

This article was downloaded by: [University of Bath]

On: 13 February 2014, At: 10:16

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

Ectosymbionts of the non-indigenous Asian shore crab, *Hemigrapsus sanguineus* (Decapoda: Varunidae), in the western north Atlantic, and a search for its parasites

John J. Mcdermott ^a

^a Department of Biology , Franklin and Marshall College , Lancaster, PA

Published online: 03 Dec 2010.

To cite this article: John J. Mcdermott (2007) Ectosymbionts of the non-indigenous Asian shore crab, *Hemigrapsus sanguineus* (Decapoda: Varunidae), in the western north Atlantic, and a search for its parasites, *Journal of Natural History*, 41:37-40, 2379-2396, DOI: [10.1080/00222930701630691](https://doi.org/10.1080/00222930701630691)

To link to this article: <http://dx.doi.org/10.1080/00222930701630691>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms &

Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

Ectosymbionts of the non-indigenous Asian shore crab, *Hemigrapsus sanguineus* (Decapoda: Varunidae), in the western north Atlantic, and a search for its parasites

JOHN J. MCDERMOTT

Department of Biology, Franklin and Marshall College, Lancaster, PA, USA

(Accepted 30 July 2007)

Abstract

Over 560 Asian shore crabs, *Hemigrapsus sanguineus*, collected mainly in the spring of 2005 and 2006 from rocky intertidal locations in southern New Jersey, were examined for epibionts. Small numbers of the sympatric green crab, *Carcinus maenas*, and the Atlantic mud crab, *Panopeus herbstii*, were examined for epifauna to compare with *H. sanguineus*. Blue mussel spat, *Mytilus edulis*, and the encrusting, cheilostome bryozoan, *Conopeum tenuissimum*, were the dominant ectosymbionts of the shore crab, with prevalences of 22.2 and 32.1%, respectively; ranges of intensity were 1–146 spat/crab and 1–31 colonies/crab. Both species are incidental symbionts. Larger crabs had higher prevalences and intensities of *C. tenuissimum* colonies, and these colonies displayed a distinct pattern of attachment to the carapace which seemed to be related to crab morphology and habitat. Much less common was the encrusting, ctenostome bryozoan *Alcyonidium albescens*, a facultative symbiont species with a prevalence of 3.4%. Other epibionts were the encrusting, cheilostome *Membranipora tenuis*, the tubicolous polychaetes *Hydroides dianthus*, *Sabellaria vulgaris*, and *Spirorbis* sp., the barnacles *Balanus improvisus* and *Semibalanus balanoides*, and unidentified thecate hydroids, all incidental symbionts with prevalences from 0.2 to 3.2%. The total number of known ectosymbionts of *H. sanguineus*, including additional species found previously in the USA and the western Pacific, is 13. *Carcinus maenas* and *P. herbstii* share some of the same symbionts. Rhizocephalan externae were not observed in any of the crab species used in this study, nor were gill parasites or internal parasites found among 248 specimens of *H. sanguineus*.

Keywords: Asian shore crab, Bryozoa, *Carcinus*, Decapoda, ectosymbionts, *Hemigrapsus sanguineus*, *Mytilus*, New Jersey, *Panopeus*, Varunidae

Introduction

Hemigrapsus sanguineus (de Haan, 1853) was found for the first time in waters of eastern USA along the coast of New Jersey in 1988 (Williams and McDermott 1990; McDermott 1991). Since then it has been reported from Maine to North Carolina (McDermott 1995, 1998a, 1998b, 1999, 2000; Lohrer and Whitlatch 1997; Lohrer 2001; Seeley and McDonald 2003). The biology and life history of *H. sanguineus* in its native range in the

northern west Pacific Ocean is known from the studies of Kurata (1962), Fukui (1988), Hwang et al. (1993) and others, along with more recent research on its ecology and interspecific interactions with sympatric brachyurans in Japan (Lohrer et al. 2000a, 2000b). Following the introduction of *H. sanguineus* into the northern west Atlantic Ocean, many aspects of its natural history have been studied, e.g. reproduction (McDermott 1998b), larval biology (Saigusa and Kawagoye 1997; Epifanio et al. 1998; Kopin et al. 2001; Park et al. 2004); feeding biology and predation (McDermott 1999; Brousseau et al. 2000, 2001; Tyrrell and Harris 2000; Ledesma and O'Connor 2001; Lohrer and Whitlatch 2002a; Bordeau and O'Connor 2003; Brousseau and Baglivo 2005); ecology (Lohrer and Whitlatch 1997, 2002a, 2002b; McDermott 1998a, 2000; Gerard et al. 1999; Jensen et al. 2002). The worldwide distribution of *Hemigrapsus sanguineus* now includes European waters after being introduced to the region in or before 1998 (Breton et al. 2002; Udekem d'Acoz and Faassee 2002).

McDermott (1998a) recorded the presence of the following ectosymbionts on *Hemigrapsus sanguineus* collected at primarily intertidal locations along the coast of New Jersey from 1988 to 1997: the bivalve mollusc *Mytilus edulis* Linnaeus, 1758; the barnacles *Balanus improvisus* Darwin, 1854, *Chelonibia patula* Ranzani, 1818, and *Semibalanus balanoides* (Linnaeus, 1767); the encrusting bryozoans *Alcyonidium albescens* Winston and Key, 1999 (Ctenostomata) and *Conopeum tenuissimum* Canu, 1908 (Cheilostomata). Most of the crabs with symbionts were collected during the spring months (March to June). Crabs collected in southern New Jersey during the late winter and spring months of 1997 and 1998 were cursorily examined for ectosymbionts, revealing again the presence of *Mytilus* and the two species of bryozoans (J. J. McDermott, unpublished data).

No internal symbionts were observed in the 1988–1997 study of *H. sanguineus*. This negative parasite load may be partially responsible for the crab's phenomenal success in the rocky intertidal communities in the western north Atlantic (Torchin et al. 2001, 2002, 2003). In the native range of *H. sanguineus* in the western Pacific Ocean, however, it may be infected with the metacercariae of the digenetic trematode *Maritrema setoensis* Bridgman, 1971 (Bridgman 1971) and the rhizocephalan barnacle *Polyascus polygena* (Lützen and Takahashi, 1997) (Takahashi and Matsuura 1994; Yamaguchi et al. 1994; Lützen and Takahashi 1997; Takahashi et al. 1997; Yamaguchi and Aratake 1997; Takahashi and Lützen 1998; Glenner et al. 2003). Interestingly, Isaeva et al. (2001) found two bivalve molluscs, *Mytilus trossulus* Gould, 1850 and *Hiatella arctica* (Linnaeus, 1767), attached to the abdomen or sternum of some crabs with externae of *P. polygena*, but never in unsacculinized crabs.

Although brachyurans are well-known hosts for a variety of ectosymbionts (e.g. Lewis 1976; Paul and Paul 1986; Abello et al. 1990; Abello and Corbera 1996; Becker 1996; Key et al. 1996, 1997, 1999; Dick et al. 1998; McGaw 2006; Savoie et al. 2007), no studies dealing with the ectosymbionts of *Hemigrapsus sanguineus*, except for McDermott (1998a), or other members of the genus appear in the literature. The purpose of the present research was to determine the species diversity, prevalence, and intensity of epibionts on this introduced intertidal crab and their possible preferences for certain locations on the crab's exoskeleton. A subsample of crabs was examined for internal parasites. Comparisons are made also with the epibionts found on two sympatric brachyurans, *Carcinus maenas* (Linnaeus, 1758) and *Panopeus herbstii* H. Milne Edwards, 1834.

Materials and methods

Crabs were collected in 2005 and 2006 from rocky intertidal locations at Townsends Inlet and Hereford Inlet (Great Channel Bridge), Cape May County, New Jersey, the two main

sites of previous biological studies of *H. sanguineus* (McDermott 1998a, 1998b, 1999). At these locations monthly water temperature and salinity ranged from approximately 1 to 28°C and 29 to 32‰, respectively; lowest temperatures were from December to February and the highest were from July to September (McDermott 1998a). Most of the collections were made in the spring when low water temperatures minimized moulting and consequent shedding of organisms attached to the exoskeleton; one other collection was made in the fall of each year. Crabs were preserved in 10% seawater formalin and later transferred to 70% ethyl alcohol. All crabs were sexed and their carapace widths (CW) were measured with vernier calipers to 0.1 mm; all crab measurements, unless otherwise noted, refer to this parameter. Crabs were examined dorsally and ventrally for the presence of epibionts, including the cephalothorax, sternum, abdomen (dorsal and ventral), and the five pairs of pereopods (chelipeds and walking legs). Small symbionts (e.g. zooids of bryozoan colony, minute barnacles) were measured to 0.01 mm with a calibrated ocular micrometer. Symbionts were identified to the lowest taxon. The terms prevalence and intensity, as defined by Bush et al. (1997), were used to describe the populations of symbionts on *H. sanguineus*. Two other sympatric species of brachyurans, *Carcinus maenas* (Portunidae) and *Panopeus herbstii* (Xanthidae), were collected and their epifauna compared with that of the Asian crabs. Crabs used for photography were dried at room temperature in order to produce better contrast between attached symbionts, such as calcareous bryozoans, and the crab exoskeleton.

