

PREDATION BY THE NONINDIGENOUS ASIAN SHORE CRAB *HEMIGRAPSPUS SANGUINEUS* ON MACROALGAE AND MOLLUSCS

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ABSTRACT - Prey selection and consumption of common molluscs and macroalgae by the Asian shore crab, *Hemigrapsus sanguineus*, were investigated in the laboratory. Crabs of three size classes (12–18, 19–25, 26–31 mm carapace width) collected from the rocky intertidal from May to November 1998, and were offered three mollusc species: the mussel *Mytilus edulis*, the clam *Mercenaria mercenaria*, and the snail *Littorina littorea*. Equal numbers of prey from three size classes or two species were offered concurrently to individual crabs. Crabs consumed small molluscs, large males opening larger molluscs than did females and smaller males. Male crabs consumed both mussels and clams. Females opened only mussels, but ate flesh from previously opened clams. Very few *L. littorea* were consumed. The macroalgae *Codium fragile* ssp. *tomentosoides*, *Enteromorpha* spp., *Chondrus crispus*, *Fucus* spp., and *Ascophyllum nodosum* were presented to individual crabs separately to determine consumption rates and together to ascertain species preference. Crabs preferred the green algae *C. fragile* ssp. *tomentosoides* and *Enteromorpha* spp.

INTRODUCTION

Through predation on native communities, nonindigenous species can have measurable and often detrimental effects by altering food webs (Herbold and Moyle 1986, Zaret and Paine 1973) and by causing local and regional extinction of native species (Clarke et al. 1984). In the northeast U.S. coast, the Asian shore crab *Hemigrapsus sanguineus* (De Haan), first found in Cape May, New Jersey in 1988 (Williams and McDermott 1990), has spread rapidly along the eastern coast from North Carolina to Maine (McDermott 1998; pers. comm., A. Phillippi, Walpole, ME). In some rocky intertidal communities, *H. sanguineus* is the dominant crab species, reaching densities greater than those of all resident crab species combined (Ahl and Moss 1999; Lohrer and Whitlatch 1997; unpubl. data, N. O'Connor). Until recently, little was known about the feeding habits and natural diet of this species.

While other intertidal crabs of the family Grapsidae prey heavily on green algae (Birch 1979, Hiatt 1948, Kennish et al. 1996, Kramer 1967),

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gut content analyses of *H. sanguineus* reveal a diversity of plant and animal food, including blue mussel, littorinid snails, and an assortment of macroalgal species (Ledesma and O'Connor 2001, Lohrer and Whitlatch 1997, McDermott 1999). The crab also readily consumes soft-shell clams (*Mya arenaria*) and oysters (*Crassostrea virginica*) (Brousseau et al. 2001).

Crab species typically inhabiting the rocky intertidal zone of New England include green crabs (*Carcinus maenas*, another non-indigenous species) and mud crabs in the family Xanthidae (Lohrer and Whitlatch 1997; unpubl. data, N. O'Connor). Although prey types in gut contents of different crab species overlap, green and mud crabs generally consume more animal matter than does the Asian shore crab (Brousseau et al. 1999, Lohrer and Whitlatch 1997); in the latter, algae and plant material are common in gut contents (Ledesma and O'Connor 2001, Tyrrell and Harris 1999). Differences in prey preferences of Asian and resident crabs could lead to changes in prey communities as *H. sanguineus* becomes established in northeastern North America.

Prey selection is an important aspect of the foraging behavior of crabs. Crabs feeding on molluscs often prefer certain species (Choy 1986, DuPreez 1984, Elner and Raffaelli 1980, Lawton and Hughes 1985) and sizes (reviewed by Juanes 1992). Similarly, crabs feeding on macroalgae exhibit clear preferences in the field and the laboratory (Birch 1979, Hiatt 1948, Kennish and Williams 1997, Lee 1988). Moreover, animal tissue is frequently found in the stomachs of crabs considered to be primarily herbivorous, and certain species assimilate nutrients from animal matter more efficiently than from plant material (reviewed by Wolcott and O'Connor 1992). Herbivorous crabs may also prefer animal to plant or algal prey (Choy 1986).

