Home and away: comparisons of resource utilization by a marine species in native and invaded habitats

Andrew M. Lohrer[1,5,*], Robert B. Whitlatch[2], Keiji Wada[3] & Yasuo Fukui[4]

[1]*Department of Ecology and Evolutionary Biology, University of Connecticut Box U-3043, Storrs, CT 06269, USA;* [2]*Department of Marine Sciences, University of Connecticut, Groton, CT 06340, USA;* [3]*Department of Biological Science, Faculty of Science, Nara Women's University Kitauoya-nishi-machi, Nara 630 Japan;* [4]*Course of General Education, Naniwa College, 2-14-19 Yata, Higashi-sumiyoshi, Osaka 546 Japan;* [5]*Present address: Baruch Marine Field Laboratory, University of South Carolina, P.O. Box 1630, Georgetown, SC 29442, USA;* *Author for correspondence (e-mail: lohrer@belle.baruch.sc.edu; fax: +1-843-546-1632)*

Abstract

The exotic Asian shore crab, *Hemigrapsus sanguineus*, was recently introduced to the northeastern coast of North America and during the 1990's breeding populations were established throughout southern New England. In 1997–1998, ecological studies of several co-occurring brachyuran crabs were conducted in native (Tanabe Bay, Japan) and invaded (Long Island Sound, USA) habitats of *H. sanguineus*. Standardized comparisons of *H. sanguineus* were made between the 2 habitats using data on crab sizes, utilization of space, and food habits. Results revealed that (1) the resource use of *H. sanguineus* was quite different from that of other resident species in its invaded habitat, and (2) there were no substantial changes in resource utilization by *H. sanguineus* after it became established in the invaded habitat (relative to native Tanabe Bay). Differing patterns of resource use by *H. sanguineus* and other crabs in the invaded habitat, the lack of restriction in resource use by *H. sanguineus* following its introduction, and the climatological and physical similarities between native and invaded regions likely contributed to the successful invasion of *H. sanguineus* into rocky intertidal habitats in southern New England.

Abbreviations: LIS – Long Island Sound, USA (in the invaded range of *H. sanguineus*); TB – Tanabe Bay, Japan (in the native range of *H. sanguineus*); NH, MS, BP, PJ – the 4 invaded study sites referring to New Haven, Millstone, and Bluff Point, CT, and Point Judith, RI; CW – carapace width (size of crab)

Introduction

A major research priority is to understand factors influencing invasion success by exotic species. Several investigators have attempted to identify species traits (i.e., life-history strategies, trophic positions) which are correlated with invasion success (O'Connor 1986; Ehrlich 1986, 1989; Rejmánek and Richardson 1996; Williamson and Fitter 1996). Others have suggested that attributes of a community (i.e., species diversity, level of disturbance) affect its ability to resist invasion by exotic species (e.g., Hobbs 1989; Case 1990; Tilman 1997; Stachowicz et al. 1999). Results from theoretical studies and correlative data from terrestrial systems provide most of the information used by invasion ecologists (Carlton 1995; reviews by Elton 1958; Hengefeld 1989; Drake et al. 1989; Williamson 1996). Since no compelling patterns have emerged to inspire consensus (Wiser et al. 1998), careful examination of invasions on a case-by-case basis may ultimately prove more

useful than the broad correlative approaches attempted previously.

Successful invasion by a particular species is likely contingent upon multiple complementary factors, one of which is the availability of essential resources in the invaded habitat. Resource availability may differ greatly between native and invaded habitats because of resource supply discrepancies and/or because patterns of resource utilization by other species differ between regions. Depending on the types of species in each region, interactions with other species may differ in intensity or outcome after an alien arrives in a new habitat. Therefore, the ecological milieu in invaded and native habitats likely dictates whether (a) the resource use patterns of an alien species remain essentially unchanged after it invades a new habitat or (b) whether resource use is expanded or contracted relative to the native habitat. To differentiate among these invasion scenarios, resource use must be compared systematically in native and invaded habitats. While this approach shows promise, published accounts of native-invaded comparisons (e.g., Suarez et al. 1999) are extremely rare, especially in the marine biological literature (JT Carlton, personal communication).