All specimens of *H. sanguineus* and the sympatric brachyurans collected during this two-year study were examined for the externae of rhizocephalans, and about half of the Asian crabs were examined for macroscopic parasites in the gill chambers and the organs of the haemocoel.

Results

Prevalence and diversity of symbionts

Table I lists the numbers of male and female Asian shore crabs collected on each date and their combined mean CW and range. The male/female sex ratio was 1.06. In the spring of 2005 (late March to early May) only four species of symbionts were found among 120 crabs examined (Table II). The 75% prevalence of *Mytilus edulis* spat in March coincided with the usual, large, recruitment of young mussels on rocks and shells in the immediate area. Mussel intensity on the crabs was 4.7 ± 5.1 mussels/crab ($n=75$, range 1–16). Mean length of 65 mussels removed from crabs was 1.00 ± 0.23 mm (0.39–1.60 mm), which corresponded to the 1.10 ± 0.34 mm (0.74–2.62 mm; $n=52$) length of mussels in the surrounding habitat. Prevalence of mussel spat decreased to 24.3% in April (intensity 0.7 ± 1.9 , $n=50$) and 11.8% in May (intensity 0.2 ± 0.6 , $n=8$). Mean length of 41 mussels attached to crabs in April was 1.34 ± 0.55 mm (0.7–3.5 mm); the two largest mussels, 2.8 and 3.3 mm, were from under the abdomen of a female crab. Half of the mussels in the May collection were still recent recruits, i.e. <1.0 mm long. A slightly gaping abdomen of an 18.0 mm male was invaded by three mussels. All parts of the exoskeleton of crabs, but mainly the bases of the walking legs (incurrent areas to the branchial chambers) and sockets of the antennae and eyes, were sites for mussel attachment. No young *Mytilus* spat occurred among the 54 crabs examined in October 2005.

The encrusting, calcareous bryozoan *Conopeum tenuissimum* was not found in March but was prominent in April and May (prevalence 17.3%, 18 of 104 crabs) (Table II). This

Table I. Mean carapace widths, ranges, and sex ratios of male (M) and female (F) Asian shore crabs, *Hemigrapsus sanguineus*, collected in New Jersey in 2005 and 2006 and examined for ectosymbionts.

Date	No. of crabs		Mean CW \pm SD; range (mm)
	Total	M/F	
2005			
30 March	16	7/9	16.2 \pm 2.7; 11.7–21.1
22/23 April	70	44/26	16.5 \pm 4.9; 8.9–30.8
6 May	34	24/10	16.0 \pm 4.9; 7.5–28.0
17 October	54	23/31	20.7 \pm 4.5; 10.4–35.8
2006			
5 March	9	3/6	9.2 \pm 2.6; 5.4–13.5
29 March	214	102/112	16.7 \pm 5.5; 5.3–29.4
26 April	67	35/32	17.4 \pm 6.8; 6.3–30.1
8/9 June	54	30/24	14.9 \pm 5.6; 5.7–30.1
7 September	46	22/24	17.8 \pm 5.5; 6.3–28.2
Total	564	290/274	

bryozoan was the most common and conspicuous symbiont in the entire study, its colonies being attached to most regions of the crab's exoskeleton (Figure 1A). No colonies were present in October. The distribution and intensity of *C. tenuissimum* on *H. sanguineus* will be presented below.

Whereas there was heavy recruitment of *Semibalanus balanoides* intertidally in March 2005 (J. J. McDermott, unpublished data), only six of 120 crabs (5.0%) collected that spring harboured individuals of this species. Fifteen barnacles were recorded; mean carino-rostral length of 13 individuals was 2.45 ± 1.08 mm (1.21–4.42 mm); the other two barnacles had just metamorphosed, and were less than 1.0 mm. Barnacles attached locally to shells and rocks had a mean length of 1.21 ± 0.34 mm (0.82–2.21 mm, $n=60$), and

Table II. Prevalence of ectosymbionts on *Hemigrapsus sanguineus* (males and females) in intertidal collections from two adjacent locations in southern New Jersey during the years 2005 and 2006.

Date	Total no. of crabs	No. of crabs with symbionts								
		<i>Me</i>	<i>Ct</i>	<i>Aa</i>	<i>Mt</i>	B	H	<i>Hd</i>	<i>Sv</i>	S
2005										
30 March	16	12								
22/23 April	70	17	13			5			1	
6 May	34	4	5			1				
17 October	54				10	1 ^a	1	1	5	11
Total	174	33	18	0	10	7	1	1	6	11
2006										
5 March	9		1							
29 March	214	81	119	12			3			6
26 April	67	10	37	7			4			1
8/9 June	54	1	6				1			
7 September	46				2		3			
Total	390	92	163	19	2	0	11	0	0	7
Grand total	564	125	181	19	12	7	12	1	6	18

Me, *Mytilus edulis*; *Ct*, *Conopeum tenuissimum*; *Aa*, *Alcyonidium albescens*; *Mt*, *Membranipora tenuis*; B, barnacles, ^a*Balanus improvisus*, all others *Semibalanus balanoides*; H, hydroids; *Hd*, *Hydroides dianthus*; *Sv*, *Sabellaria vulgaris*; S, *Spirorbis* sp.

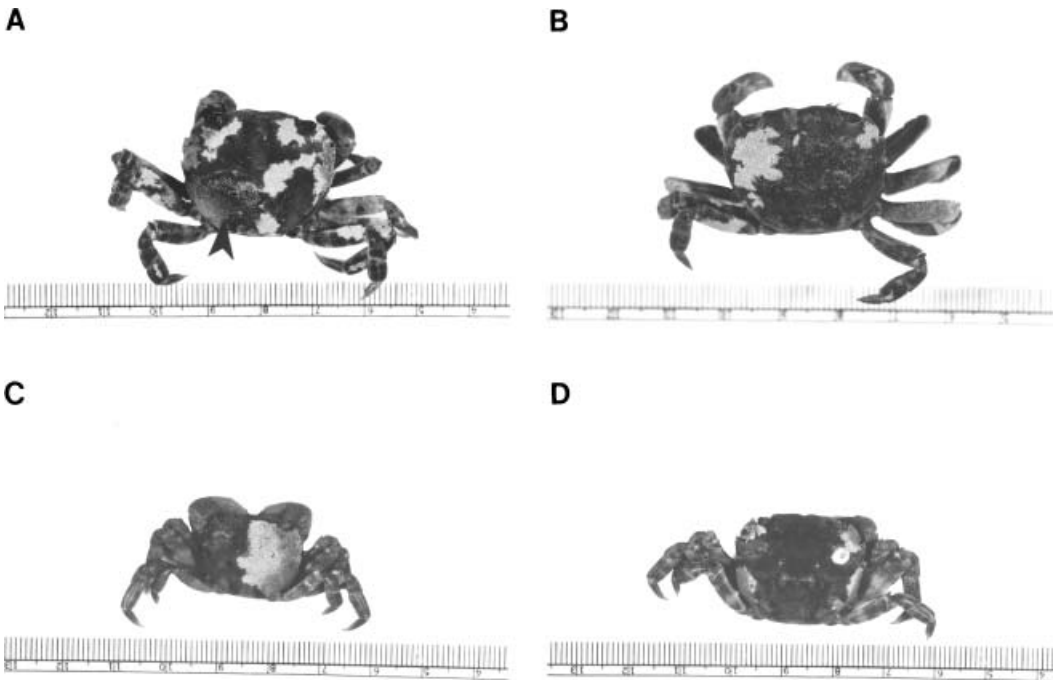


Figure 1. Dorsal views of *Hemigrapsus sanguineus* with colonies of *Conopeum tenuissimum* and other ectosymbionts, collected intertidally in New Jersey. (A) Female (27.4 mm CW; first left walking leg missing) with several colonies on the carapace and on the pereopods. Arrow shows a large colony of *Alcyonidium albescens* covering the left posterior quadrant of the carapace. (B) Female (26.1 mm CW; same crab with mussels under abdomen, Figure 2) showing *Conopeum tenuissimum* colony spanning the left hepatic-branchial region of the carapace, a small medial colony and a colony in the right hepatic region, plus numerous colonies on the pereopods. (C) Male (18.5 mm CW) with a single colony of *Conopeum tenuissimum* covering more than half of the carapace, with some smaller colonies on the pereopods. (D) Female (24.9 mm CW; left cheliped missing) with four colonies of *Conopeum tenuissimum* on the carapace, two in hepatic and two in branchial areas. Barnacle is *Semibalanus balanoides*.

cyprid larvae were seen undergoing metamorphosis or searching for favourable sites on the substrata.