In the present study, prey selection and consumption by *H. sanguineus* were investigated in laboratory experiments to assess the potential of this non-indigenous species to alter New England rocky intertidal ecosystems through predation on common molluscs and macroalgae. Laboratory experiments were conducted to (1) investigate consumption of bivalve and gastropod mollusc prey of different sizes and species, and (2) determine the algal prey preference of the crab.

METHODS

Sampling and maintenance of test organisms

Hemigrapsus sanguineus

Crabs were collected by hand from the rocky intertidal zone of two southeastern Massachusetts, USA sites: Gooseberry Island, Westport (41°29'N, 71°02'W) and Clark's Cove, New Bedford (41°35'N,

70°55'W), from May to November 1998. Crabs of both sexes were used for experimentation; those with missing or small regenerated chelipeds or walking legs were not used. Individuals were measured and grouped into one of three size classes (12–18 mm, 19–25 mm, 26–32 mm) based on carapace width (CW), then placed into covered plastic aquaria containing 2–5 cm of natural seawater at a salinity of 29–31‰. Aquaria were tilted so that a portion of the aquarium floor was exposed to air. Crabs were starved for 24 h prior to feeding trials. Experiments were run at constant temperature (18 °C) under fluorescent lights on a 12 h light: 12h dark photoperiod. Each crab was used only once in an experiment.

Mollusc prey

Prey species included the mussel *Mytilus edulis* (L.) and the gastropod snail *Littorina littorea* (L.), chosen for their high relative abundance in rocky intertidal zones, and the hard-shelled clam *Mercenaria mercenaria* (L.) selected for its commercial importance. Mussels were collected by hand from the middle of a rocky intertidal zone in Bourne, MA, in May 1998 and maintained in mesh netting suspended in the water column from a pier in Clark's Cove over the course of the study. Snails, collected from the rocky mid-intertidal zone at Gooseberry Island and hard-shelled clams, donated by Cape Cod Oyster Co. and the Westport Shellfish Constable, were obtained 24 to 48 h prior to experimentation and maintained in plastic aquaria containing seawater under the same light and temperature conditions as the crabs. Bivalve shell length was measured from the tip of the umbo to the edge of the margin at its greatest distance from the umbo. Gastropod shell height was measured from spire tip to posterior tip of the siphonal canal. Only undamaged individuals were used for experimentation.

Algal prey

Species of macroalgae, chosen for their high relative abundance during the experimental period, were collected regularly by hand from the shores of Gooseberry Island from August to November 1998. Species used as prey were *Codium fragile* (Suringar) ssp. *tomentosoides* (Goor), *Enteromorpha* (L.) spp., *Chondrus crispus* Stackh., *Fucus* (L.) spp., and *Ascophyllum nodosum* (L). Algae were obtained 24 h prior to use in feeding trials and maintained in the laboratory in plastic aquaria with aerated ambient seawater.

Prey size selection

Individual crabs from the three size classes were concurrently offered three size classes of molluscs of a particular species, placed arbitrarily over the aquarium bottom. Constant numbers were maintained by replacing prey that were injured or eaten each day. Experiments were run for 5 d. Seawater was replaced daily.

Individual small ($n = 8$), medium ($n = 8$) and large ($n = 8$) male crabs were offered mussels of three size classes (4–8, 12–16, 20–24 mm shell length, $n = 12$ for each size class). In a second experiment, small ($n = 6$), medium ($n = 6$) and large ($n = 6$) crabs were presented with clams from three size classes: 4–6, 8–10, 12–14 mm shell length ($n = 9$ for each size class). In a similar experiment, small ($n = 8$), medium ($n = 8$) and large ($n = 8$) males were offered three size classes of snails: 2–4, 6–8, 10–12 mm shell height ($n = 12$ for each size class). Due to their ability to climb the aquaria walls, snails were immobilized prior to experimentation by immersing them in freshwater at 40 °C for 15 minutes then immediately placing them in ambient seawater for ten minutes, a procedure used by Lawton and Hughes (1985) and Creswell and McLay (1990).