Hemigrapsus sanguineus, a grapsid shore crab indigenous to Japan and other western Pacific regions, was recently introduced to the Atlantic coast of North America (McDermott 1991). First reported in southern New Jersey in 1988 (Williams and McDermott 1990), the crab now ranges from North Carolina to New Hampshire (McDermott 1998b; AH Hines and MC Tyrrell, personal communications). *H. sanguineus* is frequently the most abundant crab in a variety of rocky intertidal habitats in southern New England (Lohrer and Whitlatch 1997). Rigorous comparisons of *H. sanguineus* in native and invaded habitats have not been possible because basic ecological parameters are still largely undescribed in both geographical locations (Kikuchi et al. 1981; but see Fukui 1988; Lohrer and Whitlatch 1997; McDermott 1998a,b; Lohrer et al. 2000; Gerard et al. 1999).

Many of the same physical and climatological conditions that occur along Japan's eastern coastline also occur along the United States' eastern coastline (McDermott 1998b). The current latitudinal range of *H. sanguineus* in North America (36° N to 42° N) is well within its observed latitudinal range in Asia (roughly 20° N to 50° N) (Sakai 1976; Takahashi et al. 1985; McDermott 1998b). While the exact location of the source population from Asia is not known,

H. sanguineus apparently survives well in intertidal areas during cold winters and hot summers in its native range; minimum intertidal temperatures are well below freezing in the north (e.g., Takahashi et al. 1985) and maximum temperatures are $30 + {}^\circ$C in the southern part of its Asian range (e.g., Pillay and Ono 1978). Within a given area, *H. sanguineus* can tolerate a wide range of physical conditions (e.g., Depledge 1984) and it has thrived in climatologically dynamic portions of New England (McDermott 1998b; AM Lohrer, personal observations). The similarity in regimes of physical stress in native and invaded habitats (i.e., 'donor' and 'recipient' regions – Carlton 1996; Williamson 1996) may be an important reason for the successful establishment of *H. sanguineus* in North America.

Several observations suggest that biological factors may also have affected the success of *H. sanguineus* in invaded habitats. For example, populations of *H. sanguineus* in its native habitat are often heavily infested by a rhizocephalan barnacle species that inhibits growth and reproduction, whereas crabs are apparently free from this damaging parasite in the invaded range of *H. sanguineus* (Takahashi and Matsuura 1994; Lützen and Takahashi 1997; Takahashi et al. 1997; Kuris, pers. comm.). Furthermore, *H. sanguineus* comes from a region of extremely high crab diversity (Sakai 1976; Fukui and Wada 1983) relative to the eastern coastline of the US (Williams 1984) and, therefore, interference from other crabs may be less important for populations of *H. sanguineus* in its invaded range.

This investigation primarily focuses on biological/ecological factors that may have influenced this invasion, specifically, patterns of resource use and partitioning by the guild of crabs in the invaded habitat of *H. sanguineus* relative to patterns of resource use and partitioning in the native habitat of this alien. *H. sanguineus* was ideal for use in this exercise because: (1) the appearance of *H. sanguineus* in Long Island Sound (LIS) (USA) was noted only 6 or 7 years ago (Carlton 1993), (2) *H. sanguineus* is a common and conspicuous member of rocky intertidal communities in both regions, and (3) *H. sanguineus* usually co-occurs with other brachyuran crab species in these habitats (i.e., patterns of resource overlap among the guild of crabs in each habitat can be quantified). While native-invaded comparisons across a broad range of latitude in each geographic region are ultimately desired, this study was conducted as a preliminary step toward that goal.