In October of 2005, 18.5% of the crabs harboured recently settled colonies of the encrusting, calcareous bryozoan *Membranipora tenuis* Desor, 1848. In addition, an unidentified thecate hydroid and three tubicolous polychaetes, *Hydroides dianthus* (Verrill, 1873), *Sabellaria vulgaris* (Verrill, 1873), and *Spirorbis* sp., were noted. Whereas spirorbids were found on the carapace, subhepatic area, and pereopods of 11 crabs (20.4%), a total of only 20 young worms was recorded (most were <1 mm diameter; maximum 1.5 mm); one crab had six worms. Recently metamorphosed specimens of *Sabellaria* were present on five crabs, one of which (35.8 mm male) had 35 worms on the carapace, subhepatic surface, chelipeds, and walking legs.

The diversity of species on *Hemigrapsus sanguineus* in the spring of 2006 (early March to early June) was about the same as in 2005 (Table II). Attached mussels were common during late March and April 2006 (Table II), again coinciding with recent local recruitment. Prevalence in March was 2.5 times that in April and only one crab had mussels in June. There was no significant difference in the prevalence of *M. edulis* between males and females in the 29 March collection ($\chi^2=0.012$, $P>0.05$, $df=1$; 40 of 102 males

and 41 of 112 females). Mean length of mussels taken from crabs in March was 0.90 ± 0.39 mm (0.40–2.68 mm, $n=94$). Of the 731 mussels removed from all crabs, 85% were from the March collection. The mean intensities of mussels attached to crabs in March and April were 8.0 ± 18.1 (644 mussels on 81 crabs, range 1–146) and 8.5 ± 9.6 (85 mussels on 10 crabs, range 1–26), respectively. The crab with 146 mussels was a 30.3 mm male collected in March; these minute mussels had no apparent effect on the condition of the crab. Mussels attached not only to the bases of the walking legs and depressions such as the sockets occupied by antennae and eyes, but also to the edges or under the female abdomen and often attached to the pleopods. One female crab (26.1 mm) had an abnormally gaping abdomen due to the presence of several relatively large mussels whose byssus threads entwined and immobilized many of the pleopods (mean mussel length = 2.2 ± 1.8 mm, range 0.6–9.5 mm, $n=28$) (Figure 2). Stumps of autotomized pereopods were often sites for spat attachment.

Prevalence of *Conopeum tenuissimum* colonies in March and April was nearly equal (55.6 and 55.2%, respectively), but was greatly diminished in June. The gelatinous, encrusting bryozoan *Alcyonidium albescens* was present on 6.8% of the 281 crabs collected in March and April (Table II), occurring on the carapace, subbranchial surfaces, pereopod segments, and stumps of autotomized pereopods (Figure 1A). The intensity of the *A. albescens* was 1.6 ± 1.3 , range 1–6. Adjacent colonies of *Conopeum* were partially overgrown by four of 29 *Alcyonidium* colonies.

Membranipora tenuis was found only on crabs in October 2005 and in September 2006 (4.4%) (Table II). Unidentified thecate hydroids (6.5%) and *Spirorbis* sp. (6.5%) were also found.

Only 2.0% of the 344 crabs examined from the spring collections of 2006 had spirorbids attached. Eleven worm tubes were 0.86 ± 0.26 mm in diameter (0.60–1.15 mm). These worms were found on pereopods and in subhepatic areas. Unidentified thecate hydroids (short, dead stalks) were present on 2.3% of these crabs.

Host distribution and intensity of *Conopeum tenuissimum*

This bryozoan was found on *Hemigrapsus sanguineus* in all spring collections except that of 30 March 2005 (Table II). Colonies were more frequent on larger (i.e. older) crabs (Figure 3A). There were no significant differences in the prevalence of *Conopeum tenuissimum* between male and female crabs in the total spring collection of 2006



Figure 2. Ventral view of *Hemigrapsus sanguineus* female (26.1 mm CW; same crab as Figure 1B) with a gaping abdomen caused by the accumulation of young blue mussels *Mytilus edulis* attached to the pleopods (white arrow shows largest mussel, 9.5 mm long). Colonies of the calcareous bryozoan *Conopeum tenuissimum* present on many of the pereopods. Black arrow points to the polychaete *Spirorbis* sp.

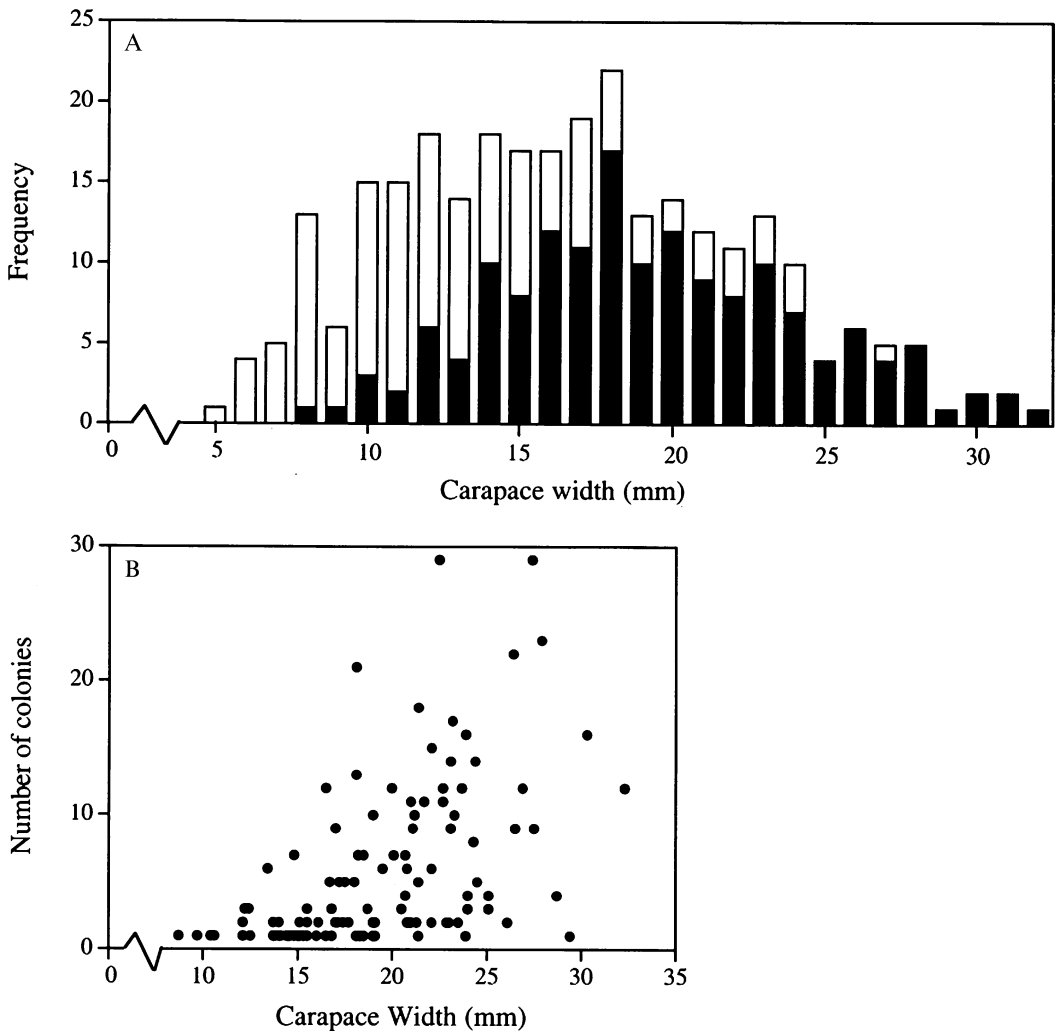


Figure 3. (A) Frequency of *Conopeum tenuissimum* versus CW (1.0 mm classes) of *Hemigrapsus sanguineus* collected March and April 2006 at Townsends Inlet, New Jersey. Open bars, total crabs examined ($n=281$); shaded bars, crabs with bryozoans ($n=156$). (B) Number of colonies of *Conopeum tenuissimum* ($n=638$) on specimens of *Hemigrapsus sanguineus* ($n=119$; 1.0 mm CW classes) collected March 2006 at Townsends Inlet, New Jersey. Regression equation: y (no. colonies) = $-7.518 + 0.681x$ (CW); $r^2 = 0.281$, $p \leq 0.0001$, $n = 119$.