Similar experiments were conducted using female crabs. Small ($n = 12$) and medium ($n = 12$) crabs were offered either mussels or snails of two size classes: 4–8 and 12–16 mm shell length for mussels, 2–4 and 6–8 mm shell height for snails ($n = 18$ for each size class). In another experiment, small ($n = 9$) and medium ($n = 9$) females were offered clams from two size classes: 4–6, 8–10 mm shell length ($n = 12$ for each size class). Large females were excluded from experimentation due to their scarcity in the field. The chi-square test of independence was used to test the null hypothesis that equal numbers of prey of different sizes were consumed. Separate chi-square tests were performed on the data from each experiment.

Because female crabs did not open any clams (see Results), an additional experiment was conducted to determine whether females would eat clam flesh if offered. Ten female crabs (14–22 mm CW) were offered two clams each (size range 4–8 mm shell length) that were intact ($n = 2$), opened with flesh exposed ($n = 4$), or one intact plus one unopened clam ($n = 4$). Crabs were allowed to feed for 17 h overnight.

Critical prey size

Individual large males ($n = 7$) were offered a single bivalve from the smallest size class for each species. If eaten, the prey was replaced with another individual of greater (+ 1 mm) shell height or length. Replacement continued until 5 d had passed without consumption of the prey. Identical experiments were run for each of the three mollusc species.

Prey species selection

Individual male ($n = 5$) and female ($n = 5$) crabs of various sizes were presented with 18 mussels and 18 clams simultaneously from one size class (4–6 mm shell length). The number of prey consumed during 24 h was determined. The chi-square test of independence was used to test the null hypothesis that equal numbers of the different prey species were consumed.

Algal preference

In the first series of experiments individual crabs of both sexes from all size classes ($n = 12$) were offered only one species of macroalga (no choice), and in the second test each crab ($n = 12$) was offered all five algal species simultaneously (multiple choice). Prior to all tests, algae were rinsed in filtered seawater, all epiphytes were removed, and algae were blotted dry and weighed to the nearest 0.001 g. Similar algae were maintained concurrently in the same type of aquarium but without a crab predator as a control for autogenic weight change. Sizes and weights of each algal species were kept as similar as each species' morphology would allow. Approximately 15 g (range = 13–17 g) of algae were provided for crabs in both experiments. Crabs were allowed to forage for 24 h, then all algal fragments from test and control aquaria were collected, blotted dry, and reweighed. Differences between control and test algal weights were determined to calculate the amount eaten by the crab. Two measurements were calculated, mass change (g) and % consumed, as the latter is sensitive to differences in size and weight of the test algae (Coen 1988, Kennish and Williams 1997).

No choice

Twelve crabs of both sexes were used to examine consumption of each of the five algal species. Differences in mass change were analyzed using ANOVA, followed by Fisher's PLSD multiple comparisons test. Differences in % consumed among algal species were analyzed using the Kruskal-Wallis test because the data were heteroscedastic even after arcsine transformation. Dunn's test, a multiple comparison procedure, was performed to compare differences in % consumption between species.

Multiple choice

Individual crabs of both sexes ($n = 12$) were offered each of the five test algae simultaneously. The experiment was repeated twice, each time using both control and test aquaria. Differences in loss of mass and % consumed in randomly paired control and test aquaria for each type of algae were examined using Mann-Whitney U-tests.

