus*; Tv = *Tripneustes ventricosus*. Decapods by row: Hc = unidentified hermit crab; Mv = *Mithrax verrucosus*; Pa = *Panulirus argus*; Pg = *Percnon gibbesi*; Pd = *Plagusia depressa*; Sh = *Stenopus hispidus*; Ss = *Stenorhynchus seticornis*.

	Da	El[a]	Ev	Et	Lv	Tv
n	799	8349	862	746	12	1167
Hc	1.13 (0.014)	0.37 (0.004)	0.12 (0.001)	1.47 (0.015)	—	0.60 (0.006)
Mv	—	0.01 (0.0001)	—	—	—	—
Pa	0.38 (0.004)	—	—	—	—	—
Pg	5.01 (0.054)	0.80 (0.009)	0.12 (0.001)	—	—	0.09 (0.0009)
Pd	0.13 (0.001)	0.08 (0.0008)	—	—	—	0.09 (0.0009)
Sh	1.13 (0.016)	—	—	0.13 (0.001)	—	0.09 (0.0009)
Ss	3.00 (0.031)	0.02 (0.0002)	—	0.13 (0.001)	—	—

[a] An unidentified small, gray decapod (possibly *Pitho* sp.) associated with 0.04% of *E. lucunter* (0.0004 per urchin)

Differences in association among decapod species

We observed 239 decapods of at least eight species associating with echinoids. The decapods differed significantly in their frequency of association with echinoids ($\chi^2 = 361.45$, df = 7, P < 0.001; Table 1). The plagusiid crab *Percnon gibbesi* (H. Milne Edwards, 1853) was the most common associate of echinoids, comprising 48.5% of the decapods observed. It associated with four species of echinoids and occurred most frequently with the longest-spined species, *D. antillarum* ($\chi^2 = 379.07$, df = 5, p < 0.001; Table 1), usually alone (93.6%) but sometimes with a second individual (6.4%). We very rarely observed it apart from echinoids. Unidentified hermit crabs (Paguridae) of an unknown number of species accounted for 27.2% of the decapods. They associated with five species of echinoids and occurred most frequently with *E. lucunter* (Table 1), but the data for this and the remaining species were insufficient for statistical tests of the frequency of association with echinoid species. Usually they were alone (90%) but sometimes a second was present (10%). We often observed them apart from echinoids. The inachid crab *Stenorhynchus seticornis* (Herbst, 1788) comprised 11.7% of the decapods. It associated with three species of echinoids and occurred most fre-

quently with *D. antillarum* (Table 1), nearly always alone (96.3%) and rarely with a second individual (3.7%). We rarely observed it apart from echinoids. The stenopid shrimp *Stenopus hispidus* Olivier, 1811 represented 6.3% of the decapods. It associated with three species of echinoids and occurred most frequently with *D. antillarum* (Table 1), either alone (63.6%) or with a companion (36.4%). We often observed it apart from echinoids. The plagusiid crab *Plagusia depressa* (Fabricius, 1775) comprised 3.3% of the decapods. It associated with three species of echinoids and occurred most frequently with *E. lucunter* (Table 1), but one shuttled back and forth between a *D. antillarum* and a *T. ventricosus*, and it was always alone. We often observed it apart from echinoids. The panulirid lobster *Panulirus argus* Latreille, 1804 represented 1.3% of the decapods. Three juveniles associated with *D. antillarum* (Table 1), always alone. We often saw adults, none of which associated with echinoids, but we rarely saw a juvenile apart from an echinoid. An unidentified small, gray decapod (possibly *Pitho* sp.) accounted for 1.3% of the decapods, associating only with *E. lucunter* (Table 1) and always alone. We never observed any apart from an echinoid, but it is easily overlooked. One mithracid crab *Mithrax verrucosus* H. Milne Edwards, 1832, comprising

0.4% of the decapods, associated with an *E. lucunter* (Table 1). We did not observe any apart from echinoids. Two species associated with an echinoid on only one occasion: an unidentified hermit crab and a *P. gibbesi* associating with an *E. lucunter*.