($\chi^2 = 0.74$, $P > 0.05$, $df = 1$; 76 of 170 males and 86 of 174 females) or the smaller collections of 2005 ($\chi^2 = 3.6$, $P > 0.05$, $df = 1$; 13 of 68 males and 5 of 36 females).

On 29 March 2006 the mean intensity of *Conopeum tenuissimum* was 5.6 ± 6.0 colonies/crab (660 colonies on 119 crabs, range 1–29 colonies). The 29 colonies on a 27.4 mm female were distributed on the pereopods (21), carapace (7), and abdomen (1), and the host also harboured five colonies of *Alcyonidium albescens* on the pereopods and one on the carapace. Intensity of *C. tenuissimum* in crabs on 29 March showed a significant positive correlation with crab CW (Figure 3B). Mean intensity in April was 7.8 ± 9.4 colonies/crab (290 colonies on 37 crabs, range 1–31 colonies). The relationship between intensity and CW was also significant for crabs in the April collection (regression equation:

$y = -13.328 + 0.989x$; $r^2 = 0.377$, $P \leq 0.0001$, $n = 37$). There was a significantly greater intensity of *Conopeum* colonies (in March 2006) on the carapace of female crabs compared to males ($\chi^2 = 25.2$, $P < 0.001$, $df = 1$; 87 on 42 males and 167 on 64 females).

Location of *Conopeum tenuissimum* colonies

The dorsal carapace of *Hemigrapsus sanguineus* was the major site for attachment of colonies to the cephalothorax of crabs (Figure 1B). Many colonies that began their growth on the lateral parts of the dorsal carapace often continued development ventrally on to the subhepatic and subbranchial regions of the cephalothorax. Some subhepatic and subbranchial colonies, however, originated in these locations. *Conopeum tenuissimum* was seldom found on the sternum, abdomen, or the third maxillipeds, but chelipeds and walking legs were common sites for attachment; some colonies completely covered the individual segments of these appendages. Colonies ranged from those recently settled (1–10 zooids) to large colonies with hundreds of zooids, some covering one-half of the carapace (Figure 1C).

An analysis of the number of *Conopeum tenuissimum* colonies at different locations on the dorsal carapace of *Hemigrapsus sanguineus* showed that the colonies occurred primarily on the hepatic and branchial areas—basically at the four corners of the carapace (Table III; Figures 1D, 4). In many cases the colonies at each of these locations coalesced to produce a lateral band from the anterior to the posterior end of the carapace (Figure 1B). Colonies were relatively fewer and less developed on mid-carapace locations (i.e. frontal, protogastric, cardiac, etc.). Among the 119 crabs infested with *Conopeum tenuissimum* from the 29 March 2006 collection, there were 254 colonies on the dorsal carapace and 406 on the chelipeds and walking legs for a total of 660 (intensity = 5.6 ± 6.0). Colonies on the ventral carapace were not included in this tabulation.

Symbionts on sympatric brachyurans

Green crabs (*Carcinus maenas*) and mud crabs (*Panopeus herbstii*) were examined for ectosymbionts. Eighty-six green crabs were collected in spring and fall of 2005 and 2006

Table III. Percentages of *Conopeum tenuissimum* colonies attached to various locations on the carapace of *Hemigrapsus sanguineus* based on the occurrence of 336 colonies from 134 crabs collected 29 March 2006 and 26 April 2006 at Townsends Inlet, New Jersey.

Location on carapace	No. of colonies		Total	%
	29 March	26 April		
Frontal	16	8	24	7.1
Hepatic (left)	22	6	28	8.3
Hepatic (right)	32	12	44	13.1
Branchial (left)	70	20	90	26.8
Branchial (right)	65	20	85	25.3
Hepatic-branchial (left)	13	6	19	5.7
Hepatic-branchial (right)	9	3	12	3.6
Protogastric	6	2	8	2.4
Mesogastric	14	4	18	5.4
Cardiac	3	1	4	1.2
Intestinal	4	0	4	1.2
Total	254	82	336	100.0

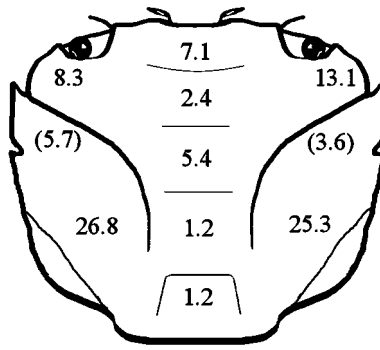


Figure 4. Percentages of colonies of *Conopeum tenuissimum* at various locations on the carapace of *Hemigrapsus sanguineus* based on 336 colonies from 134 crabs (Table III) collected 29 March 2006 and 26 April 2006 at Townsends Inlet. Anterolaterally are hepatic areas, posterolaterally are branchial areas; numbers in parentheses are for colonies that span the hepatic-branchial regions. Medially from anterior to posterior are frontal, progastric, mesogastric, cardiac, and intestinal locations.

($n=49$ and 37 , respectively); 43 were males (mean = 42.3 ± 20.8 mm, range 10.0 – 72.1 mm) and 43 were females (mean = 36.0 ± 16.7 mm, range 10.1 – 61.3 mm). Approximately half of the crabs were immature, i.e. <40 mm. Green crabs harboured many of the same symbionts observed on *H. sanguineus*. *Mytilus edulis*, *C. tenuissimum*, and *A. albescens* had the greatest prevalences, 37.2 , 31.4 and 26.7% , respectively. The intensities of *A. albescens* and *C. tenuissimum* colonies were 12.2 ± 10.2 (257 colonies on 31 crabs, range 1 – 31) and 7.5 ± 5.8 (172 colonies on 23 crabs, range 1 – 21), respectively. Intensity for *M. edulis* was not determined because not all mussels were counted; there were hundreds on some crabs. *Hydroides dianthus*, *Sabellaria vulgaris*, *Semibalanus balanoides*, and unidentified thecate hydroids had low prevalences (2.3 – 11.6%) and intensities. *Spirorbis* sp. occurred only on *H. sanguineus*, whereas the gastropod molluscs *Crepidula convexa* Say, 1822, *C. fornicata* (Linnaeus, 1758), and *Corambe obscura* (Verrill, 1870), and the bryozoans *Anguinella* sp. and a “*Triticella*-like” sp. were found only with green crabs, all of which were of low prevalence (1.2 – 3.5%) and intensity.

All surfaces of green crabs, particularly the legs, were prone to the development of *Conopeum* and *Alcyonidium* colonies, and colonies of the latter tended to overgrow those of *Conopeum*. Barnacle and polychaete larvae tended to metamorphose in the grooves of the green crab’s carapace (Figure 5A).

Two of 19 mud crabs (11 males, mean = 24.6 ± 5.1 mm, range 15.8 – 33.7 mm; eight females, mean 20.5 ± 2.3 mm, range 17.5 – 23.9 mm) collected in October 2005, and examined for ectosymbionts, had one recently settled *Sabellaria vulgaris* on their carapace. Some of the 15 mud crabs (eight males, mean = 23.0 ± 4.6 mm, range 17.9 – 27.3 mm; seven females, mean = 19.3 ± 2.2 mm, range 16.4 – 22.2) collected in the spring and fall of 2006 had the following symbionts: *Mytilus edulis*, *Alcyonidium albescens*, *Conopium tenuissimum*, and a “*Triticella*-like” species of bryozoan (Figure 5B). Colonies of the last were found on the pereopods of six crabs.

