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HABITAT AND DIET OF THE NON-NATIVE CRAB *HEMIGRAPSUS SANGUINEUS* IN SOUTHEASTERN NEW ENGLAND

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ABSTRACT — Intertidal distribution, habitat, and diet of the recently introduced western Pacific shore crab *Hemigrapsus sanguineus* (De Haan) were studied in southern New England. *H. sanguineus* was found in rocky intertidal coastal and estuarine environments, in salinities as low as 24 ppt. *H. sanguineus* was more abundant in lower and middle than in upper intertidal elevations, and abundance increased with rock cover. Gut contents of *H. sanguineus* included a variety of food items, particularly crustacean remains, algae, and vascular plants, indicating an omnivorous diet. *H. sanguineus* abundances and sizes at different sites suggested a trend of northward expansion of its range.

INTRODUCTION

The non-indigenous shore crab, *Hemigrapsus sanguineus* (De Haan, 1835), is becoming an abundant member of the rocky intertidal community in New England. First noticed in New Jersey in 1988 (Williams and McDermott 1990), the crab is now well established in southern New England (Ahl and Moss 1999, Lohrer and Whitlatch 1997). Its native range in the western Pacific extends from Sakhalin, Russia to Hong Kong (Williams and McDermott 1990). It is likely that *H. sanguineus* was introduced by release of larvae in ballast water transported from the western North Pacific Ocean to the mid-Atlantic coast of the United States (Carlton and Geller 1993).

H. sanguineus has several distinguishing characteristics (Sakai 1976, Williams and McDermott 1990; see Fig. 1). The carapace, somewhat square in shape, is usually patterned and dark in color, ranging from brownish orange to greenish black. Each side of the carapace has three distinct anterolateral teeth. *H. sanguineus* has a readily observable banding pattern on the walking legs. Male crabs possess a fleshy knob at the base of the dactyl of the cheliped, as well as relatively larger and more robust claws than females (McDermott 1999, Sakai 1976, Williams and McDermott 1990). The abdomen of mature females is wider than that of male crabs (McDermott 1998a). Ecological and behavioral data concerning *H. sanguineus* are scant, although it is one of the most

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common crabs found intertidally along the Japanese shoreline (Arikawa et al. 1987, Fukui 1988). Life history studies suggest that the crab has a high reproductive potential, facilitating a rapid rate of dispersal and colonization of new areas (Fukui 1988; McDermott 1991, 1998a).

The present study was designed to acquire baseline ecological data on *H. sanguineus* in southern New England. Objectives were to determine: 1) the distribution and abundance of *H. sanguineus* with respect to substrate composition (sedimentary, vegetated marsh, and rocky) and salinity; 2) the distribution and abundance of *H. sanguineus* with respect to intertidal height; and 3) the composition of the diet of crabs in the field.

MATERIALS AND METHODS

Density with respect to substrate type and salinity

Thorough searches along the southeastern Massachusetts coastline no shorter than 30 minutes in duration per locality were conducted during daytime low tides. Four intertidal substrate types (sandy, vegetated marsh, rocks next to marsh, and rocky areas) and one shallow subtidal habitat (seagrass beds) in coastal and estuarine habitats in areas with seawater of various salinities were intensively searched for the presence of *H. sanguineus*. At locations where the substrate was sandy, a hand rake was used to sift through the substrate to ensure that no crabs were shallowly buried. At vegetated marsh sites, at least five transects approximately one meter in width and running the length of each marsh area perpendicular to the water line were randomly delineated and searched. Random checks of smaller marsh areas were also performed.

Figure 1. *Hemigrapsus sanguineus*, male. Illustration by Sarah Richardson.

Rocky intertidal areas were searched at various intertidal heights by lifting cobbles and boulders, and probing the area underneath.

Because pilot data suggested that the abundance of *H. sanguineus* was related to the amount of rocky intertidal substratum in an area, we determined the influence of rock cover on crab density at Gooseberry Island in Westport, MA, during daytime low tides in September 1996. A 0.5 m^2 quadrat was placed on 29 areas of similar intertidal elevation but differing in rock cover. At least two people made visual estimates of the rock cover in the quadrat, taking into account only cobble-sized ($\geq$6 cm) or larger rocks, and the estimates were averaged. Each quadrat was searched and the number of *H. sanguineus* found per quadrat was recorded. The relationship between crab density and percent rock cover was examined using linear regression.