Differences in association by water depth

The frequency of decapods associating with *D. antillarum* did not differ between water <5 m deep (10.3%, n = 687) and water >5 m deep (13.4%, n = 112; $\chi^2 = 0.65$, df = 1, p = 0.42). However, the crab *P. gibbesi* associated with *D. antillarum* more frequently in water <5 m deep (5.8%) than in water >5 m deep, where it was not observed (0%; $\chi^2 = 5.70$, df = 1, p = 0.017). In contrast, the crab *S. seticornis*, which was the only decapod associating with echinoids >5 m deep, associated more frequently with *D. antillarum* in water >5 m deep (13.4%) than in water <5 m deep (1.3%; Fisher exact p <0.001). We encountered only one other echinoid species, *E. viridis*, in water >5 m deep, but no decapods associated with the dozen echinoids observed.

Differences between sites

In water <5 m deep, decapods associated with *D. antillarum* more frequently at West End (11.70%, n = 581) than at nearby West Bay (2.44%, n = 82; $\chi^2 = 6.53$, df = 1, p = 0.02), and decapods associated more frequently with *E. lucunter* at West End (1.53%, n = 5364) than at distant Paya Bay (0.83%, n = 2278; $\chi^2 = 5.40$, df = 1, P = 0.02). The frequency of decapods associating with echinoids was too low to permit statistical comparisons between other sites for these two species and between sites for other species.

■ Discussion

Ecology of decapod-echinoid associations

None of the decapod species observed in this study associates exclusively with echinoids or

is specialized for associating with echinoids (Williams, 1984; Keith, 1985; Hendler *et al.*, 1995). However, *P. gibbesi* associates almost exclusively with *E. lucunter* (e.g., Schmalfuss, 1976; Humann & DeLoach, 2002). Several species, including hermit crabs, *S. seticornis*, *S. hispidus*, and *P. argus*, often associate with *D. antillarum* in the eastern Caribbean (Hayes *et al.*, 2006; Hayes, 2007). Juvenile *P. argus* in the Virgin Islands have been observed associating with *D. antillarum* as they move across seagrass beds and quickly return to them when removed and released several m away (Davis, 1971). Although crustaceans often appear to associate intentionally with echinoids, some of the associations we observed may have been incidental rather than intentional.

Decapods associated with the longest-spined species, *D. antillarum*, at a rate more than six times higher than that of any other echinoid species, providing strong evidence that the decapods seek shelter among the spines of echinoids to benefit from decreased predation. Our results are consistent with controlled experiments demonstrating that the shrimp *T. neglecta* and the crab *S. seticornis* consistently prefer to associate with the longest-spined echinoid, *D. antillarum*, when given a choice among several echinoid species (Castro, 1974; Joseph *et al.*, 1998). However, test and spine fragments of small *D. antillarum* have been reported in the gut of the spiny lobster *P. argus* (Randall *et al.*, 1964), suggesting that the association of adult *P. argus* with echinoids, which has been reported in the Virgin Islands (Hayes, 2007), may represent a predatory rather than a defensive relationship. It remains unknown whether the echinoids benefit from the decapods. Echinoids may potentially benefit from decapods cleaning their tests or spines, which has been reported in the apogonid fish *Siphamia versicolor* (Smith & Radcliffe in Radcliffe, 1912) (Eibl-Eibesfeldt, 1961). The decapod-echinoid relationship documented in this study is best regarded as a facultative asso-

ciation rather than an obligatory commensalism (Hayes, 2007).

How decapods locate echinoids and assess their value for protection from predators remains unknown, although visual cues are probably the most important. Experiments with echinoid models revealed that the palaemonid shrimp *Tuleariocaris zanzibarica* Bruce, 1967 uses visual cues to find *Diadema setosum* (Leske, 1778) hosts, preferring dark rather than pale spines, vertical rather than horizontal spines, and dense spines rather than sparse spines (Fricke & Hentschel, 1971). Further experiments revealed that the endoparasitic larva of the pilumnid crab *Echinoecus pentagonus* (A. Milne Edwards, 1879) use both visual and chemical cues to locate echinoid hosts (Castro, 1978). Acoustic sounds generated by foraging echinoids may also help guide decapods to echinoids (Radford *et al.*, 2008, 2010).

New records of association

We recorded nine new records of association (13 if unidentified hermit crabs are included) between decapods and echinoids. At least ten species of decapods have been reported associating with *D. antillarum*, including *Mithraculus sculptus* (Lamarck, 1818), *P. argus*, *P. gibbesi*, *Periclemenes* sp., *Petrolisthes galathinus* (Bosc, 1802), *Stegopontonia* sp., *S. hispidus*, *S. seticornis*, *Tuleariocaris neglecta*, and an unidentified hermit crab (Randall *et al.*, 1964; Chace, 1969; Davis, 1971; Castro, 1974; Gooding, 1974; Schmalfuss, 1976; Criales, 1984; Hayes *et al.*, 1998; Wirtz, 2004; Hayes, 2007). Our study adds *P. depressa* as an associate.