Parasites

Externae of rhizocephalans were not found on any of the crabs in this study. Two hundred and forty-eight specimens of *H. sanguineus* were examined for gill and internal parasites

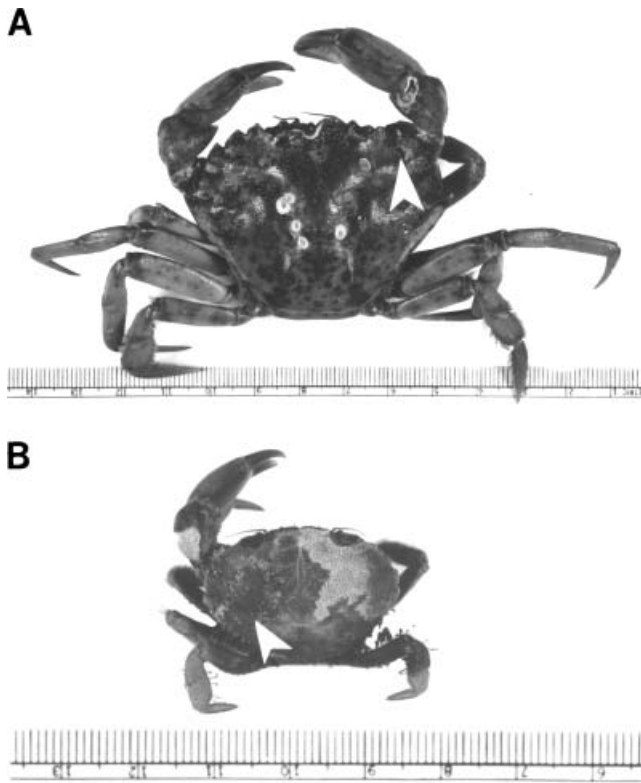


Figure 5. (A) Dorsal view of *Carcinus maenas* male (56.4 mm CW; injury to carpus of right cheliped) with five barnacles *Semibalanus balanoides* located in grooves around the mesogastric region of the carapace. Small colonies of *Conopeum tenuissimum* are scattered on the carapace. Arrow points to the opening of a *Sabellaria vulgaris* tube in the right hepatic area. (B) Dorsal view of *Panopeus herbstii* female (23.5 mm CW; right cheliped and two left walking legs missing) with large *Conopeum tenuissimum* colony on right side spanning frontal, progastric, hepatic, and branchial areas; another colony on carpus of the left cheliped. One large colony of *Alcyonidium albescens* on left side (arrow).

(136 males, 112 females (11 ovigerous); mean CW = 14.4 ± 4.3 mm, range = 5.3–28.2 mm). No bopyrid or entoniscid isopods, nemertean egg-predators (*Carcinonemertes* spp.), or metacercarial cysts of digenetic trematodes were present. A 23.0 mm male with carapace damage and gill damage on the left side harboured two *Mytilus* spat in its gill chamber.

Discussion

Diversity, prevalence, and intensity

In the present study, 10 species of ectosymbionts were recorded from *Hemigrapsus sanguineus* (Table II)—a bivalve mollusc, three species of encrusting bryozoans, three species of polychaetes, two barnacles, and an unidentified hydroid(s). The occurrence of attached hydroids refers to possibly more than one species, but all were so damaged (consisting of short dead stalks) that specific identification was not possible. *Alcyonidium albescens* was listed as *A. polyoum* (Hassall, 1841) in my previous biological studies of *H. sanguineus* (McDermott 1998a), but Winston and Key (1999) determined that *A. polyoum* was of European origin, and thus created the new species *A. albescens*. Five of the 10

ectosymbionts found in the present study (*Mytilus*, *Balanus*, *Semibalanus*, *Alcyonidium*, *Conopeum*) were noted in earlier studies (McDermott 1998a; J. J. McDermott, unpublished data), but hydroids and the polychaete worms, *Hydroides*, *Sabellaria*, *Spirorbis*, were not noted previously. The barnacle *Chelonibia patula* was found only in the earlier studies; it occurred on the carapace of the largest *H. sanguineus* ever recorded, a 43.9 mm male that had likely reached terminal ecdysis (McDermott 1998a, 1999). Thus, the Asian shore crab is host to 11 species of ectosymbionts in the waters of the USA. Worldwide, with addition of the bivalves *Hiatella arctica* and *Mytilus trossulus* from the western Pacific, attached only to crabs with externae of the rhizocephalan *Polyascus polygena* (Isaeva et al. 2001), the total is 13 species. Relationships of all known ectosymbionts from *H. sanguineus* are considered incidental (see Williams and McDermott 2004), except for the crab's facultative relationship with *C. patula*, a species known to have a predilection for attaching to the exoskeletons of a variety of brachyuran crabs and horseshoe crabs (Limulidae), but also found sometimes to be free-living or on gastropods, sea snakes, and sea turtles (Key et al. 1997).

There are 13 recognized species within the genus *Hemigrapsus* (McLay and Schubart 2004; Asakura and Watanabe 2005), but ectosymbionts have been reported only from *H. sanguineus*. Epibionts have not been recorded in numerous studies of intertidal members of the Grapsoidea sympatric with *H. sanguineus* from the western Pacific (e.g. Kikuchi et al. 1981; Fukui 1988; Lohrer et al. 2000a).

Information in Table II shows clearly that *Mytilus edulis* and *Conopeum tenuissimum* were the most prevalent species among the 564 crabs examined in this two-year study (22.2 and 32.1%, respectively). *Alcyonidium albescens* had a prevalence of 3.4%, although not found in any of the 174 crabs examined in 2005. It was not surprising that the two basically free-living species of bryozoans were found on the non-indigenous *H. sanguineus*, because they have been recorded frequently from other benthic brachyurans and horseshoe crabs [*Limulus polyphemus* (Linnaeus, 1758)] (Watts 1957; Key et al. 1996, 1999; J. J. McDermott, personal observations). The Asian horseshoe crab, *Tachypleus gigas* (Müller, 1819), has a high prevalence of similar, encrusting, cheilostome bryozoans (Key et al. 1996). The presence of bryozoans on the sympatric green crabs and mud crabs mentioned here emphasizes that *H. sanguineus* is not a unique arthropod host. Colonies of *Membranipora* found only in the fall collections of 2005 and 2006 were all recently settled and of low intensity. The other ectosymbiotic species (barnacles, polychaetes, and hydroids) covered only minute areas on the exoskeleton of *H. sanguineus*.

It was also not surprising that *Mytilus* spat were so prevalent on *H. sanguineus* and *C. maenas* in the spring because most other hard or soft (algae) surfaces in the intertidal zone were heavily covered with these newly attached mussels. There they remain attached and grow rapidly, unlike their relatively ephemeral existence on the exoskeleton of crabs, especially young crabs with their short intermoult periods. Bryozoans and all the other attached organisms suffer the same fate. This was the reason for collecting crabs in the spring for evaluating the ectosymbiont load, when moulting was expected to be minimal, thus preserving organisms that may have accumulated on crabs during their lower intertidal or subtidal existence during the colder months of the year. More year-round data are needed to substantiate this point, but the present information (Table II) and previous observations with large numbers of crabs suggest that the spring affords a more fruitful period for studying the crab's epibionts. The present study suggests that annual differences in the prevalence of ectosymbionts is probably due, at least in part, to the size of the existing free-living populations and the many environmental factors related to their recruitment.

Rhizocephalan barnacles are known usually to prevent moulting or prolong normal intermoult periods of infected crabs. *Hemigrapsus sanguineus* is host for the rhizocephalan *Polyascus polygenea*, originally described as *Sacculina polygenea* by Lützen and Takahashi (1997) with a later generic change to *Polyascus* by Glenner et al. (2003). Isaeva et al. (2001) found ectosymbionts only on sacculinized *H. sanguineus* collected at Vistok Bay, Sea of Japan. To date, however, externae of *P. polygenea* have not been found in crabs collected in the Atlantic Ocean in previous studies (McDermott 1998a; Torchin et al. 2001) or in the 564 crabs examined in the present study. Abello and Corbera (1996) showed that infestations with the bryozoan *Triticella flava* Dalyell, 1848 were significantly greater in *Goneplax rhomboides* (Linnaeus, 1758) infected with an unidentified parasitic barnacle. That rhizocephalan infections can be an unequivocal factor in increasing the prevalence and intensity of epibionts in *Carcinus maenas* from Danish waters was shown by Mouritsen and Jensen (2006). In >1100 crabs examined, 75% of sacculinized crabs (*Sacculina carcini* Thompson, 1836) had a variety of epibionts compared to only 29% of the uninfected animals. The normal burying response of *C. maenas* was reduced by more than half in infected crabs in the laboratory, which would make the exposed crabs more vulnerable to epibionts. Such an effect on behaviour was shown also in another portunid crab, *Charybdis longicollis* Leene, 1938, infected with the rhizocephalan *Heterosaccus dollfusi* Boschma, 1960 (Innocenti et al. 1998).

It was expected that ectosymbionts would have a greater prevalence and intensity in larger Asian crabs because of their longer intermoult intervals and possibly due to their greater size. Figure 3A, B shows this relationship to be true for the prevalence and intensity of *Conopeum tenuissimum* colonies. Such relationships have been demonstrated for the epifauna of other species of brachyurans, e.g. the deep-water portunids *Bathynectes superbus* (Costa, 1853) (Lewis 1976) and *B. piperitus* Manning and Holthuis, 1981 (Abello et al. 1990), the tanner crab *Chionocetes bairdi* Rathbun, 1924 in Alaska (Dick et al. 1998), the Cancroid crabs *Cancer gracilis* Dana, 1852, *C. magister* Dana, 1852, and *C. productus* Randall, 1839 (McGaw 2006), and the New Zealand portunid *Ovalipes catharus* White, 1843 (Miller et al. 2006). Abello and Corbera (1996), however, found that juvenile males of *Goneplax rhomboides* had lower prevalences of *Triticella flava* than mature crabs, but that there was no difference in the female population. On the other hand, in the blue crab, *Callinectes sapidus* Rathbun, 1896, Key et al. (1997, 1999) showed that *Chelonibia patula* and bryozoan epifauna were not more prevalent on older crabs. In both of these studies, however, unlike the Asian crabs examined in the present study, no juvenile crabs were used in their analyses.

How do the prevalences and intensities of ectosymbionts associated with *Hemigrapsus sanguineus* compare with those observed in other brachyurans? A variety of factors need to be considered in making interspecific comparisons. Most other brachyurans whose epibionts have been studied are strictly aquatic, whereas the Asian crab is mainly intertidal and exposed to the air for substantial periods during the tidal cycle and for considerable periods during the whole year. This difference should favour larger ectosymbiont loads in the aquatic species. *Carcinus maenas* is basically an aquatic species, but some crabs spend periods in the lower intertidal usually under the cover of rocks (often used as a refuge for moulting; personal observations). The present study showed that the prevalence and intensity of epibionts in the larger green crab were noticeably greater than in the Asian crab. *Panopeus herbstii* is aquatic, but may be found periodically in burrows in the lower rocky intertidal often covered with mud. The information presented here for *Panopeus* is inadequate for any quantitative comparison with the Asian shore crab.

Recently Miller et al. (2006) compared the epifauna on two portunid crabs from New Zealand, the non-indigenous species *Charybdis japonica* (A. Milne-Edwards, 1861) and the native *Ovalipes catharus*. Nearly 100% of the native species were infested with the obligate bryozoan epibiont *Triticella capsularis* Gordon and Wear, 1999, a species not found on the alien crab. *Charybdis japonica*, however, was host only for serpulid polychaetes and balanomorph barnacles. Substrate preferences and differences in burying behaviour of the crabs seemed to be responsible for this disparity. Whether innate differences between the two portunids are in some way responsible for susceptibility to attachment of the obligate *T. capsularis* is not known.

Although there were no significant differences in the prevalence of *Conopeum tenuissimum* between male and female Asian crabs, the intensity of this bryozoan was significantly greater in females. This difference may be related to the overall longer intermoult periods in females, associated with reproduction. Key et al. (1999) found, for an unexplained reason, that only female blue crabs harboured bryozoans. Perhaps the higher salinity water occupied by females compared to males may be involved in this difference.

Another factor to consider in determining prevalence of epibionts is the effect of the particular method of collection (e.g. trawls, baited traps, gill nets, hand collecting) on the age distribution of the host population. In some cases only mature crabs are recovered (Paul and Paul 1986; Key et al. 1997, 1999; Dick et al. 1998; McGaw 2006; Savoie et al. 2007) while others may include both immature and mature specimens (Lewis 1976; Abello et al. 1990). Lower prevalence values are expected with greater numbers of immature crabs. As in the present study, prevalence of ectosymbionts may vary seasonally, especially in relation to peak ecdysial periods when all attached epibionts are shed with exoskeletons. Crabs collected during periods of prolonged anecdysis or those species known to have a terminal ecdysis are likely to yield large prevalence and intensity values (Lewis 1976; Abello et al. 1990; Savoie et al. 2007).

It is to be understood that the prevalence and intensity values reported here for the epibionts of *Hemigrapsus sanguineus* are minimal because of missing pereopods due to autotomy. For interspecific comparisons of the diversity and prevalence of brachyuran symbionts, concentration only on the carapace and ventral aspects of crabs may yield more comparable data (Key et al. 1999).

Distribution of bryozoan colonies

Distinct distributional patterns of epibionts living on a number of brachyurans and horseshoe crabs have been reported (Abello et al. 1990; Abello and Corbera 1996; Key et al. 1997, 1999, 2000; Dick et al. 1998; Dietl et al. 2000; McGaw 2006). *Conopeum* colonies on the carapace of *Hemigrapsus sanguineus* are more frequently attached laterally, often extending to subhepatic and subbranchial locations (Figures 1B, D, 4). This crab lives mainly in narrow crevices in rocky intertidal areas where its carapace comes in contact with the overlying rocks (Fukui 1988; McDermott 1998a). Since the carapace slopes laterally, the medial regions of the carapace have greater contact with the rocks, which likely minimizes the attachment and growth of bryozoan colonies. Scratch marks on the carapace are more conspicuous medially. Bryozoan larvae that metamorphosed medially in the grooves separating the distinctive regions of the carapace usually produced only small colonies in these locations. The chelipeds and walking legs were prime sites for the attachment of the bryozoan colonies, but they were less common on the two distal segments (propodus and dactylus), which are in greater contact with the substratum than the more proximal segments.

Colonies of *Alcyonidium albescens* were less common on the dorsal carapace of *H. sanguineus*, occurring more frequently on the ventral aspects of the carapace and locomotory pereopods and chelipeds. Key et al. (1999) reported that *A. albescens* preferred settling on lateral portions of the dorsal carapace of *Callinectes sapidus*, but that colonies also attached ventrally. The tendency of *A. albescens* colonies to overgrow those of *C. tenuissimum* requires further study, but such interspecific dominance is common among encrusting species of bryozoans (Jackson 1979; McKinney and Jackson 1989).

The nudibranch *Corambe obscura* is a known predator of *Alcyonidium albescens* colonies that encrust the gastropod shells harbouring hermit crabs (McDermott 2001), colonies of *Conopeum tenuissimum* (Franz 1967; Dudley 1973), and other bryozoan species (Franz 1967). This nudibranch was found with some of the sympatric green crabs infested with *A. albescens* and *C. tenuissimum* but not with *H. sanguineus*. It seems likely, however, that the larvae of *C. obscura* may at times attach and metamorphose on shore crabs bearing these bryozoans.

What are the costs and benefits of the *Hemigrapsus sanguineus*–ectosymbiont relationships described? It is unlikely that any of the epibionts described here in any way benefit the crab host. Perhaps the bryozoan colonies might be considered to have some camouflage effect, but this would appear to be unnecessary for the survival of animals that lead a secretive existence in their rocky habitat. The ecdysis-prone exoskeleton substrate of crabs does not usually allow for the accumulation of a heavy epibiont growth that would provide a more useful disguise for avoiding predation. Older brachyurans and those in terminal anecdysis are more likely to have heavier growths of epibionts, but in most cases do not accumulate the heavy growths of symbionts seen on the appropriated shells of many hermit crabs (Stachowitsch 1980; Williams and McDermott 2004). Are there any advantages gained by the ectosymbionts of *Hemigrapsus sanguineus*? Almost all of them are basically free-living species that usually have more than ample substrates to which they may attach, compared to the relatively minute surface areas provided by the ephemeral body surface of shore crabs. However, the exoskeleton of crabs in terminal anecdysis may be a protective refuge from predators and sedimentation and provide time for the completion of their life cycles.

What are the possible adverse effects of these symbionts on *Hemigrapsus sanguineus*? It appears that only *Mytilus edulis* has the potential for producing harmful effects on this crab. Mussels attached to the underside of the abdomen of older females in anecdysis may grow sufficiently to cause gaping, entanglement of the pleopods with byssus threads, and interference with normal attachment and development of embryos (Figure 2). Although *H. sanguineus*, in the laboratory, is known to produce viable, successive broods from previously stored sperm (McDermott 1998b), normal copulation in females would be inhibited in cases of heavy mussel infestation.

Parasitism in Hemigrapsus sanguineus

The Asian shore crab has been a member of rocky intertidal communities in the northwestern Atlantic for at least 20 years (McDermott 1998a), but there is still no evidence of parasitism. As with several other introduced species of brachyurans, *H. sanguineus* remains released from its native parasite load, i.e. the rhizocephalan *Polyascus polygenea* and the trematode metacercaria *Maritrema setoensis* (Bridgman 1971; McDermott 1998a, present study; Torchin et al. 2001). *Charybdis japonica*, introduced into New Zealand from the northwestern Pacific, is without its native rhizocephalan *Heterosaccus papillosus* Boschma, 1933 (Miller et al. 2006), whereas *C. longicollis*, a Lessepsian migrant to

the eastern Mediterranean from the Red Sea, brought with it *H. dollfusi* (Galil and Lützen 1995; Innocenti et al. 1998). It remains to be seen if *H. sanguineus* in the Atlantic will ever become reassociated with its native parasites or modify its resistance to similar parasites in its new environment.