Density with respect to intertidal height

Two monthly sampling sites were established in different areas where rocks were present throughout the intertidal zone (Fig. 2): 1) Gooseberry Island (41°29'N, 71°02'W) in Westport, MA, a small elon-

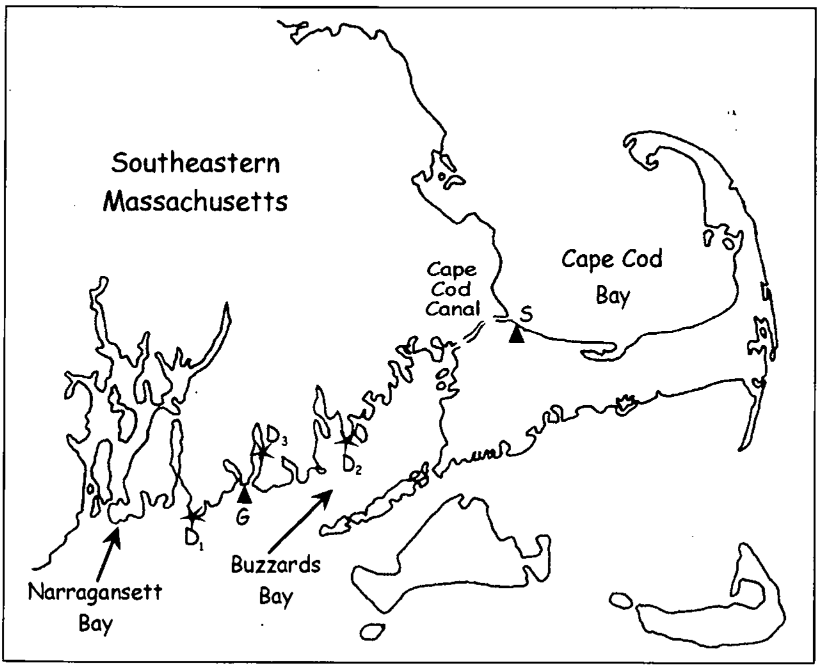

Figure 2. Map of southeastern Massachusetts, showing sites of monthly sampling of *H. sanguineus* (G = Gooseberry Island, Westport, MA; S = Town Beach, Sandwich, MA), and collection sites for diet analysis (D1 = Briggs Beach, Little Compton, RI; D2 = Fairhaven, MA; D3 = Hillcrest Acres, Westport, MA).

gated island at the southwestern end of Buzzards Bay having a tidal range of approximately 1.07 m, and 2) Sandwich Town Beach (41°46'N, 70°29'W) in Sandwich, MA, located on Cape Cod Bay near the east entrance to the Cape Cod Canal. The tidal range is approximately 2.65 m. The site sampled was a large rocky expanse located adjacent to a groin.

Each of the sites was sampled once monthly during a daytime low tide for several months in 1996. Gooseberry Island was sampled over a period of six months (June through November) at three different intertidal heights: 0.05 m, 0.16 m, and 0.68 m above mean lower low water (MLLW). Sandwich Town Beach was sampled at four intertidal heights (0.13 m, 0.53 m, 1.34 m, and 1.65 m above MLLW) over a period of five months (July through November) in 1996 and once in May 1997.

At each intertidal height of each sampling site, five replicate 2 m^2 square quadrats made of PVC pipe were placed randomly on rocky areas where less than one quarter of the quadrat was composed of sand. Every boulder, cobble, and pebble that could be lifted was lifted, and the area underneath and around the rocks was searched. Rocks that were located more than halfway out of the quadrat were not lifted or searched. Rocks and boulders were then replaced to minimize disturbance of other organisms (Chapman and Underwood 1996). All species of crab found inside the quadrat were captured manually and placed in labeled containers with water and algae to keep them moist. After all the quadrats were searched, the number of *H. sanguineus*, the sex of each crab, and the number of ovigerous females present in each quadrat were determined. Carapace width (CW) of each crab was measured with vernier calipers. On each sampling date, water temperature and salinity were noted. The crabs were then released at the approximate intertidal height from which they were captured.

Mean numbers of *H. sanguineus* and variances for each of the monthly sampling dates were calculated for each intertidal height of each sampling site. Because variances were heterogeneous (F_{max} test) even when the data were transformed, median densities among intertidal heights were compared using the Kruskal-Wallis non-parametric analysis of variance. When the Kruskal-Wallis test was significant ($p < 0.05$), Dunn's post-hoc tests (Daniel 1990) were performed to identify which sites were different from others.

Temporal changes in population characteristics

Monthly size-frequency distributions of *H. sanguineus* were constructed for each sampling site to examine temporal changes in sizes of crabs. Likewise, temporal trends in sex ratios (male:female) of crabs greater than 10 mm CW, the size at which gender could be identified with certainty, were calculated. The percentage of ovigerous females at each site and sampling date was determined for those crabs above 12 mm CW, the size at which females become sexually mature (McDermott 1998a).