The only species of decapod reported to associate with *E. tribuloides* is *S. seticornis* (Hayes *et al.*, 1998b). Our study adds *S. hispidus* and an unidentified hermit crab as associates.

The only species of decapod reported to associate with *L. variegatus* is *Gnathophylloides mineri* Schmitt, 1933 (Lewis, 1956). We did not find any decapods associating with *L. variegatus*, although our sample was very small.

Two species of decapods have been recorded associating with *T. ventricosus*, including *G. mineri* and *M. sculptus* (Lewis, 1956; Criales, 1984; Patton *et al.*, 1985; Hayes, 2007; Wirtz *et al.*, 2009). We added *P. gibbesi*, *P. depressa*, *S. hispidus*, and an unidentified hermit crab as associates.

Five species of decapods have been reported associating with *E. lucunter*, including *Clastotoechus vanderhorsti* (Schmitt, 1924), *Gnathophyllum ascensione* Manning & Chace, 1990, *P. gibbesi*, *Teleophrys pococki* Rathbun, 1924, and *T. neglecta* (Manning & Chase, 1990) (Schoppe, 1991; Schoppe & Werding, 1996; Hayes *et al.*, 1998b; Monroy López & Solano, 2006; Giribet & Lemer, 2014). Our study adds *M. verrucosus*, *P. depressa*, *S. seticornis*, and an unidentified hermit crab as associates.

No species of decapods have been reported associating with *E. viridis*. Our study adds *P. gibbesi* and an unidentified hermit crab as associates.

Geographic variation of association

Given the heterogeneity of coastal habitats on any given island, local variation in the frequency of decapods associating with echinoids can be expected (Hayes *et al.*, 2006; Hayes, 2007). Substantial regional variation has been documented in the frequency of decapods associating with *D. antillarum* in shallow water (<5 m deep) of the Caribbean Sea. The frequency of association on Roatán (10.3% of echinoids, 0.12 decapods per echinoid, n = 687) was slightly but significantly higher than in the Virgin Islands, where Hayes (2007) reported that 6.4% of *D. antillarum* (n = 1800) hosted decapods with an average of 0.09 individuals per echinoid ($\chi^2 = 10.63$, df = 1, P = 0.001). However, the frequency of association on Roatán was nearly three times lower than in islands of the southeastern Caribbean (Grena-

dines, Grenada, Barbados, and Tobago), where Hayes *et al.* (2006) reported that 30.1% of *D. antillarum* (*n* = 991) hosted decapods with an average of 0.49 individuals per echinoid (χ^2 = 90.98, df = 1, P < 0.001).

The proportions of decapod species associating with *D. antillarum* in shallow water (< 5 m deep) were similar among the three regions of the Caribbean Sea, with four species consistently ranking among the most frequent decapods. In all three regions *P. gibbesi* was the most common decapod associating with *D. antillarum*, comprising 56.3% of the decapods (n = 80) in Roatán, 48.8% in the Virgin Islands (n = 164; Hayes, 2007), and 79.1% in the Southeastern Caribbean (n = 487; Hayes *et al.*, 2006). Unidentified hermit crabs represented 13.8% of the decapods in Roatán, 30.5% in the Virgin Islands, and 8.2% in the southeastern Caribbean; *S. seticornis* accounted for 12.7% in Roatán, 11.0% in the Virgin Islands, and 7.0% in the southeastern Caribbean; and *S. hispidus* comprised 16.3% in Roatán, 5.5% in the Virgin Islands, and 0% in the southeastern Caribbean.

Substantial regional variation also occurs in the frequency of decapods associating with *E. lucunter*. In separate studies along the coast of Colombia, Schoppe and Werding (1996) reported that *C. vanderhorsti* associated with 20.4% of *E. lucunter* (n = 820) and Monroy López & Solano (2006) reported that *C. vanderhorsti* associated with 60.5% and *T. pococki* associated with 3.5% of *E. lucunter* (n = 2587). Neither *C. vanderhorsti* nor *T. pococki* has been recorded from Roatán (Keith, 1985), where we recorded decapods of six species associating with only 1.3% of *E. lucunter* (n = 8349; Table 1).

The environmental factors responsible for local, regional, and temporal variation in the frequency of decapods associating with echinoids, which may include either or both abiotic and biotic factors, remain unknown. Hayes *et al.* (2006) and Hayes (2007) suggested that geo-graphic and temporal variation in the frequency of decapods associating with *D. antillarum* in the Caribbean Sea may be affected by regional differences in the population growth rate of *D. antillarum* following the 1983 mass mortality event (see review by Lessios, 2015).

■ Literature Cited

Britayev, T. A., Bratova, O. A., & Dgebuadze, P. Y., 2013. Symbiotic assemblage associated with the tropical sea urchin, *Salmacis bicolor* (Echinoidea: Temnopleuridae) in the An Thoi archipelago, Vietnam. Symbiosis, 61: 155–161.

Bruce, A. J., 1976. Shrimps and prawns of coral reefs, with special reference to commensalism. In: O. A. Jones, & R. Endean (eds.), Biology and Geology of Coral Reefs. Vol. 3. Biology 2. Academic Press, New York, pp. 37–94.

Bruce, A. J., 1982. The shrimps associated with Indo-West Pacific echinoderms, with the description of a new species in the genus *Periclimenes* Costa, 1844 (Crustacea: Pontoniinae). Australian Museum Memoir, 16: 191–216.

Campos, E., de Campos, A. R., & de León-González, J. A., 2009. Diversity and ecological remarks of ectocommensals and ectopar-

asites (Annelida, Crustacea, Mollusca) of echinoids (Echinoidea: Mellitidae) in the Sea of Cortez, Mexico. Parasitology Research, 105: 479–487.

Carpenter, R. C., 1997. Invertebrate predators and grazers. In: A. Birkeland (ed.), Life and Death of Coral Reefs. Chapman and Hall, London, pp. 198–229.

Castro, P., 1974. A new host and notes on the behavior of *Tuleariocaris neglecta* Chace, 1969 (Decapoda, Palaemonidae, Pontoniinae), a symbiont of diadematid sea urchins. Crustaceana, 26: 318–320.

Castro, P., 1978. Settlement and habitat selection in the larvae of *Echinoecus pentagonus* (A. Milne Edwards), a brachyuran crab symbiotic with sea urchins. Journal of Experimental Marine Biology and Ecology, 34: 259–270.

Chace, F. A. Jr., 1969. A new genus and five new species of shrimps (Decapoda, Palaemonidae, Pontoniinae) from the western Atlantic. Crustaceana, 16: 251–272.

Clark, A. M., 1976. Echinoderms of coral reefs. In: O. A. Jones, & R. Endean (eds.), Biology and Geology of Coral Reefs. Vol. 3. Biology 2. Academic Press, New York, pp. 95–123.

Comely, C. A., & Ansell, A. D., 1988. Invertebrate associates of the sea urchin, *Echinus esculentus* L., from the Scottish west coast. Ophelia, 28: 111–137.

Coppard, S. E., & Campbell, A. C., 2004. Organisms associated with diadematid echinoids in Fiji. In: T. Heinzeiller, & J. H. Nebelsick (eds.). Echinoderms: München. Taylor & Francis, London, pp. 171–176.

Criales, M. M., 1984. Shrimps associated with coelenterates, echinoderms, and molluscs in the Santa Marta region, Colombia. Journal of Crustacean Biology, 4: 307–317.

Davis, G. E., 1971. Aggregations of spiny sea urchins, *Diadema antillarum*, as shelter for young spiny lobsters, *Panulirus argus*. Transactions of the American Fisheries Society, 100: 586–587.

Eibl-Eibesfeldt, I., 1961. Eine Symbiose zwischen Fischen (*Siphamia versicolor*) und Seei-

geln. Zeitschrift für Tierpsychologie, 18: 56–59.

Felder, D. L., Álvarez, F., Goy, J. W., & Lemaitre, R., 2009. Decapoda (Crustacea) of the Gulf of Mexico, with comments on the Amphionidacea. In: D. L. Felder, & D. K. Camp (eds.), Gulf of Mexico—Origins, Waters, and Biota. Vol. 1. Biodiversity. Texas A&M University Press, College Station, TX, pp. 1019–1104.

Fricke, H. W., 1970. Ein mimetisches Kollektiv— Beobachtungen an Fischschwärmen, die Seeigel nachahmen. Marine Biology, 5: 307–314.

Fricke, H. W., & Hentschel, M., 1971. Die Garnelen-Seeigel-Partnerschaft—eine Untersuchung der optischen Orientierung der Garnele. Zeitschrift für Tierpsychologie, 28: 453–462.