Consumption of molluscan vs. algal prey

Individual crabs of both sexes from all size classes ($n = 12$) were simultaneously presented with 12 mussels of one size class (4–6 mm) and preweighed (3–4 g) algae and given 24 h to feed. The first experiment was performed using *Codium fragile* as the test alga, the second with *Enteromorpha* spp. Controls without the crab were run simultaneously in the same type of aquaria. Each experiment was repeated twice. Because of differences in the response variables (number and mass change) the data were not analyzed statistically.

RESULTS

Prey size selection

When presented with three size categories of mussels, male crabs, regardless of size, consumed small individuals (Chi square = 136.06, 487.29, 259.86, $df = 2$, $P < 0.0001$ for small, medium and large crabs respectively; Fig. 1). Crabs did not eat large mussels. Males also consumed small clams (Chi square = 291.98, 321.98, 106.29, $df = 2$, $P < 0.0001$ for small, medium and large crabs respectively; Fig. 2), with large males also including medium and large clams in their diet. Small and medium crabs did not eat clams > 6 mm shell length. Twenty-four male crabs, each offered 180 littorine snails, consumed a total of only seven small individuals.

Female crabs presented with mussels ate small prey (Chi square = 199.02, 470.49, $P < 0.0001$ for small and medium crabs respectively;

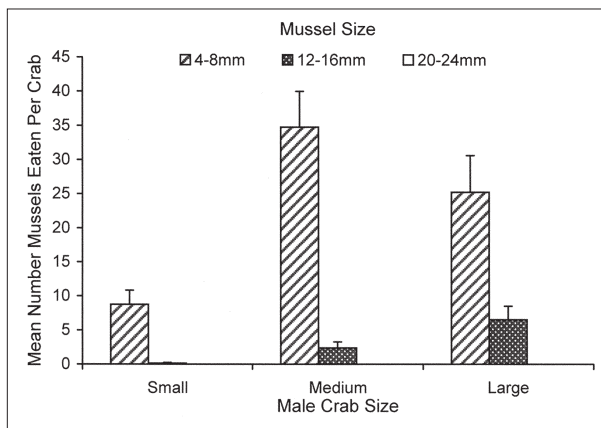


Figure 1. Consumption of *Mytilus edulis* by male *Hemigrapsus sanguineus*. Mean number of mussels eaten per crab over five days (+1 S.E.M.) by small (12–18 mm), medium (19–25 mm) and large (26–32 mm) crabs ($n = 8$ for each crab size class).

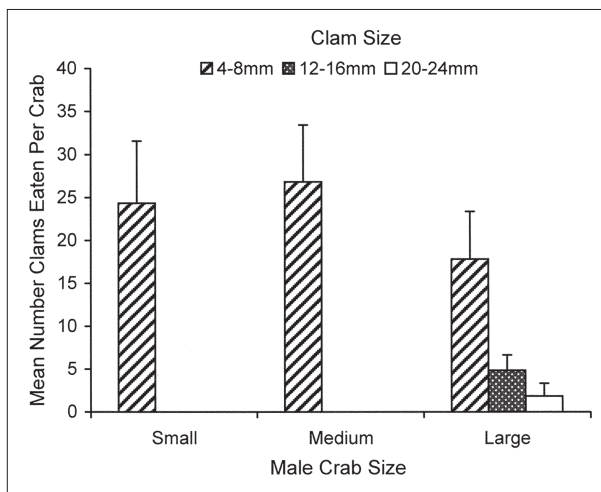


Figure 2. Consumption of *Mercenaria mercenaria* by male *Hemigrapsus sanguineus*. Mean number of clams eaten per crab over five days (+1 S.E.M.) by small, medium and large crabs ($n = 6$ for each crab size class).

Fig. 3). No female crabs consumed any clams or snails. In the experiment in which female crabs were offered opened clams, all the flesh was eaten, but none of the females opened any of the intact clams, and no marks suggesting an attempt to open the clams were visible on the shell margins.