Methods

At sites within the native and invaded ranges of
H. sanguineus, data were collected on (1) population
size-structure of co-occurring crabs, (2) the use of
space by crabs at 2 different spatial scales, and (3) the
patterns of food utilization by crabs. These 3 dimen-
sions of the niche were likely important to the fitness
of *H. sanguineus* in both habitats and data collection
was standardized to make proper comparisons between
regions. While crab size is not a resource *per se*, it
potentially affects shelter requirements (e.g., Eggleston
et al. 1990; Beck 1995, Lohrer et al. 2000) as well as
agonistic and predator–prey interactions of the crabs
(e.g., Elner and Hughes 1978; Eggleston 1990; Lee
and Seed 1992; Fernandez et al. 1993, Moksnes et al.
1998; see also Hutchinson 1957). The principal param-
eters examined in this study were chosen to satisfy

2 goals: (1) to gain insight into how *H. sanguineus*
successfully invaded rocky intertidal habitats in eastern
North America, and (2) to provide basic ecological data
from which the future impacts and invasion potential
of this species can be predicted.

Study areas

Comparable and representative sites within the native
and invaded ranges of *H. sanguineus* were selected
and standardized sampling methods were used in both
regions. Sampling in the invaded range was con-
ducted at 4 locations in eastern LIS, USA (41° N,
73–71° W; Figure 1). Spanning an east–west distance
of approximately 160 km, these sites varied in sub-
strate composition, exposure level, tidal amplitude,
and dominant macro-flora/fauna (Lohrer and Whitlatch
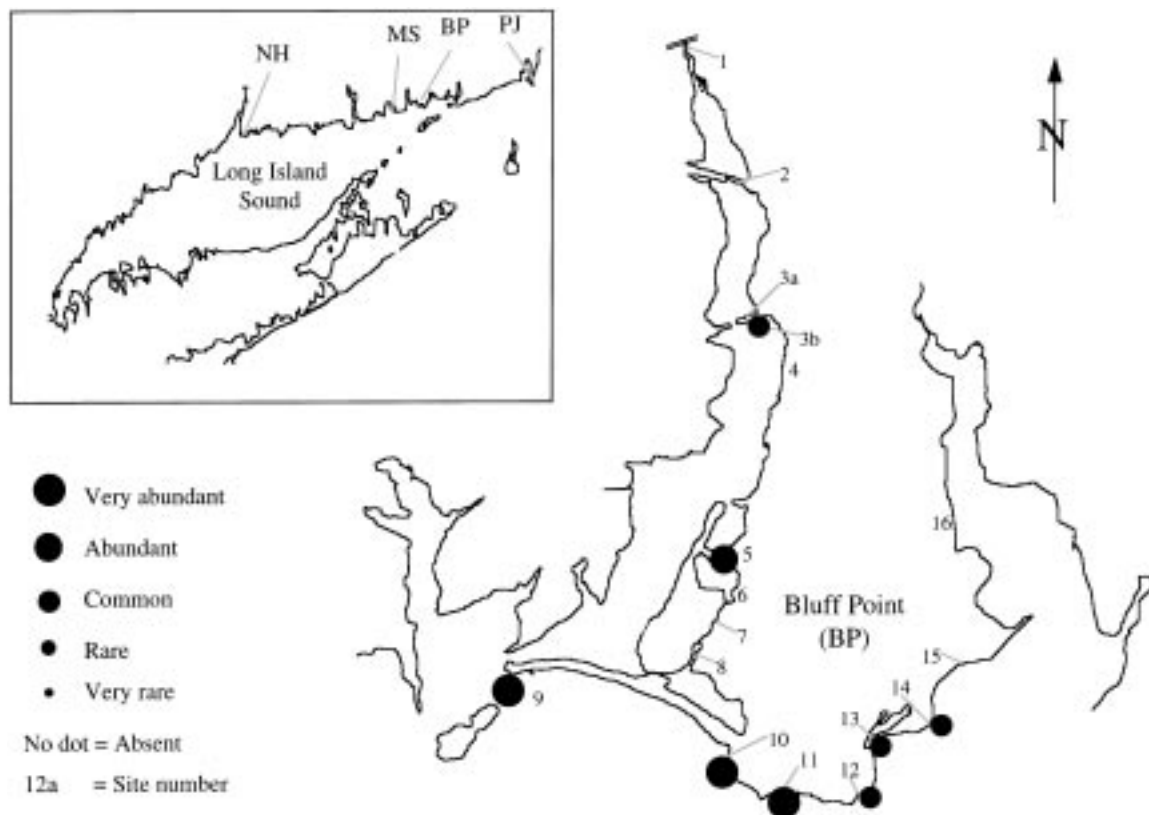1997). Sampling in the native range of *H. sanguineus*