Giribet, G., & Lemer, S., 2014. On the occurrence of *Tuleariocaris neglecta* Chace, 1969 (Decapoda, Palaemonidae, Pontoniinae) on *Echinometra lucunter* (Linnaeus, 1758) (Echinodermata, Echinoidea, Echinometridae) in the archipelago of Bocas del Toro, Panama. Crustaceana, 87: 634–638.

Glynn, P. W., & Enochs, I. C., 2011. Invertebrates and their roles in coral reef ecosystems. In: Z. Dubinsky, & N. Stambler (eds.), Coral reefs: an Ecosystem in Transition. Springer, Berlin, pp. 273–325.

Gooding, R. U., 1974. Animals associated with the sea urchin, *Diadema antillarum*. In: T. J. Bright & L. H. Pequegnat (eds.), Biota of the West Flower Garden Bank. Gulf Publishing, Houston, pp. 333–336.

Gould, A. L., Harii, S., & Dunlap, P. V., 2014. Host preference, site fidelity, and homing behavior of the symbiotically luminous cardinalfish, *Siphamia tubifer* (Perciformes: Apogonidae). Marine Biology, 161: 2897–2907.

Hayes, F. E., 2007. Decapod crustaceans associating with the sea urchin *Diadema antillarum* in the Virgin Islands. Nauplius, 15: 81–85.

Hayes, F. E., Joseph, V. L., Gurley, H. S., &

Wong, B. Y. Y., 1998a. Selection by two de-capod crabs (*Percnon gibbesi* and *Stenorhynchus seticornis*) associating with an urchin (*Diadema antillarum*) at Tobago, West Indies. Bulletin of Marine Science, 63: 241–247.

Hayes, F. E., Joseph, V. L., Gurley, H. S., & Wong, B. Y. Y., 2006. Geographic variation in the association of decapod crabs with the sea urchin *Diadema antillarum* in the southeastern Caribbean Sea. Nauplius, 14: 31–35.

Hayes, F. E., Joseph, V. L., & Trimm, N. A. Jr., 1998b. New records and levels of association for decapod crabs and sea urchins in Tobago, West Indies. Caribbean Marine Studies, 6: 37–38.

Hendler, G., Miller, J. E., Pawson, D. L., & Kier, P. M., 1995. Sea stars, sea urchins, and allies: echinoderms of Florida and the Caribbean. Smithsonian Institution Press, Washington DC.

Hétérier, V., De Ridder, C., David, B., & Rigaud, T., 2004. Comparative biodiversity of ecto-symbionts in two Antarctic cidarid echinoids, *Ctenocidaris spinosa* and *Rhynchocidaris triplopora*. In: T. Heinzeller, & J. H. Nebelsick (eds.), Echinoderms: München. Taylor & Francis, London, pp. 201–205.

Hopkins, T. S., Thompson, L. E., Walker, J. M., & Davis, M., 2004. A study of epibiont distribution on the spines of the cidaroid sea urchin, *Eucidaris tribuloides* (Lamarck, 1816) from the shallow shelf of the eastern Gulf of Mexico. In: T. Heinzeller, & J. H. Nebelsick (eds.), Echinoderms: München. Taylor & Francis, London, pp. 207–211.

Humann, P., & DeLoach, N., 2002. Reef creature identification: Florida, Caribbean, Bahamas. New World Publications, Jacksonville, FL.

Joseph, V. L., Hayes, F. E., & Trimm, N. A. Jr., 1998. Interspecific selection of three potential urchin host species by the arrow crab *Stenorhynchus seticornis* (Crustacea, Decapoda, Brachyura). Caribbean Marine Studies, 6: 31–34.

Keck, J., undated. Instructor's guide: planning a field course. Roatán Institute for Marine Sciences, Roatán.

Keith, D. E., 1985. Shallow-water and terrestrial brachyuran crabs of Roatán and the Swan Islands, Honduras. Sarsia, 70: 251–278.

Lallemant, H. G., & Gordon, M., 1999. Deformation history of Roatán Island: implications for the origin of the Tela Basin (Honduras). In: P. Mann (ed.), Caribbean Basins. Sedimentary Basins of the World. Vol 4. Elsevier, Amsterdam, pp. 197–218.

Lessios, H. H., 2015. The great *Diadema antillarum* die-off: 30 years later. Annual Review of Marine Science, 8: 267–283.

Lewis, J. B., 1956. The occurrence of the macruran *Gnathophylloides minerii* Schmitt on the spines of the edible sea-urchin *Tripneustes esculentus* Leske in Barbados. Bulletin of Marine Science, 6: 288–291.

Magnus, D. B. E., 1967. Ecological and ethological studies and experiments on the echinoderms of the Red Sea. Studies in Tropical Oceanography, 5: 635–664.

Manning, R. B., & Chace, F. A. Jr., 1990. Decapod and stomatopod crustaceans from Ascension Island, south Atlantic Ocean. Smithsonian Contributions to Zoology, 503: 1–91.

McBirney, A., & Bass, M., 1967. Geology of Bay Islands, Gulf of Honduras. In: McBimey A (ed) Tectonic Relationships of Northern Central America and the Western Caribbean—the Bonacca Expedition. American Association of Petroleum Geologists Memoir, 11: 229–243.

Monroy López, M., & Solano, D. O., 2006. Estado poblacional de *Echinometra lucunter* (Echinoida: Echinometridae) y su fauna acompañante en el litoral rocoso del Caribe Colombiano. Revista de Biología Tropical, 53: 291–297.

Ory, N. C., Dudgeon, D., & Thiel, M. 2013. Host-use patterns and factors influencing the choice between anemone and urchin hosts by a caridean shrimp. Journal of Experimental Marine Biology and Ecology, 449: 85–92.

Patton, W. K., Patton, R. J., & Barnes, A., 1985. On the biology of *Gnathophylloides mineri*, a shrimp inhabiting the sea urchin *Tripneustes ventricosus*. Journal of Crustacean Biology, 5: 616–626.

Radford, C. A., Jeffs, A. G., Tindle, C. T., & Montgomery, J. C., 2008. Resonating sea urchin skeletons create coastal choruses. Marine Ecology Progress Series, 362: 37–43.

Radford, C. A., Stanley, J. A., Tindle, C. T., Montgomery, J. C., & Jeffs, A. G., 2010. Localised coastal habitats have distinct underwater sound signatures. Marine Ecology Progress Series, 401: 21–29.

Randall, J. E., Schroeder, R. E., & Starck, W. A. II., 1964. Notes on the biology of the echinoid *Diadema antillarum*. Caribbean Journal of Science, 4: 421–433.

Ross, D. M., 1983. Symbiotic relations. In: F. J. Vernberg, & W. B. Vernberg (eds), The Biology of Crustacea. Vol. 7. Behavior and Ecology. Academic Press, New York, pp. 163–212.

Schmalfuss, H., 1976. Ökologish-funktionsmorphologische Untersuchungen an karibischen Krabben (Decapoda, Brachyura) I. *Percnon gibbesi* (H. Milne-Edwards, 1837) (Grapsidae, Plagusiinae). Studies on Neotropical Fauna and Environment, 11: 211–222.

Schoppe, S., 1991. *Echinometra lucunter* (Linnaeus) (Echinoidea, Echinometridae) als wirt einer komplexen lebensgemeinschaft im Karibischen Meer. Helgoländer Meeresuntersuchungen, 45: 373–379.

Schoppe, S., & Werding B., 1996. The boreholes of the sea urchin genus *Echinometra* (Echinodermata: Echinoidea: Echinometridae) as a microhabitat in tropical South America. Marine Ecology, 17: 181–186.

Strasburg, D. W., 1966. Observations on the ecology of four apogonid fishes. Pacific Science, 20: 338–341.

Tamura, R., 1982. Experimental observations on the association between the cardinalfish (*Siphamia versicolor*) and the sea urchin (*Diadema setosum*). Galaxea, 1: 1–10.

Wells, S. M. (ed), 1988. Coral Reefs of the World. Vol. 1. Atlantic and Eastern Pacific. United Nations Environment Programme and International Union for Conservation of Nature and Natural Resources, Cambridge, UK. 373 pp.

Williams, A. B., 1984. Shrimps, Lobsters and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington DC. 550 pp.

Wirtz, P., 2004. Four amphi-Atlantic shrimps new for São Tomé and Príncipe (eastern central Atlantic). Arquipélago—Life and Marine Sciences, 21A:83–85.

Wirtz, P., De Melo, G., & De Grave, S., 2009. Symbioses of decapod crustaceans along the coast of Espírito Santo, Brazil. Marine Biodiversity Records, 2 e162:1–9.

Zar, J. H., 2009. Biostatistical Analysis, 5th edn. Pearson Prentice Hall, Upper Saddle River, NJ. 756 pp.

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