Critical prey size

Large male crabs were capable of opening and consuming mussels over 20 mm in length (Table 1). The largest mussel (31 mm) opened and consumed was attacked by a male 32.6 mm CW. The largest clam (17 mm) opened and consumed was manipulated by a male 30.5 mm CW.

Prey species selection

Large male crabs presented with equal numbers of mussels and clams consumed both species equally (Chi square = 2.246, df = 1, P >

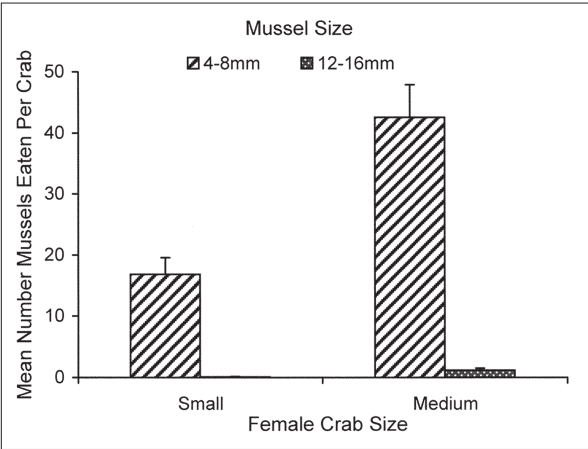


Figure 3. Consumption of *Mytilus edulis* by female *Hemigrapsus sanguineus*. Mean number of mussels eaten per crab over five days (+1 S.E.M.) by small and medium crabs (n = 12 for each crab size class).

Table 1. Maximum bivalve size (shell length) opened and consumed by large (> 26mm carapace width) male *Hemigrapsus sanguineus* within 5 d.

Crab Carapace Width (mm)	Shell Length (mm)	
	<i>Mytilus</i>	<i>Mercenaria</i>
<i>Hemigrapsus</i>		
26.3	27.6	-
26.8	-	12.0, 14.0
27.5	22.0	-
28.2	30.0	-
28.3	-	13.0
29.9	21.2	-
30.1	22.8	13.0
30.5	-	17.0
31.1	-	16.0
31.2	-	12.0
32.6	31.0	-
34.2	20.3	-

0.1294; Table 2). Female crabs consumed only mussels (Chi square = 82, df = 1, $P < 0.0001$; Table 2).

Attack methods

H. sanguineus exhibited variable shell opening tactics for bivalves. Smaller bivalves were crushed outright. Larger bivalves were opened using a variety of techniques including: (1) umbo crushing where force was applied to the umbo end of the shell, (2) posterior crushing in which force was applied across the valve plane at the posterior end of the shell, and (3) edge clipping involving the application of force to the perimeter of the posterior end of the shell with minimal shell damage. The umbo was the most frequently broken shell region of larger prey. The remains usually consisted of a large piece of one valve plus a fragment of the other valve attached by a virtually intact hinge. In contrast, smaller prey were shattered into small fragments by haphazard crushing.

Algal preference: No choice

Crabs exhibited clear differences in the relative consumption of each of the five macroalgal species ($F = 8.602$, df = 4, $P < 0.0001$; $H = 19.957$, df = 4, $P = 0.0005$, for g consumed and % loss respectively). The highest consumption with respect to % loss (Fig. 4) and g consumed (Fig. 5) was of *Codium fragile*, slightly less for *Enteromorpha* spp. Little or none of the remaining three algal species was eaten. The green algae were consumed in significantly greater amounts than the red or brown species (Fisher's PLSD and Dunn's tests, $p < 0.05$).

Table 2. Mean number of prey eaten per crab in 24 h, when offered small (4–6 mm shell length) mussels and clams (18 of each). SD = standard deviation, n = number of crabs used.