Figure 1. Map of habitat use survey sites in the invaded range of *H. sanguineus*. Inset shows the location of Bluff Point (BP) and 3 quantitatively sampled sites in eastern Long Island Sound, USA: NH = New Haven, MS = Millstone, and PJ = Point Judith. Relative abundance of *H. sanguineus* is denoted with black dots of various size. For definition of dot size see lower left of figure and explanation in text. Information about each numbered site contained in Appendix 1.
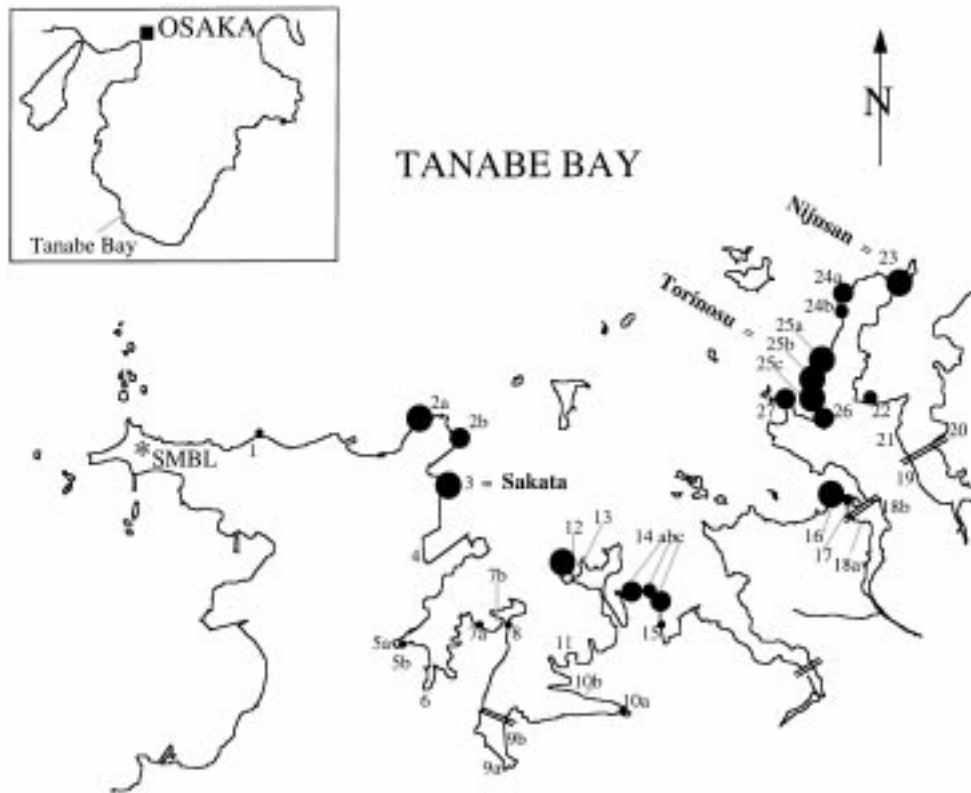
44

Figure 2. Map of habitat use survey sites within the native range of *H. sanguineus*. Sakata, Nijusan, and Torinosu were the 3 collection sites for crab diet studies, and Torinosu was used to assess crab species vertical distributions. Methods of data collection in TB were the same as in LIS. See previous figure for map legend.

was conducted in Tanabe Bay (TB), Japan (33.5° N, 135° W). While TB is significantly smaller and farther south than LIS, the area was chosen for a variety of reasons: First, TB, on the Pacific coast of central Japan, is near the middle of this species' geographic range, and habitats differing in substrate type, exposure regime, and species composition were available for study (Ohgaki et al. 1997) (Figure 2). Second, *H. sanguineus* is common in TB (Fukui and Wada 1983) and previous studies on *H. sanguineus* and other co-occurring grapsid crabs have been conducted in this area (Fukui 1988).

Habitat use by H. sanguineus

In 1998, a systematic survey over a wide range of habitat types was conducted in TB and around Bluff Point (BP), in eastern LIS (Figures 1 and 2). Roughly equal amounts of shoreline (≈ 5 km) were covered in both

surveys. Because of the more convoluted coastline and greater diversity of habitats in TB, more sites were sampled there ($n = 36$) than were sampled at BP ($n = 17$). All sites around TB and BP were sampled using the same protocol. While standing at the upper tide mark of each site, a visual estimate of stone cover was made over a broad area (roughly 10 m × 5 m). The predominant sediment type of the habitat (e.g., mud, sand, gravel, or shellhash), and the level of stone burial in sediments (none, low, moderate, high) was qualitatively assessed. The exposure level of the habitat was indexed from low (e.g., protected embayments) to high (e.g., exposed headlands). Brackish conditions were noted where appreciable inputs of freshwater occurred (e.g., streams, storm drain run-off). After the site was characterized, active searching for *H. sanguineus* (> 8 mm carapace width) was undertaken for 5 min. The relative abundance of *H. sanguineus* was described using an index: absent, very rare (1 individual found), rare (2–5 individuals), common (10–20 crabs), abundant

($\approx$ 25–50 crabs), very abundant ($\approx$ 50–100 crabs). The TB and BP surveys were carried out over 2–3 days, and were duplicated (> 1 month later) at both locations.

Within-habitat spatial distributions
of rocky intertidal crab species

The vertical distributions of several co-occurring crab species were determined by sampling 5 randomly positioned quadrats at each of 4 tidal heights within a site (quadrat size = $1\,\text{m}^2$; n_{total} = 20; see Lohrer and Whitlatch 1997). Two of the equally-spaced tidal heights were below the mid-tide level and 2 were above it. Three intertidal habitats were quantitatively sampled in LIS, each done during spring low tides in both June and August, 1997. One comparable shoreline was sampled in TB (Torinosu, site 25, Figure 2) during a spring low tide in late March 1998. Sampling spanned 200–300 m of similarly-sloped cobble shoreline at each site.

Prior to searching a quadrat for crabs, relative cover (% within $1\,\text{m}^2$) of 4 stone size-categories (boulders, large cobbles, small cobbles, and rocks) was estimated. Additionally, sediment type beneath the stones was noted, species lists of conspicuous organisms (e.g., barnacles, mussels, filamentous algae) were compiled, and % coverage of canopy-forming macroalgal species was estimated. These data were used to characterize shelter and food availability at the sites. Stones were removed during quadrat sampling, and all brachyuran crabs were identified, sexed, checked for general condition (e.g., gravid, parasitized, missing chelae, postmolt), measured, and then released again. Handling mortality was < 1%. Mean densities ($\pm$ 1 S.E.) of all common brachyuran species were calculated at each of 4 tidal heights within all sites on every sampling date.

Diet studies

Collections for gut content analysis of crabs were done at or before dawn on ebbing tides since intertidal crabs generally forage during darkness while submerged (e.g., Lindberg 1980; Willason 1981; Batie 1983; Depledge 1984; Saigusa and Kawagoye 1997). Crabs were immediately placed on ice and frozen within an hour in the laboratory. Crabs clearly in pre- and post-molt condition (Vigh and Fingerman 1985) were excluded from analysis. Following removal of the gastric mill under a dissecting microscope, the percent fullness of the gut was estimated. Stomach contents were placed in a petri dish and food items were identified. Visually, each item was ranked (by volume) relative to the other food items found with it. The percent contribution of each food item to the overall diet of a species was calculated using gut fullness as a weighting factor (e.g., Hines 1982).

The diet of *H. sanguineus* in TB and LIS was assessed at 3 locations in each region. In 1997, collections were made adjacent to the NH, MS, and PJ sampling sites in LIS (Figure 1) since crab densities, food types present, and exposure levels of these sites were well characterized. Collections were made from a comparable set of sites in TB in 1998 (Figure 2). Sakata, Nijusan, and Torinosu (like the 3 LIS sites) were well-studied rocky intertidal habitats where *H. sanguineus* was common. Sakata was chosen for its similarity to the NH site, and Torinosu–MS and Nijusan–PJ were also comparable. Guts from 96 and 71 *H. sanguineus* were analyzed from LIS and TB, respectively.

Diet overlap analyses of co-occurring brachyuran crabs were limited to numerically dominant species at 2 sites in LIS and 1 site in TB: *Eurypanopeus depressus*, a native xanthid, and *H. sanguineus* co-exist at NH (Figure 3); *Carcinus maenas*, a portunid introduced to New England almost 200 years ago (Say 1817; Cohen et al. 1995), and *H. sanguineus* co-occurred at MS (Figure 3); Three species (*Gaetice depressus* [Grapsidae], *Leptodius exaratus* [Xanthidae], and *H. sanguineus*) were all collected from the Torinosu site in TB. Dietary comparisons were made through analysis of 20–30 non-empty guts from each co-occurring species at each site.

Comparative analyses of resource use

A number of indices (i.e., niche metrics) are available to quantify the breadth of resource utilization by a single species and the overlap in resource utilization for pairs of species (e.g., Levins 1968; Colwell and Futuyma 1971; Schoener 1974; Hulbert 1978; Petraitis 1979). These metrics were calculated in order to compare resource use by crabs in native and invaded ranges of *H. sanguineus*. Most niche metrics examine the proportional utilization of available resources by species (the relative exclusivity or generality in use over a variety of resource choices). Following Hines (1982), the 2 simplest indexes were used. The niche breadth (*B*) of species '*i*' is given by
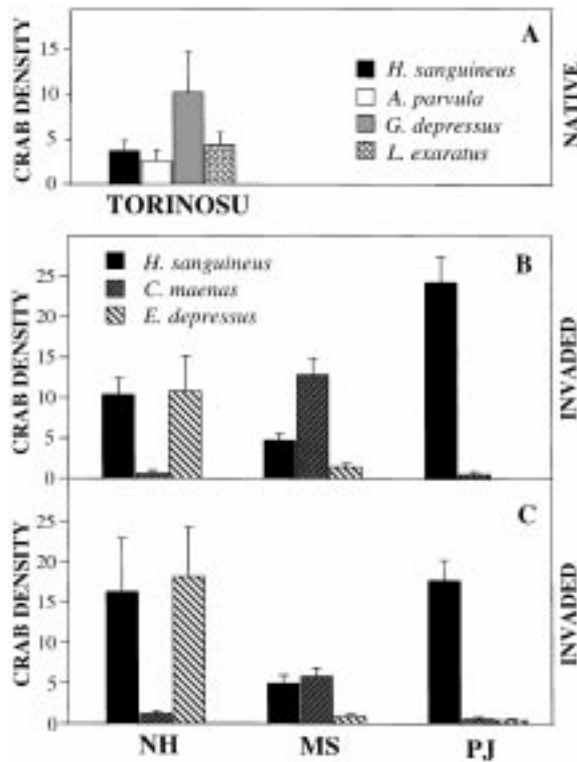
$$B_i = 1/\sum p_{ij}^2$$

Figure 3. Overall densities (# crabs m^{-2}, mean + 1 S.E.) of *H. sanguineus* (black bars) and several other brachyuran species inhabiting 4 rocky intertidal sites: A = Torinosu, March 1998; B = NH, MS, and PJ, June 1997; C = same invaded sites, August 1997.

where p_{ij} is the proportion of individuals of species 'i' associated with resource state 'j'. The niche overlap (C) between species 'h' and 'i' is given by

$$C_{ih} = 1 - 1/2 \sum \left| p_{ij} - p_{hj} \right|$$

where p_{ij} is the same as above and p_{hj} is the proportional use of resource 'j' by species 'h'. Overlap calculations are bounded by 0 (no overlap) and 1 (complete overlap). The designation of various resource categories was standardized in both native and invaded habitats in order to reduce a number of potential biases (Colwell and Futuyma 1971). To calculate crab size-overlap, the values p_{ij} and p_{hj} were taken as the proportion of crabs in different 5 mm size-categories of carapace width (CW). For spatial niche breadth and overlap, the proportion of crabs found at 4 intertidal heights within sites was used for p_{ij} and p_{hj} values. For food use, the proportional contributions of the food categories to crab diets yielded p_{ij} and p_{hj} values. Crabs were lumped into 2 groups (i.e., *H. sanguineus* and

'all others') in order to compare *H. sanguineus* overlap values in native and invaded habitats.

It appeared likely, *a priori*, that *H. sanguineus* had low overlap with other co-occurring crabs in the invaded habitat. To conservatively test this idea, the analyses were constrained so that overlap values would be maximized. Furthermore, resource availability likely affects resource utilization and, therefore, sampling protocol and data analyses were designed to account for this to the greatest possible extent. For example, while there were differences in collection dates between native and invaded sites (which could affect vertical distributions, size-structures, and diets of the co-occurring crabs), the bias was reduced by calculating breadth and overlap values for crabs *within* sites and *within* dates. Presumably, crabs present at the same site on the same date had the same types/amounts of resources available to them; this reduced the likelihood that resource availability alone explained the observed patterns of resources use. When multiple sites and dates were used (i.e., in the invaded habitats), the metrics were averaged after being calculated separately (and, thus, estimates of variance were also available in some cases).

Results

Crab species richness and taxonomic relatedness in native and invaded habitats

There were significant differences in species richness and taxonomic relatedness of crabs in the native and invaded ranges of *H. sanguineus*. Surveys in intertidal cobble habitats of TB revealed 20+ crab species, mostly Grapsidae and Xanthidae (personal observations; Fukui and Wada 1983), and 11 species co-occurred with *H. sanguineus* at various densities during this study (i.e., at least 1 individual per species was collected from a quadrat containing *H. sanguineus*). In addition to the relatively high diversity of crabs, there were a number of species in the same subfamily as *H. sanguineus* and at least one congener (*Hemigrapsus penicillatus*). In contrast, relatively few crab species inhabited rocky intertidal habitats in LIS: *H. sanguineus*, *E. depressus*, and *C. maenas* were the only crabs commonly found in this habitat type. These three species, each from separate crab families (Grapsidae, Xanthidae, and Portunidae, respectively), made up > 99% of the crabs found. Two species

of cancrid crabs (*Cancer borealis*, *Cancer irroratus*) occasionally co-occurred with *H. sanguineus* at PJ, and *Panopeus herbstii* (Xanthidae) occasionally co-occurred with *H. sanguineus* at NH.

Relative use of various habitat types by
H. sanguineus

At TB and BP, habitat utilization patterns by *H. sanguineus* were quite similar. *H. sanguineus* was predominantly found on moderately-exposed shores in both locations, and was rare or absent in protected sites (Figures 1 and 2). Other factors apparently governing relative abundance patterns of *H. sanguineus* were also consistent between native and invaded sites. For example, the presence of loose stones atop the substrate appeared important, as this species was always found beneath stones during daytime low tides in TB and LIS and was most abundant where cobble and boulder piles provided structure (see also Kikuchi et al. 1981; Fukui and Wada 1983; