Geographic variation in the association of decapod crabs with the sea urchin *Diadema antillarum* in the southeastern Caribbean Sea

Floyd E. Hayes; Joseph V. L.; Gurley H. S. and Brian Y. Y. Wong

(FEH, VLJ, HSG, BYYW) Department of Biology, Caribbean Union College, P.O. Box 175, Port of Spain, Trinidad and Tobago, West Indies.
(FEH) Department of Life Sciences, University of the West Indies, St. Augustine, Trinidad and Tobago, West Indies.
(FEH) Current address: Department of Biology, Pacific Union College, 1 Angwin Ave., Angwin, CA 94508, USA.
E-mail: floyd_hayes@yahoo.com
(VLJ) Quarry Hill, Liberta Village, Antigua and Barbuda, West Indies. E-mail: vjosephlib@yahoo.com
(HSG) Department of Biological Sciences, Western Michigan University, 1903 W. Michigan Ave., Kalamazoo, MI 49008-5410, USA. E-mail: gordon.gurley@wmich.edu
(BYYW) Department of Biology, Pacific Union College, 1 Angwin Ave., Angwin, CA 94508, USA. E-mail: bwong@puc.edu

Abstract

Geographic variation in the degree of association of decapod (brachyuran and anomuran) crabs with the sea urchin *Diadema antillarum* was investigated in fringing coral reefs (< 5 m deep) of Bequia, Mayreau, Grenada, Barbados and Tobago in the southeastern Caribbean Sea. Of 991 *D. antillarum* urchins inspected, 298 (30.07%) hosted decapod crabs with an average of 0.49 crabs per urchin. The frequency of crabs associating with urchins varied geographically, being highest in Bequia (56.68%) and Grenada (40.74%), and lowest in Barbados (6.73% and 5.63% at two sites) and Mayreau (13.33%). Of 487 crabs observed, *Percnon gibbesi* was the most common species (79.05% of all crabs) followed by unidentified (possibly *Pagurus* spp.) hermit crabs (8.21%), *Stenorhynchus seticornis* (6.98%), and unidentified greyish (5.75%) and reddish (0.82%) crabs (possibly *Mithraculus coryphe* and *M. forceps,* respectively). The causes of geographic as well as temporal variation in the association of crabs with urchins remain obscure. However, the rarity of crabs in Barbados might be attributable to the frequent use of motorized water craft. Long-term temporal trends in the association of crabs with urchins may be linked with large-scale population dynamics of *D. antillarum.*

Key words: Caribbean Sea, associates, Decapod crabs, *Diadema antillarum,* geographic variation, *Mithraculus* spp., *Pagurus* spp., *Percnon gibbesi, Stenorhynchus seticornis.*

Introduction

Although crustaceans form symbiotic relationships with a variety of echinoderm hosts (e.g., Ross 1983; Williams, 1984; Hendler *et al.,* 1995), the ecological relationships of most symbioses remain poorly studied. In the Caribbean Sea, the spines of the long-spined urchin *Diadema antillarum* (Philippi, 1845) have been reported to provide refuge for a variety of facultative associates, including an anemone, a flatworm, a copepod, a mysid shrimp, the young of many fish species, and a variety of decapod (brachyuran and anomuran) crustaceans (Randall *et al.,* 1964; Chace 1969; Clifton *et al.,* 1970; Davis 1971; Castro 1974; Gooding 1974; Serafy 1979; Criales 1984; Hayes *et al.,* 1998a, b). At least one species, a decapod crab (*Stenorhynchus seticornis*), has been demonstrated to prefer associating with *D. antillarum* more than with other species of urchins, presumably because its longer, mildly toxic spines provide more protection from potential predators than the shorter, nontoxic spines of other urchins (Joseph *et al.,* 1998).

Given the variable environments in which these organisms occur, the degree of association between facultative associates and their urchin hosts may be expected to vary in both space and time. In this paper we document geographic variation in the degree of association of decapod crabs with *D. antillarum* in the southeastern Caribbean Sea, and discuss the potential causes and implications of variation.

Study Areas and Methods

The association of crabs with *D. antillarum* was studied at the following sites and dates in the southeastern Caribbean Sea (from north to south, east to west): Lower Bay, Bequia, Grenadines, 23 December 2001; Saline Bay, Mayreau, Grenadines, 27 December 2001; Folkestone Underwater Park, Barbados, 18 July 2000; Paynes Bay, Barbados, 19 July 2000; Mourne Rouge Bay, Grenada, 31 July 2000; Mount Irvine, Tobago, 22 and 24 March 1995 and repeated on 7 August 2002; Arnos Vale, Tobago, 24 March 1995; Bloody Bay, Tobago, 5 September 1996; and Charlotteville, Tobago, 23 March 1995 and repeated on 5 August 2002. Each site was located on the leeward side of the island and was characterized by a moderate growth of fringing coral reefs on a rocky coastal platform. The coastal marine environment and coral reefs of these sites are described in further detail by Wells (1988) and Agard and Gobin (2000).

With the use of a stick, each urchin was probed underneath to facilitate examination for associating crabs. Each crab observed (some may have been overlooked) was either identified or described based on Colin (1978), Sefton and Webster (1986), and Humann (1992) and the number of crabs of each species at each urchin was recorded on an underwater writing slate. A few crabs found nearby, but not associated with urchins, were later collected and identified by Rafael Lamaitre. All urchins were accessed with standard snorkeling equipment in shallow water < 5 m deep.

The percent frequency of urchin hosts occupied by crabs and the mean number of crab individuals per urchin host were calculated. Statistical comparisons among sites (data pooled for different years in Tobago) and between years (two sites on Tobago only) were computed using two-sample chi-square tests (χ^2 statistic; Zar 1984) based on frequency data. Because the number of crabs per urchin at each site was not normally distributed and the number of tied ranks were excessive in nonparametric tests comparing abundance, the results of such tests are not presented here. All statistical analyses were computed with Statistix 3.1 software (Anonymous 1990).

Results

Of 991 *D. antillarum* urchins inspected during this study, 298 (30.07%) hosted decapod crabs with an average of 0.49 crabs per urchin. The frequency of crabs associating with urchins varied geographically ($\chi^2 = 147.4$, df = 8, $P < 0.001$), being highest in Bequia (56.68%) and Grenada (40.74%), and lowest in Barbados (6.73% and 5.63% at two sites) and Mayreau (13.33%; see Table I).

The urchin crab *Percnon gibbesi* (Milne-Edwards, 1837) was the most common species, comprising 79.05% of the 487 associate crabs observed. It associated with 22.70% of the urchins with an average of 0.38 crabs per urchin. Its frequency of association varied geographically ($\chi^2 = 235.5$, df = 8, $P < 0.001$), being highest in Bequia where up to eight crabs associated with a single urchin (exceeding previous high of four; Hayes *et al.,* 1998b), and lowest in Barbados (Table I). Its frequency of occurrence did not vary significantly between sites in Barbados ($\chi^2 = 0.00$, df = 1, $P = 1.00$) or in Tobago ($\chi^2 = 7.57$, df = 3, $P = 0.06$; Table I). At the latter island it associated with a higher proportion of urchins in Charlotteville in 2002 than in 1995 ($\chi^2 = 11.98$, df = 1, $P < 0.001$), but did not differ in its frequency of association at Mount Irvine between 1995 and 2002 ($\chi^2 = 3.30$, df = 1, $P = 0.07$; Table I).

Unidentified hermit crabs (infraorder Anomura), probably representing *Pagurus* spp. (*P. marshi* and *P.* cf. *brevidactylus* were collected in western Tobago), accounted for 8.21% of the associate crabs. Hermit crabs associated with 2.02% of the urchins with an average of 0.04 crabs per urchin. Although hermit crabs did not associate with urchins in the Grenadine Islands of Bequia and Mayreau, their frequency of association did

Table I. Percent frequency of urchin (*Diadema antillarum*) hosts occupied by crabs and mean number of crab individuals per urchin host in the southeastern Caribbean Sea.

	Stenorhynchus seticornis		*Percnon gibbesi*		*Mithraculus* spp.		Hermit crab spp.		No crab	
Locality	%	x̄	%	x̄	%	x̄	%	x̄	%	n
Grenadines										
Bequia	0.81	0.01	55.87	1.12	–	–	–	–	43.32	247
Mayreau	3.33	0.03	10.00	0.10	–	–	–	–	86.67	30
Grenada										
Morne Rouge Bay	7.41	0.07	30.86	0.40	–	–	–	–	59.26	81
Barbados										
Folkestone Underwater Park	–	–	2.89	0.03	–	–	3.85	0.06	93.27	104
Paynes Bay	–	–	2.99	0.03	–	–	2.82	0.04	94.37	71
Tobago										
Mount Irvine (1995)	6.36	0.06	11.82	0.14	1.81	0.02	–	–	80.00	110
Mount Irvine (2002)	11.6	0.12	6.20	0.06	13.18	0.14	3.88	0.11	69.77	129
Arnos Vale	–	–	19.35	0.26	6.45	0.06	–	–	74.19	31
Bloody Bay	–	–	21.43	0.29	–	–	–	–	78.57	42
Charlotteville (1995)	2.63	0.03	2.63	0.04	–	–	–	–	94.74	76
Charlotteville (2002)	1.43	0.01	22.86	0.26	12.86	0.14	8.57	0.26	60.00	70

not vary geographically ($\chi^2 = 13.70$, df = 8, $P = 0.09$; Table I). Their frequency of occurrence did not vary significantly between sites in Barbados ($\chi^2 = 0.00$, df = 1, $P = 1.00$) or in Tobago ($\chi^2 = 3.79$, df = 3, $P = 0.28$; Table I). In Tobago, hermit crabs were significantly more common in 2002 than in 1995 in Charlotteville ($\chi^2 = 4.49$, df = 1, $P = 0.03$) but not in Mount Irvine ($\chi^2 = 2.67$, df = 1, $P = 0.10$; Table I). However, they may have been overlooked during the 1995 and 1996 surveys in Tobago, where the occurrence of hermit crabs with *D. antillarum* was first detected in 1997 (Hayes *et al.,* 1998b). Up to five hermit crabs associated with a single urchin at both Mount Irvine and Charlotteville, Tobago.

The arrow crab *Stenorhynchus seticornis* (Herbst, 1788) accounted for 6.98% of the crabs. It associated with 3.43% of the urchins with an average of 0.03 crabs per urchin. Its frequency of association with urchins varied significantly ($\chi^2 = 41.97$, df = 8, $P < 0.001$); it occurred most frequently in Grenada and in Mount Irvine, Tobago, and did not associate with urchins in Barbados (Table I). Its frequency of occurrence varied significantly among sites in Tobago ($\chi^2 = 13.99$, df = 3, $P = 0.003$), where it was most common at Mount Irvine and absent at Arnos Vale and Bloody Bay (Table I). In Tobago, its frequency of occurrence did not vary between 1995 and 2002 at either Mount Irvine ($\chi^2 = 1.39$, df = 1, $P = 0.24$) or Charlotteville ($\chi^2 = 0.00$, df = 1, $P = 1.00$; Table I). In this study no more than one *S. seticornis* was ever found with an urchin.

Unidentified crabs found associating with *D. antillarum* included 28 greyish individuals, accounting for 5.75% of all crabs, at Mount Irvine and Charlotteville, Tobago, in 2002, and four reddish individuals (0.82% of all crabs) at Mount Irvine and Arnos Vale, Tobago, in 1995. These crabs probably represented *Mithraculus* spp. (similar appearing grayish and reddish crabs collected in western Tobago were later identified as *M. coryphe* and *M. forceps,* respectively). The greyish individuals associated with 2.83% of the urchins with an average of 0.03 crabs per urchin. The reddish individuals associated with only 0.02% of the urchins with an average of < 0.01 crabs per urchin. Although the frequency of occurrence of greyish crabs did not vary significantly among sites in Tobago ($\chi^2 = 5.38$, df = 3, $P = 0.15$), the frequency of occurrence of reddish crabs did vary ($\chi^2 = 12.80$, df = 3, $P = 0.005$; Table I). The greyish crabs were more common in 2002 than in 1995 at both Charlotteville ($\chi^2 = 4.65$, df = 1, $P = 0.03$) and Mount Irvine, Tobago ($\chi^2 = 13.68$, df = 1, $P < 0.001$; Table I), where they were unlikely to have been overlooked in 1995 and 1996. The reddish crabs were equally rare in 1995 and 2002 at Mount Irvine, Tobago ($\chi^2 = 0.68$, df = 1, $P = 0.41$; Table I). No more than one reddish and two greyish crabs, respectively, associated with a single urchin.

Discussion

Geographic variation in the frequency of decapod crabs associating with *D. antillarum* is undoubtedly attributable to environmental differences among the sites, such as the availability of food, abundance of predators, extent of alternative sites to hide from predators, physical properties of water (e.g., turbidity), etc. However, given the absence of comparative environmental data, it remains impossible to determine which factors contribute to such variation. A possible explanation for the low frequency of crabs associating with urchins in the Barbados sites is the frequent use of motorized water craft, which were more numerous in Barbados than in any other site. Further studies should be conducted to assess the impact of motorized water craft on the association of decapod crabs with *D. antillarum* in shallow coastal waters.

Temporal variation in the frequency of decapod crabs associating with *D. antillarum* may well be seasonal as well as diel, as biotic or physical conditions change. However, data documenting temporal variation, such as in this study, are scarce and difficult to interpret. For example, in June and July 1997, Hayes *et al.* (1998b) estimated that up to 30% of *D. antillarum* at Mount Irvine, Tobago, hosted *S. seticornis,* and reported observing up to three individuals associating with a single urchin; obviously *S. seticornis* was more common at this site in June and July 1997 than when sampling for this study was conducted in March 1995 and August 2002. Obviously an understanding of temporal trends in crab-urchin associations will be premised upon frequent sampling of crabs and urchins simultaneously with monitoring the biotic and physical properties of the environment.

Finally, long-term temporal trends in the association of crabs with urchins may well be linked to the large-scale population dynamics of *D. antillarum*. In 1983, an unknown epizootic pathogen swept across the Caribbean from west to east, wiping out up to 97% of *D. antillarum* in some areas (Lessios *et al.,* 1984). The impacts of such an epidemic on populations of decapod crabs that routinely associate with *D. antillarum,* especially *P. gibbesi* which usually associates with *D. antillarum* (Williams 1984), remain unknown. The greater frequency of association of *P. gibbesi* with *D. antillarum* in Charlotteville, Tobago, in 2002 than in 1995 suggests that populations of *P. gibbesi* may have been increasing, but no parallel increase was found at Mount Irvine, Tobago. The potential implications of another epidemic underscore the need for monitoring not only urchin populations but their associate crab populations as well.

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