Crab	Prey	Mean no. eaten	SD	n
Male	<i>Mytilus</i>	13	2.6	5
	<i>Mercenaria</i>	10	3.6	
Female	<i>Mytilus</i>	16	2.7	5
	<i>Mercenaria</i>	0	0	

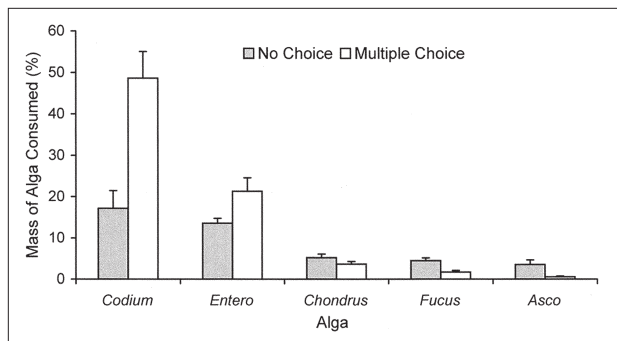


Figure 4. Feeding preference of male and female *Hemigrapsus sanguineus* for five species of macroalgae; mean % mass of alga consumed (+1 S.E.M.) in 24 h.

Algal preference: Multiple choice

When presented with five macroalgal species concurrently, *H. sanguineus* preferred green algae to red and brown algae. As in the no-choice feeding experiment, larger percentages of *Codium fragile* and *Enteromorpha* spp. were consumed (Fig. 4), and in greater amounts (Fig. 5) than the other three species. Significant differences in loss of mass (g) between control and experimental algae were found only for *Codium* and *Enteromorpha* (Mann-Whitney test, $p < 0.0001$).

Preference for mollusc or algal prey

Crabs offered small mussels and green algae simultaneously exhibited no clear preference for mollusc or algal prey (Table 3). Consumption of algae and mussels offered simultaneously was similar to consumption of each offered alone.

DISCUSSION

The Asian shore crab *Hemigrapsus sanguineus* removed small bivalves from experimental prey populations, suggesting it has the potential to alter natural prey population structure by affecting prey recruitment into adult size classes. The clam *Mercenaria mercenaria* obtained refuge from predation by male *H. sanguineus* at smaller sizes than did the blue mussel *Mytilus edulis*. Male crabs from all three size classes opened mussels from 12–16 mm in length, and the largest males were capable of opening mussels up to 31 mm. In contrast, large males typically could not open clams greater than 14 mm, and small and medium males did not consume any clams larger than 6 mm. Differ-

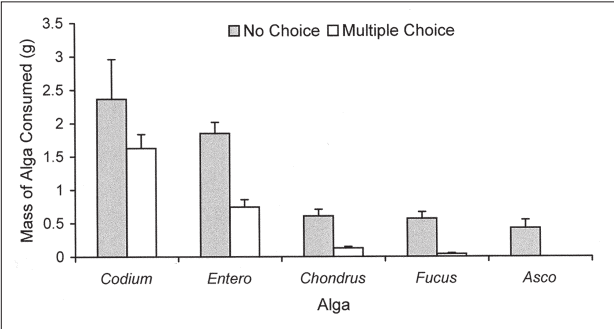


Figure 5. Feeding preference of male and female *Hemigrapsus sanguineus* for five species of macroalgae; mean mass (g) of alga consumed (+1 S.E.M.) in 24 h.

Table 3. Feeding of *H. sanguineus* presented with small *Mytilus edulis* concurrently with green algae (*Codium fragile* or *Enteromorpha* sp.). Mean mass of alga consumed (g) and mean number of mussels consumed within 24 h.

Treatment	Alga consumed (g)	Mussels consumed (# eaten)
<i>Codium fragile</i>	1.8	6.9
<i>Enteromorpha</i> spp.	0.5	9.3

ences in shell morphology of the two bivalve species may explain the different patterns of consumption. *Mercenaria mercenaria* shells are harder, thicker and presumably stronger than those of *Mytilus edulis*, so should be more resistant to crushing.