Acknowledgements

I thank Jason D. Williams, Biology Department, Hofstra University, Hempstead, NY, for reviewing a draft of the manuscript. I appreciate the taxonomic assistance of Christopher B. Boyko, American Museum of Natural History, New York, and Judith E. Winston, Virginia Museum of Natural History, Martinsville, VA. I am grateful to Alan M. Bifolck, David R. Bowne, Kirk Miller, Carroll Shearer Jr, and Mary K. Shelly, Franklin and Marshall College, for constructing graphs, reviewing the manuscript, statistical help, photography, and interlibrary loan assistance, respectively. Franklin and Marshall College continues to aid and encourage my research.

References

- Abello P, Corbera J. 1996. Epibiont bryozoans (Bryozoa, Ctenostomatida) of the crab *Goneplax rhomboides* (Brachyura, Goneplacidae) off the Ebro delta (western Mediterranean). *Miscelanea Zoologica* 19:43–52.
- Abello PR, Villanueva R, Gili JM. 1990. Epibiosis in deep sea crab populations as indicator of biological and behavioural characteristics of the host. *Journal of the Marine Biological Association of the United Kingdom* 70:687–695.
- Asakura A, Watanabe S. 2005. *Hemigrapsus takanoi*, new species, a sibling species of the common Japanese intertidal crab *H. penicillatus* (Decapoda: Brachyura: Grapsoidea). *Journal of Crustacean Biology* 25:279–292.
- Becker K. 1996. Epibionts on carapaces of some malacostracans from the Gulf of Thailand. *Journal of Crustacean Biology* 16:92–104.
- Bourdeau PE, O'Connor NJ. 2003. Predation by the nonindigenous Asian shore crab *Hemigrapsus sanguineus* on macroalgae and mollusks. *Northeastern Naturalist* 10:319–334.
- Breton G, Faasse M, Noël P, Vincent T. 2002. A new alien crab in Europe: *Hemigrapsus sanguineus* (Decapoda: Brachyura: Grapsidae). *Journal of Crustacean Biology* 22:184–189.
- Bridgman JF. 1971. The life cycle of *Maritrema setoensis* n. sp. (Trematoda: Microphallidae). *Japanese Journal of Parasitology* 20:13–23.
- Brousseau DJ, Baglivo JA. 2005. Laboratory investigations of food selection by the Asian shore crab, *Hemigrapsus sanguineus*: algal versus animal preference. *Journal of Crustacean Biology* 25:130–134.
- Brousseau DJ, Filipowicz A, Baglivo JA. 2001. Laboratory investigations of the effects of predation sex and size on prey selection by the Asian shore crab *Hemigrapsus sanguineus*. *Journal of Experimental Marine Biology and Ecology* 262:199–210.
- Brousseau DJ, Korchari PG, Pflug C. 2000. Food preference studies of the Asiatic shore crab (*Hemigrapsus sanguineus*) from western Long Island Sound. In: Pederson J, editor. *Marine bioinvasions*. Cambridge, MA: MIT Sea Grant College Program. p 200–207.
- Bush AO, Lafferty KD, Lotz JM, Shostak AW. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* 83:575–583.
- Dick MH, Donaldson WE, Vining IW. 1998. Epibionts of the tanner crab *Chionoecetes bairdi* in the region of Kodiak Island, Alaska. *Journal of Crustacean Biology* 18:519–528.
- Dietl J, Nascimento C, Alexander R. 2000. Influence of ambient flow around the horseshoe crab *Limulus polyphemus* on the distribution and orientation of selected epizoans. *Estuaries* 23:509–520.
- Dudley JE. 1973. Observations on the reproduction, early larval development, and colony astogeny of *Conopeum tenuissimum* (Canu). *Chesapeake Science* 14:270–278.
- Epifanio CE, Dittel AI, Park S, Schwalm S, Fouts A. 1998. Early life history of *Hemigrapsus sanguineus*, a non-indigenous crab in the Middle Atlantic Bight (USA). *Marine Ecology Progress Series* 170:231–238.
- Franz DR. 1967. On the taxonomy and biology of the dorid nudibranch *Doridella obscura*. *Nautilus* 80:73–79.
- Fukui Y. 1988. Comparative studies on the life history of the grapsid crabs (Crustacea, Brachyura) inhabiting intertidal cobble and boulder shores. *Publications of the Seto Marine Biological Laboratory* 33:122–162.

- Galil BS, Lützen J. 1995. Biological observations on *Heterosaccus dollfusi* Boschma (Cirripedia: Rhizocephala), a parasite of *Charybdis longicollis* Leene (Decapoda: Brachyura), a Lessepsian migrant to the Mediterranean. *Journal of Crustacean Biology* 15:659–670.
- Gerard VA, Cerrato RM, Larson AA. 1999. Potential impacts of a western Pacific grapsid crab on intertidal communities of the northwestern Atlantic Ocean. *Biological Invasions* 1:353–361.
- Glenner H, Lützen J, Takahashi T. 2003. Molecular and morphological evidence for a monophyletic clade of asexually reproducing Rhizocephala, new genus (Cirripedia). *Journal of Crustacean Biology* 23:548–557.
- Hwang SG, Lee C, Kim CM. 1993. Complete larval development of *Hemigrapsus sanguineus* (Decapoda, Brachyura, Grapsidae) reared in the laboratory. *Korean Journal of Systematic Zoology* 9:69–86.
- Innocenti G, Vannini M, Galil BS. 1998. Notes on the behavior of the portunid crab *Charybdis longicollis* Leene parasitized by the rhizocephalan *Heterosaccus dollfusi* Boschma. *Journal of Natural History* 32:1577–1585.
- Isaeva V, Kulikova V, Kasyanov I. 2001. Bivalve molluscs, *Mytilus trossulus* and *Hiatella arctica*, as facultative epibionts on the crab, *Hemigrapsus sanguineus*, infected by the rhizocephalan *Sacculina polygenea*. *Journal of the Marine Biological Association of the United Kingdom* 81:891–892.
- Jackson JBC. 1979. Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican cryptic reef environment. *Journal of Animal Ecology* 48:805–823.
- Jensen GC, McDonald PS, Armstrong DA. 2002. East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. *Marine Ecology Progress Series* 225:251–262.
- Key MM Jr, Jeffries WB, Voris HK, Yang CM. 1996. Epizoic bryozoans, horseshoe crabs, and other mobile benthic substrates. *Bulletin of Marine Science* 58:368–384.
- Key MM Jr, Jeffries WB, Voris HK, Yang CM. 2000. Bryozoan fouling pattern on the horseshoe crab *Tachypleus gigas* (Müller) from Singapore. In Herrera A, Jackson JBC, editors. *Proceedings of the 11th International Bryozoology Association Conference, 2000, Smithsonian Tropical Research Institute, Balboa, Panama*, p 265–271.
- Key MM Jr, Volpe JW, Jeffries WB, Voris HK. 1997. Barnacle fouling of the blue crab *Callinectes sapidus* at Beaufort, North Carolina. *Journal of Crustacean Biology* 17:424–439.
- Key MM, Winston JE, Volpe JW, Jeffries WB, Voris HK. 1999. Bryozoan fouling of the blue crab *Callinectes sapidus* at Beaufort, North Carolina. *Bulletin of Marine Science* 64:513–533.
- Kikuchi T, Tanaka M, Nojima S, Takahashi T. 1981. Ecological studies on the pebble crab, *Gaetice depressus* (de Haan). I. Ecological distribution of the crab and environmental conditions. Publications from the Amakusa Marine Biological Laboratory, Kyushu University, 6:23–34.
- Kopin CY, Epifanio CE, Nelson S, Stratton M. 2001. Effects of chemical cues on metamorphosis of the Asian shore crab *Hemigrapsus sanguineus*, an invasive species on the Atlantic coast of North America. *Journal of Experimental Marine Biology and Ecology* 265:141–151.
- Kurata H. 1962. Studies on the age and growth of Crustacea. *Bulletin of the Hokkaido Regional Fisheries Research Laboratory* 24:1–115.
- Ledesma ME, O'Connor NJ. 2000. Habitat and diet of the non-native crab *Hemigrapsus sanguineus* in southeastern New England. *Northeastern Naturalist* 8:63–78.
- Lewis EG. 1976. Epizoids associated with *Bathynectes superbus* (Decapoda: Portunidae). *Fishery Bulletin* 74:225–227.
- Lohrer AM. 2001. The invasion of *Hemigrapsus sanguineus* in eastern North America: a review. *Aquatic Invaders* 12:1–11.
- Lohrer AM, Fukui Y, Wada K, Whitlach RB. 2000a. Structural complexity and vertical zonation of intertidal crabs, with focus on habitat requirements of the invasive Asian shore crab, *Hemigrapsus sanguineus* (de Haan). *Journal of Experimental Marine Biology and Ecology* 244:203–217.
- Lohrer AM, Whitlach RB. 1997. Ecological studies on the recently introduced Japanese shore crab (*Hemigrapsus sanguineus*), in eastern Long Island Sound. In: Balcom NC, editor. *Proceedings of the Second Northeast Conference on nonindigenous aquatic nuisance species*. Groton: University of Connecticut. p 49–60. Connecticut Sea Grant College Program, publication nr CTSG-97-02.
- Lohrer AM, Whitlach RB. 2002a. Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. *Marine Ecology Progress Series* 227:135–144.
- Lohrer AM, Whitlach RB. 2002b. Interactions among aliens: apparent replacement of one exotic species by another in an intertidal system. *Ecology* 83:719–732.
- Lohrer AM, Whitlach RB, Wada K, Fukui Y. 2000b. Home and away: comparisons of resource utilization by a marine species in native and invaded habitats. *Biological Invasions* 2:41–57.
- Lützen J, Takahashi T. 1997. *Sacculina polygenea*, a new species of rhizocephalan (Cirripedia: Rhizocephala) from Japan, parasitic on the intertidal crab *Hemigrapsus sanguineus* (De Haan, 1935) (Decapoda: Brachyura: Grapsidae). *Crustacean Research* 26:103–108.

- McDermott JJ. 1991. A breeding population of the western Pacific crab *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae) established on the Atlantic coast of North America. *Biological Bulletin* 181:195–198.
- McDermott JJ. 1995. Geographical distribution of a western Pacific brachyuran crab, *Hemigrapsus sanguineus*, along the east coast of the United States [abstract]. Chesapeake Research Consortium Publication 149:708.
- McDermott JJ. 1998a. The western Pacific brachyuran (*Hemigrapsus sanguineus*: Grapsidae), in its new habitat along the Atlantic coast of the United States: geographic distribution and ecology. *ICES Journal of Marine Science* 55:289–298.
- McDermott JJ. 1998b. The western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic coast of the United States: reproduction. *Journal of Crustacean Biology* 18:308–316.
- McDermott JJ. 1999. The western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic coast of the United States: feeding, cheliped morphology and growth. In: Schram FR, von Vaupel Klein JC, editors. *Crustaceans and the biodiversity crisis*. Leiden: Brill. p 425–444.
- McDermott JJ. 2000. Natural history and biology of the Asian shore crab *Hemigrapsus sanguineus* in the western Atlantic: a review, with new information. In: Pederson J, editor. *Marine bioinvasions*. Cambridge (MA): MIT Sea Grant College Program. p 193–199.
- McDermott JJ, . 2001. Symbionts of the hermit crab *Pagurus longicarpus* Say, 1817 (Decapoda: Anomura): new observations from New Jersey waters and a review of all known relationships. *Proceedings of the Biological Society of Washington* 114:624–639.
- McGaw IJ. 2006. Epibionts of sympatric species of *Cancer* crabs in Barkley Sound, British Columbia. *Journal of Crustacean Biology* 26:85–93.
- McKinney FK, Jackson JBC. 1989. *Bryozoan evolution*. Boston: Unwin Hyman. 238 p.
- McLay CL, Schubart CD. 2004. On the current name for *Hemigrapsus edwardsii* (Hilgendorf, 1882) (Brachyura: Varunidae) from New Zealand. *Journal of Natural History* 38:695–704.
- Miller A, Inglis GJ, Poulin R. 2006. Comparison of the ectosymbionts and parasites of an introduced crab, *Charybdis japonica*, with sympatric and allopatric populations of a native New Zealand crab, *Ovalipes catharus* (Brachyura: Portunidae). *New Zealand Journal of Marine and Freshwater Research* 40:369–378.
- Mouritsen KN, Jensen T. 2006. The effect of *Sacculina carcini* infections on the fouling, burying behaviour and condition of the shore crab, *Carcinus maenas*. *Marine Biology Research* 2:270–275.
- Park S, Epifanio CE, Grey EK. 2004. Behavior of larval *Hemigrapsus sanguineus* (de Haan) in response to gravity and pressure. *Journal of Experimental Marine Biology and Ecology* 307:197–206.
- Paul JM, Paul AJ. 1986. Encrusting barnacles as ageable tags on Gulf of Alaska *Chionoecetes bairdi* (Decapoda). Fairbanks: University of Alaska. p 28. Alaska Sea Grant Report 86-2.
- Saigusa M, Kawagoye O. 1997. Circatidal rhythm of an intertidal crab, *Hemigrapsus sanguineus*: synchrony with unequal tide height and involvement of a light-response mechanism. *Marine Biology* 129:87–96.
- Savoie L, Miron G, Biron M. 2007. Fouling community of the snow crab *Chionoecetes opilio* in Atlantic Canada. *Journal of Crustacean Biology* 27:30–36.
- Seeley RH, McDonald EM. 2003. The Japanese shore crab moves down east: *Hemigrapsus sanguineus* in Maine, 2002 [abstract]. In: *Benthic Ecology Meeting; 2003 Mar 28–30; Groton (CT)*, 1 p.
- Stachowitsch M. 1980. The epibenthic and endolithic species associated with the gastropod shells inhabited by the hermit crabs *Paguristes oculatus* and *Pagurus cuanensis*. *Pubblicazioni della Stazione Zoologica di Napoli, Marine Ecology* 1:73–101.
- Takahashi T, Iwashige A, Matsuura S. 1997. Behavioral manipulation of the shore crab *Hemigrapsus sanguineus* by the rhizocephalan barnacle, *Sacculina polygenea*. *Crustacean Research* 26:153–161.
- Takahashi T, Lützen J. 1998. Asexual reproduction as part of the life cycle in *Sacculina polygenea* (Cirripedia: Rhizocephala: Sacculinidae). *Journal of Crustacean Biology* 18:321–331.
- Takahashi T, Matsuura S. 1994. Laboratory studies on molting and growth of the shore crab, *Hemigrapsus sanguineus* de Haan, parasitized by a rhizocephalan barnacle. *Biological Bulletin* 186:300–308.
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM. 2003. Introduced species and their missing parasites. *Nature* 421:628–630.
- Torchin ME, Lafferty KD, Kuris AM. 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasions* 3:333–345.
- Torchin ME, Lafferty KD, Kuris AM. 2002. Parasites and marine invasions. *Parasitology* 124:S137–S151.
- Tyrrell MC, Harris LG. 2000. Potential impact of the introduced Asian shore crab, *Hemigrapsus sanguineus* in northern New England: diet, feeding preferences, and overlap with the green crab, *Carcinus maenas*. In: Pederson J, editor. *Marine bioinvasions*. Cambridge, MA: MIT Sea Grant College Program. p 208–220.
- Udekem d'Acoz C d', Faassee M. 2002. De huidige status van *Hemigrapsus sanguineus* (de Haan, 1835) en *H. penicillatus* (de Haan, 1835) in de noordelijke Atlantische Oceaan, in het bijzonder in Nederland, met opmerkingen over hun biologie (Crustacea, Decapoda, Brachyura). *Het Zeepaard* 62:101–115.

- Watts E. 1957. A survey of the Bryozoa in the southwest portion of Delaware Bay, with special reference to those species occurring on the blue crab, *Callinectes sapidus*. Newark: University of Delaware Marine Laboratories. p 19. University of Delaware Marine Laboratories Reference 57-7.
- Williams AB, McDermott JJ. 1990. An eastern United States record for the western Indo-Pacific crab, *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae). Proceedings of the Biological Society of Washington 103:108–109.
- Williams JD, McDermott JJ. 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. Journal of Experimental Marine Biology and Ecology 305:1–128.
- Winston JE, Key M.M Jr. 1999. *Alcyonidium albescens* (Ectoprocta: Ctenostomata) a new species from the mid-Atlantic coast of the United States. Bulletin of Marine Science 64:509–512.
- Yamaguchi T, Aratake H. 1997. Morphological modifications caused by *Sacculina polygenea* in *Hemigrapsus sanguineus* (De Haan) (Brachyura: Grapsidae). Crustacean Research 26:125–145.
- Yamaguchi T, Tokunaga S, Aratake H. 1994. Contagious infection by the rhizocephalan parasite *Sacculina* sp. in the grapsid crab *Hemigrapsus sanguineus* (De Haan). Crustacean Research 23:89–101.