Diet composition

To ascertain what *H. sanguineus* was consuming in the field, crabs were collected from under rocks at three different locations (Fig. 2) during daytime low tides in June - Sept. 1996. Site 1, Briggs Beach is a high-energy coastal area with a rocky area adjacent to a sandy expanse located in Little Compton, RI. Site 2, Fairhaven, MA, is a low energy embayment with rocks and cobbles overlaying a silty substrate. Marsh grasses are present in the upper intertidal zone, and a dense mat of *Fucus* covers the rocky area. Site 3, Hillcrest Acres is a muddy area along the east branch of the Westport River estuary. Marsh grasses are interspersed with rocks, and large amounts of algal material are present during summer months.

The crabs collected were placed in a cooler with ice and then transported to the lab where their buccal cavities were injected with approximately 2 ml of a 10% formalin solution. Injected crabs were then placed in a freezer (-15° C) and a stomach content analysis was performed during the fall of 1996 and early winter 1997. A total of 121 crabs were examined using the following procedure: A frozen crab was defrosted and blotted dry. The dorsal part of the carapace was removed and the esophagus, cardiac stomach, and intestines (hereafter "gut") were extracted. The gut was cut open and the contents were removed and examined using dissecting and compound microscopes. Prey types were identified to the lowest possible taxonomic level. The frequency of occurrence of the food items in gut contents was calculated as a percentage of the total number of guts with food that contained each respective prey type. Although the frequency of occurrence index may over-represent prey organisms with hard or indigestible structures and under-represent rapidly-digested prey (Elner and Campbell 1987), it still provides information about the natural diet of *H. sanguineus*.

RESULTS

Density with respect to substrate type and salinity

H. sanguineus was only found in rocky areas where boulders, cobbles, or pebbles were present. The crab was not found in sandy areas in either coastal or estuarine habitats, or in seagrass beds or vegetated marshes (Table 1). *H. sanguineus* was found in the vicinity of vegetated marshes only if there were rocks present in the area bordering it. In that case, crabs were found under rocks but not within the marsh. *H. sanguineus* was found in rocky estuarine areas in salinities as low as 24 ppt.

Crab abundance increased with rock cover (Fig. 3). Regression analysis indicated a strong positive relationship between percent rock cover and the number of crabs present ($p < 0.0001$). Approximately 53% of the variance in crab abundance could be explained by variation in rock cover.

Density with respect to intertidal height

Gooseberry Island. At each sampling date, densities of crabs varied with respect to intertidal height (Fig. 4). On the whole, higher crab densities were found at lower intertidal heights (0.05 m and 0.16 m above MLLW) than at the upper intertidal height (0.68 m above MLLW). No significant differences in crab densities were found be-

Table 1. Summary of results of searches for *H. sanguineus* in five habitat types in areas of various salinities.

Habitat	# Sites Searched	Salinity Range	*H. sanguineus* Present?
Rocky Intertidal	6	30 - 32	Y
	1	24	Y
	1	12	N
Vegetated Marsh	4	28 - 30	N
	2	18 - 24	N
Rocks Next to Marsh	2	30	Y
	1	20	N
Sand/Mud Flat	3	30	N
	3	18 - 24	N
Seagrass Bed	2	30	N

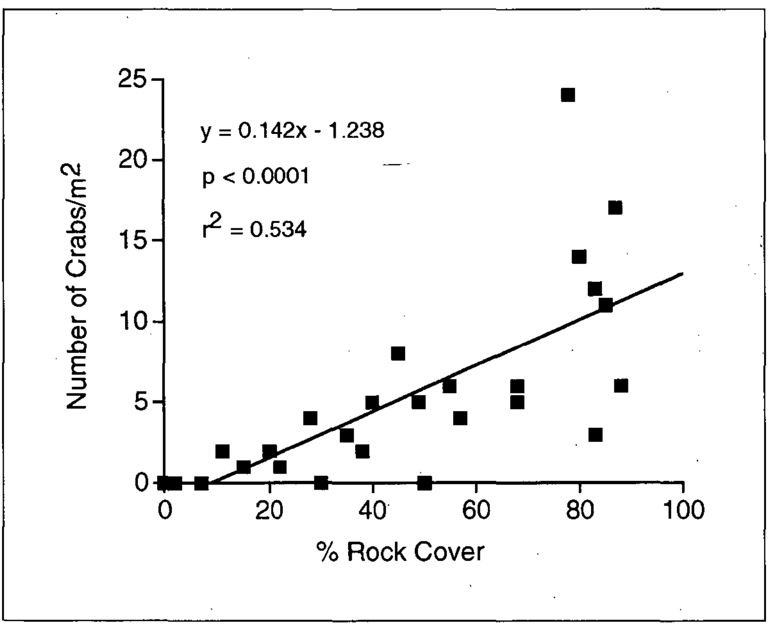

Figure 3. Density of *H. sanguineus* as a function of rock cover.

tween the two locations in the lower intertidal zone. In November, no crabs were present in the upper intertidal region.

Pooling the crab densities over six months (n = 30), each intertidal elevation differed significantly from each other (Kruskal-Wallis $p < 0.0001$). Crab densities at the elevation 0.16 m above MLLW were significantly higher than those at 0.05 m above MLLW (Dunn's test $p < 0.05$) and 0.68 m above MLLW (Dunn's test $p < 0.001$). The lowest intertidal sampling site (0.05 m above MLLW) had significantly higher crab densities than did the highest (0.68 m above MLLW) intertidal height (Dunn's test $p < 0.05$).

Sandwich Town Beach. In general, crab densities were greater at lower intertidal elevations than at the higher elevations, but only during the first and last sampling dates did densities differ significantly (Dunn's test, $p < 0.05$, Fig. 5). Early in the sampling season, significantly higher densities were found at 0.13 m above MLLW than at 1.65 m above MLLW (Dunn's test $p < 0.01$), but by the end of the five-month sampling period, in November 1996, crabs were only present in the lowest intertidal

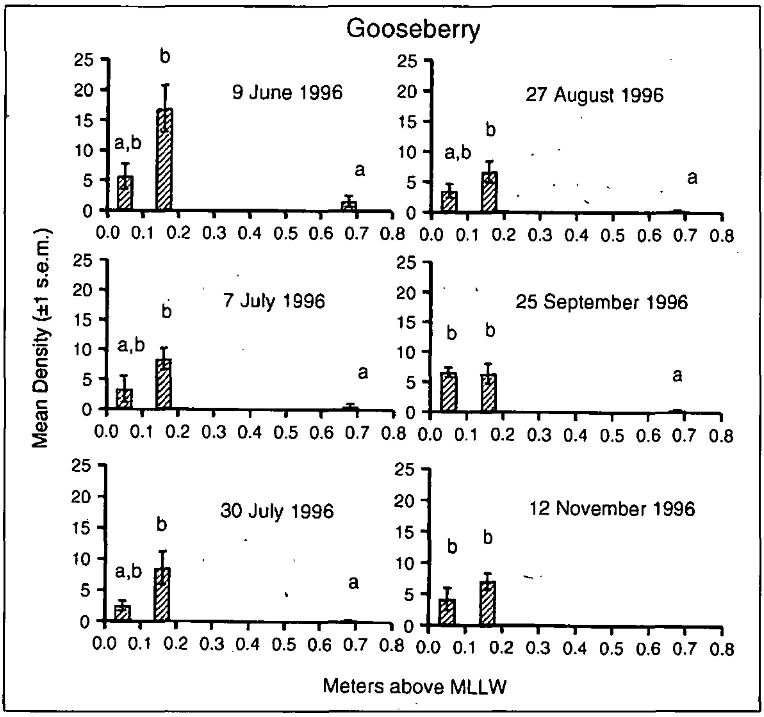

Figure 4. Mean densities of *H. sanguineus* at Gooseberry Island, Westport, MA, at three intertidal elevations: 0.05 m, 0.16 m, and 0.68 m above mean lower low water (MLLW). Significant differences are designated by differing lower case letters (a, b).

area. Early in 1997, highest crab densities were found at 0.13 m and 0.53 m above MLLW and none were present at 1.65 m above MLLW.

Crab densities at each intertidal elevation pooled over six months ($n = 30$) differed significantly (Kruskal-Wallis $p < 0.0001$). Crab densities were significantly higher at 0.13 m above MLLW than at 1.34 m and 1.65 m above MLLW (Dunn's test $p < 0.001$). In addition, there were higher densities of crabs at 0.53 m above MLLW than at 1.34 m and 1.65 m above MLLW (Dunn's test $p < 0.001$). No significant density differences were found between the two lower intertidal sampling sites 0.13 m above MLLW and 0.53 m above MLLW (Dunn's test $p > 0.05$).