Differences in bivalve shell characteristics or crab claw morphology might protect juvenile clams from predation by female *H. sanguineus*. Despite their ability to open and consume young mussels, female crabs did not consume any intact clams in the laboratory, although they readily ate the flesh from pre-opened clams. Female *H. sanguineus* have smaller chelae and face greater mechanical limitations than similar-sized males (McDermott 1999). Differences in chelal morphology associated with gender also affects predation on molluscs by *Carcinus maenas* (Elner 1980).

The present results suggest that *Mytilus edulis* is more vulnerable than *Mercenaria mercenaria* to predation by *H. sanguineus*. In addition to refuge from predation at smaller sizes, *M. mercenaria* typically occurs in sandy or muddy regions of the intertidal zone, whereas *H. sanguineus* is typically found in rocky areas (Ledesma and O'Connor 2001, Lohrer et al. 2000) and is less likely to encounter infaunal clams. Even dense 'seed clam' beds in aquaculture plots might only be susceptible to predation by male crabs. Because mussels are epifaunal and occur in dense assemblages, crabs may locate them more easily than clams. Moreover, mussels are potential prey for both male and female crabs. Mussels, whether in natural or commercial populations, may therefore endure greater predation pressure by *H. sanguineus* than would hard clams.

Although the crab readily consumed bivalves, it mostly ate smaller sizes than it is capable of opening. Larger crabs consumed larger bivalves more often than smaller crabs, but there was no relationship between crab size and prey size consumed. Selection of smaller bivalves by *H. sanguineus* is likely a product of relative shell to chela strength, a hypothesis used to explain the avoidance of large snails by the crab *Hemigrapsus nudus* (Behrens Yamada and Boulding 1998). Female crabs generally have smaller, thinner chelae than males, suggesting a lower level of crushing strength (Brown et al. 1979, Warner and Jones 1976), and mussel shell strength increases with the cube of length (Elner and Hughes 1978). As a result, females and smaller males probably select smaller prey because of fewer mechanical limitations, consuming more small prey because they yield more readily. The pattern of breakage among shell fragments from prey in the aquaria supports this hypothesis. In addition to outright crushing, females and smaller males often had to employ umbo crushing, exploiting the oldest, weakest part of the shell (Currey 1977) to open small bivalves. In contrast, larger males were capable of crushing even larger bivalves. It may be that

larger males select small bivalves to minimize handling times, an advantage in the intertidal zone where time for foraging is limited.

It remains uncertain whether *H. sanguineus* has the potential to affect populations of the gastropod snail *L. littorea* through direct predation. Results suggest *L. littorea* is protected at least in part by the morphology or thickness of its shell. In the present study few crabs consumed littorine snails in the laboratory, with only seven small snails consumed, all by large male crabs. Furthermore, those snails were not crushed outright but opened through breakage of the aperture. Many unsuccessful attempts at opening snails, in the form of clipped aperture edges and shredded operculum, were observed at the end of the feeding trial. Gastropod shells are spherical or conical in shape and generally more robust than bivalve shells due to coiling of the shell wall (Lawton and Hughes 1985). The geometric shape of the shell may influence the crab's ability to successfully open and eat the snails regardless of crab size (Lawton and Hughes 1985).

While the inability of *H. sanguineus* to consume *L. littorea* is consistent with recent studies (McNamee and Whitlatch 1999, Tyrrell and Harris 1999), *L. littorea* was found in gut contents of Asian shore crabs (Lohrer and Whitlatch 1997), and *H. sanguineus* consumed *L. littorea* in a laboratory feeding study (Gerard et al. 1999). Methods used for prey immobilization in the present study may have affected the results. Immobilizing snails caused them to draw their operculum deep within their shell, which may have restricted the crabs' ability to extract the flesh from the shell, even with extensive apertural breakage. The reaction of the snail to immobilization methods may be an exaggeration of its natural behavioral response to predation, making it more resistant to attack.

In addition to eating small bivalves, *H. sanguineus* readily consumed green macroalgae, preferring *Codium fragile* ssp. *tomentosoides* and *Enteromorpha* spp. to the red alga *Chondrus crispus* and the brown algae *Fucus* spp. and *Ascophyllum nodosum*, in both no-choice and multiple-choice feeding preference tests. Little *Chondrus*, *Fucus*, and *Ascophyllum* were consumed during the feeding trials, supporting previous studies that found intertidal grapsid crabs rely heavily on green algae for food (Birch 1979, Hiatt 1948, Kramer 1967).

Herbivore food choice is influenced by a complex array of factors (reviewed by Lubchenco and Gaines 1981). Many algae possess chemical (e.g., Conover and Sieburth 1965, Hay and Fenical 1988, Irelan and Horn 1991, Sieburth 1969, Steinberg 1985, Targett et al. 1992, Van Alstyne and Paul 1990) and structural (Kennish and Williams 1997, Littler et al. 1983) defenses that deter feeding and affect dietary preferences of marine herbivores, as do synergistic mechanisms between these defenses (Duffy and Hay 1990, Hay et al. 1994). Tannins, which influence the prey preference of detritivorous crabs (Lee 1988), occur in both

Fucus and *Ascophyllum* (Nicotri 1980), and a number of halogenated compounds, which could play an anti-herbivore role, are prevalent in red algae (Fenical 1975, Hornsey and Hilde 1974). In contrast, *Enteromorpha*, a thin, filamentous alga, has high caloric value (Paine and Vadas 1969a) and does not appear to contain secondary metabolites (Wylie and Paul 1988). Therefore *Enteromorpha* may be more palatable than *Chondrus*, *Fucus*, or *Ascophyllum*, making it more susceptible to grazing by *H. sanguineus*.

The high relative consumption of *Codium* by *H. sanguineus* was unexpected. *Codium* is typically ignored or eaten in limited quantities by generalist marine herbivores (Nicotri 1980; Santelices et al. 1981; Trowbridge 1992, 1995). Along with having low caloric value (Paine 1966), *Codium* contains calcareous deposits (Prescott 1968) and unstable chemical compounds (Trowbridge 1995) that may deter herbivory. However, preference for algal species of lower caloric content by marine herbivores is not unusual (Carefoot 1973, Coen 1988, Larson et al. 1980, Nicotri 1980, Paine and Vadas 1969b, Vadas 1977). Yet, high relative availability, a suggested basis for such selection (Kilar and Lou 1984, Nicotri 1980), does not adequately explain the selection of *Codium* by *H. sanguineus*. *Codium* is rare in the guts of wild crabs (Ledesma and O'Connor 2001, Lohrer and Whitlatch 1997), suggesting it may not be an available food resource for the crab. *Codium* is primarily a subtidal species in the western Atlantic (Hanisak 1979, 1980) and was rarely observed in the intertidal sampling sites during the course of the study. If *H. sanguineus* is using *Codium* as a food source in the field, it may be consuming drift forms, washed ashore by storms, which were very common at both sampling sites throughout the year.

In summary, *H. sanguineus* is omnivorous, feeding readily on both molluscs and macroalgae. However, the algae and molluscs used in this study represent only a portion of the prey available to the crab, and simple laboratory experiments may not be representative of natural situations where alternative prey are generally available. Both prey preference and availability of prey are likely to be important determinants of prey consumption. Tyrrell and Harris (1999) found that drift algae, drift marsh grass, and fucoids were common both in the area where *H. sanguineus* was collected and in the crabs' guts. For animal prey, the ability of the crabs to successfully attack the prey will determine consumption, and sessile forms might be more vulnerable than mobile or cryptic prey. Future studies of the potential effects of predation by *H. sanguineus* in rocky intertidal communities should prove useful as these generalist crabs are very abundant (up to 80/m², unpubl. data, N. O'Connor) and likely to impact prey populations in their new range in the northwestern Atlantic Ocean.

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