Temporal change in population characteristics

Gooseberry Island. A strong recruitment of juveniles was observed in June and early July (Fig. 6). No *H. sanguineus* under 4.0 mm CW were

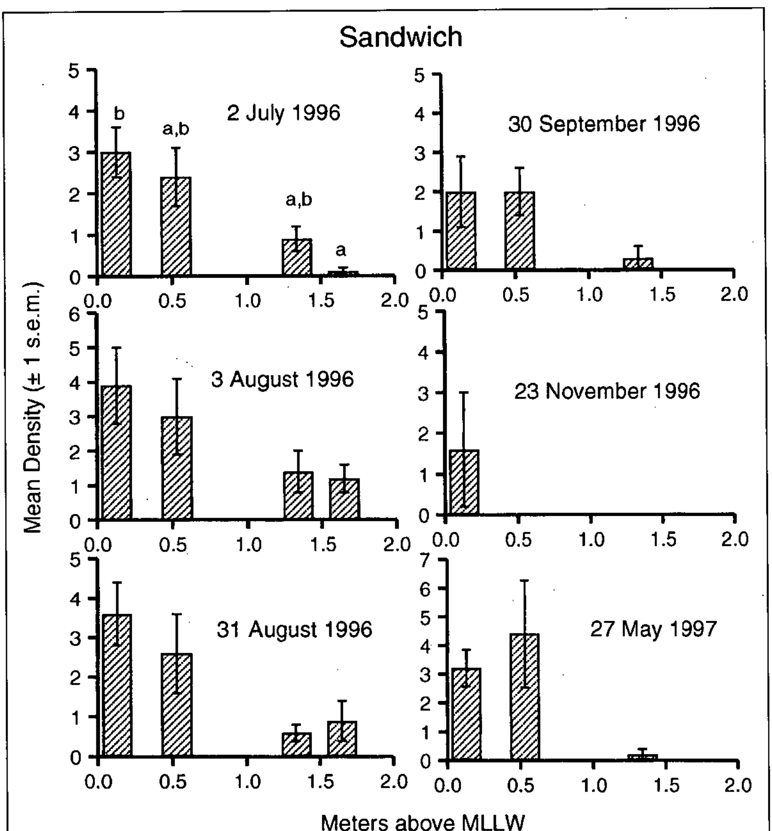

Figure 5. Mean densities of *H. sanguineus* at Sandwich Town Beach, MA, at four intertidal elevations: 0.13 m, 0.53 m, 1.34 m, and 1.65 m above mean lower low water (MLLW). Significant differences are designated by differing lower case letters (a, b).

found throughout the sampling season. As the sampling season progressed there was a noticeable shift in the mode from smaller (< 10 mm CW) to intermediate and larger-sized crabs (Fig. 6). The largest female sampled was 34.0 mm CW, and the largest male crab was 33.0 mm CW.

Male crabs above 10 mm CW were more numerous than females above 10 mm, except in June. However, the sex ratios varied over the sampling season (Table 2). The percentage of female crabs that were ovigerous peaked at 56% in late July, continued to be high in late August, then declined sharply to 7% at the end of September. No ovigerous females were captured in November.

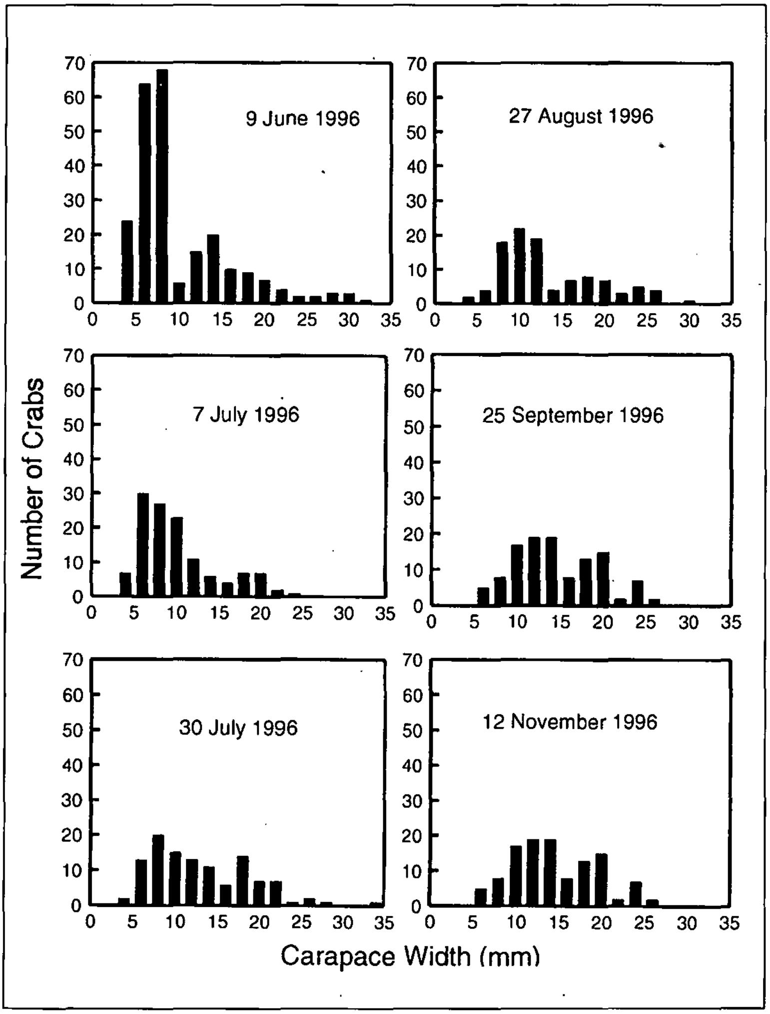

Figure 6. Size-frequency distributions of *H. sanguineus* at Gooseberry Island, Westport, MA.

Sandwich Town Beach. Unlike the phenomenon observed at Gooseberry Island, there was no strong recruitment peak observed for this population in 1996 (Fig.7), although a few very small individuals were observed during May of the following year. As the sampling season progressed from July to September, there was a shift in the mode toward larger sizes (Fig. 7). The widest range of sizes present in the population was found during May 1997, with crabs ranging from 4.4 mm to 30.2 mm in CW. Unlike the distributions observed for Gooseberry, only the first two sampling dates could be viewed as bimodal.

The sex ratios of crabs in Sandwich also varied, but males outnumbered females during the summer months (Table 2). In 1996 the percentage of ovigerous females was highest (11%) in July and decreased to 6% in early August, after which time no ovigerous females were found (Table 2). However, 22% of female crabs collected in late May of 1997 were ovigerous, suggesting that extrusion of eggs by female *H. sanguineus* occurs relatively early in the spring (Table 2).

Diet composition

H. sanguineus was omnivorous at all three sites; most guts with food items contained both plant and animal remains (Table 3). Crustacean parts (appendages and setae) were present in guts of crabs from all three sites, and were generally the most frequently observed animal food items found (Table 3). Barnacle remains such as shell plates and cirri were present in high percentages in guts from both the Fairhaven site (34%) and the Briggs Beach site (30%), but were absent in guts examined from the estuarine site at Hillcrest Acres. Bivalve remains (hinged

Table 2. Sex ratios (male : female) of *H. sanguineus* above 10 mm in carapace width (CW), and percent of female crabs ≥ 12.0 mm in CW that were ovigerous.

Location	Date	Sex Ratio	% Ovigerous
Gooseberry	6/9/96	1 : 1	38
	7/7/96	1.5 : 1	44
	7/30/96	1.1 : 1	56
	8/27/96	1.5 : 1	43
	9/25/96	1.1 : 1	7
	11/12/96	1.1 : 1	0
Sandwich	7/2/96	1.4 : 1	11
	8/3/96	1 : 1	6
	8/31/96	1.2 : 1	0
	9/30/96	1.1 : 1	0
	11/23/96	0.9 : 1	0
	5/27/97	0.9 : 1	22

shell fragments) were present in low percentages at two of the three sites. Nematodes were present in 17% of the guts from the Fairhaven site that contained food (Table 3).

Plant material was present in all guts (containing food) of crabs from Briggs Beach and Hillcrest Acres, and in almost all (93%) guts from Fairhaven (Table 3). Generally, the most frequent plant food item at all three sites was algae. One red algal species and two green algae occurred in stomachs at all three sites: *Polysiphonia* sp., *Ulva* sp., and *Enteromorpha* sp. (Table 3). In addition to high percentages of algal material, guts of crabs from Hillcrest Acres also contained high percentages of vascular plant material (44%).

DISCUSSION

H. sanguineus was most frequently found and most abundant along rocky intertidal shores in coastal environments. In addition, the crab

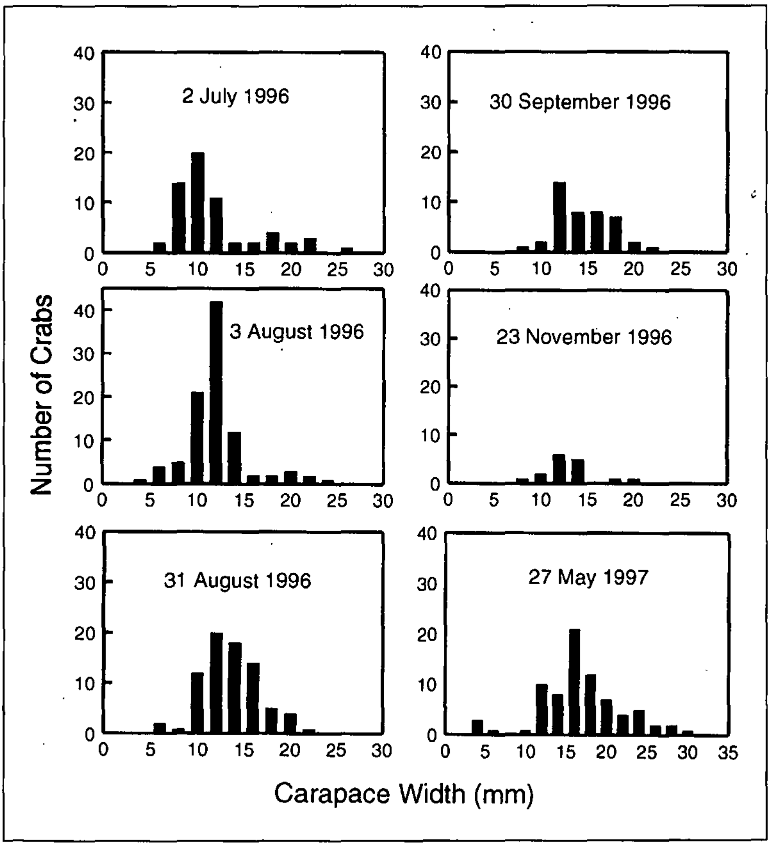

Figure 7. Size-frequency distributions of *H. sanguineus* at Sandwich Town Beach, MA.

occurred in estuarine environments among rocky substrates in salinities as low as 24 ppt. This is consistent with information about the ecological habitat of *H. sanguineus* in Japan, where *H. sanguineus* is abundant on rocky coasts but is also found in estuaries if rocks are present. However, low salinity water is physiologically stressful to *H. sanguineus*; in salinities <15 ppt, cardiac activity and locomotion decrease (Depledge 1984).

Table 3. Food types eaten by *H. sanguineus* at three sampling sites (Briggs Beach, Little Compton, RI; Fairhaven, MA; and Hillcrest Acres, Westport, MA) in summer 1996. A dashed line indicates the food item was not found. The first number shows the number of guts containing a particular food item and the number in parentheses shows the percent frequency of occurrence of the item in stomachs that contained food.

	Briggs Beach	Fairhaven	Hillcrest Acres
# Stomachs Examined	39	62	20
# Stomachs with Food	20 (51)*	41 (66)	9 (45)
Animal Remains	15 (75)	27 (66)	5 (56)
Foraminifera	-	1 (2)	-
Nematodes	-	7 (17)	1 (11)
Mollusc			
Bivalve	1 (5)	1 (2)	-
Gastropod	-	5 (12)	-
Arthropod			
Crustacean parts	5 (25)	14 (34)	3 (33)
Barnacle	6 (30)	14 (34)	-
Insect parts	1 (5)	-	2 (22)
Unidentifiable	6 (30)	6 (15)	3 (33)
Plant Remains	20 (100)	38 (93)	9 (100)
Spore	-	4 (10)	-
Green Algae			
Enteromorpha	4 (20)	12 (29)	1 (11)
Codium	-	3 (7)	-
Ulva	7 (35)	6 (15)	2 (22)
Urospora	2 (10)	-	1 (11)
Brown Algae			
Fucus	-	1 (2)	-
Red Algae			
Polysiphonia	7 (35)	16 (39)	3 (33)
Seirospira	-	1 (2)	-
Vascular Plants			
Seagrass	-	-	4 (44)
Epidermal hair	-	10 (24)	4 (44)
Detritus	-	-	1 (11)

* Number (%)

Shortly after its introduction to the eastern seaboard of the United States, *H. sanguineus* was described by McDermott (1992) as dwelling in the upper intertidal zone. McDermott (1992) suggested that interactions with native species of crabs, most of which occur lower intertidally, would therefore be limited. The present study suggests otherwise. While *H. sanguineus* was present in the upper intertidal regions in low numbers, higher densities of *H. sanguineus* occurred at the middle and lower intertidal elevations at all locations sampled. In addition, *H. sanguineus* was found co-existing with mud crabs in the family Xanthidae, juvenile green crabs (*Carcinus maenas*), and occasionally the rock crab, *Cancer irroratus*. Lohrer and Whitlatch (1997) also found highest abundance of *H. sanguineus* primarily in the lower and middle rocky intertidal regions in eastern Long Island Sound, and *H. sanguineus* co-occurred with mud, green, and rock crabs.

Reports of intertidal distributions of *H. sanguineus* in the western Pacific also differ. Although Kikuchi et al. (1981) and Takada and Kikuchi (1991) observed the species in the middle and upper intertidal zone in Japan, Saigusa and Kawagoye (1997) found it in highest abundances lower in the intertidal zone. In Korea, *H. sanguineus* occurs throughout the intertidal zone (Hwang et al. 1993). The different distributions may reflect variable amounts of shelter-providing rocks in the intertidal areas sampled as crab abundance is directly proportional to rock cover (Fig. 3). Alternatively, shifts in distribution may be caused by interactions with other species.

Total intertidal abundance of *H. sanguineus* declined from the summer to the late fall. In addition, densities of crabs at upper intertidal elevations decreased as winter approached. Similar temporal changes were found in Japan and eastern Long Island Sound. Fukui (1988) found that densities of *H. sanguineus* exhibited seasonal changes with higher densities in the upper intertidal during spring and summer months, shifting to the lower intertidal regions during autumn and winter months. Lohrer and Whitlatch (1997) also found the highest densities of crabs in the lower half of the intertidal zone of eastern Long Island Sound, especially during winter months. Seasonal changes in distribution may reflect migration to escape harsh winter conditions such as freezing and ice scouring, which are more likely in the upper intertidal regions. Perhaps crabs move to shallow subtidal areas during the winter. Even though *H. sanguineus* was not found in subtidal habitats during the summer (present study), McDermott (1998b) found epifaunal organisms on the carapaces of *H. sanguineus* in New Jersey in the spring, and suggested that crabs had spent some time subtidally. In Japan, *H. sanguineus* will dwell in shallow areas up to 3 m in depth if rocks are present (Takahashi et al. 1985). Recently, *H. sanguineus* was found associated with subtidal fouling communities on floating platforms in the Westport River estuary (pers. obs., O'Connor).

McDermott (1998a) suggested that the length of the reproductive period of *H. sanguineus* is related to latitude and therefore water temperature. In southern parts of Japan, the breeding season is 8 months long (Fukui 1988), whereas in northern Japan, it lasts 3 months (Takahashi et al. 1985). Whereas breeding occurred through September at Gooseberry in Buzzards Bay, ovigerous females were found only until early August in Sandwich in Cape Cod Bay. However, ovigerous *H. sanguineus* were found in early September, 1999 in Marshfield, Massachusetts, slightly north of Sandwich (unpub. data, O'Connor), suggesting that the breeding season is similar in Buzzards Bay and Cape Cod Bay.

The present study of gut contents of crabs from Massachusetts and prior studies in Connecticut (Lohrer and Whitlatch 1997) and New Jersey (McDermott 1999) confirm that *H. sanguineus* is an omnivore. However, the taxonomic composition of gut contents varied among locations, perhaps reflecting differences in availability of potential prey items. For example, mussel (*Mytilus edulis*) shell fragments were commonly consumed by crabs in New Jersey but not at sites in Massachusetts, where mussels were not especially abundant. Yet *H. sanguineus* readily consumes mussels (and other bivalves) in laboratory feeding experiments (Bourdeau and O'Connor 1999; Brousseau et al. 1999; McDermott 1999). In addition, a crab found in a clam propagation tray in Westport contained clam shell remains in its gut (unpub. data, Ledesma).

H. sanguineus was first observed near Cape May, New Jersey, in 1988 (Williams and McDermott 1990). By 1994, the species was common in Buzzards Bay (pers. obs., O'Connor). Comparisons of densities at several sites in New England illustrate the northward spread of the crab. In 1996, average densities of *H. sanguineus* in Long Island Sound ranged from 20 - 40/m^2 (Lohrer and Whitlatch 1997). Mean densities at Gooseberry Island, northeast of Long Island Sound, were 5 - 15/m^2, whereas those at Sandwich, on the north side of Cape Cod, were only 2 - 4/m^2. Likewise, crab sizes decreased northward along the coast of Long Island Sound (Lohrer and Whitlatch 1997), and crabs at Gooseberry were generally larger than those at Sandwich, where the largest crabs were observed in the following spring. These data suggest that the species spread north from Long Island Sound to Buzzards Bay to Cape Cod Bay, likely through the Cape Cod Canal. Also in 1996, *H. sanguineus* was present in low numbers in Plymouth, MA, north of the canal, but increased greatly in abundance during the next two years (O'Connor et al. 1999). If the physiological tolerance of *H. sanguineus* to cold temperatures in the western Atlantic is the same as in the western Pacific, the species could spread into Maine (McDermott 1998b), where rocky intertidal substrata are abundant.

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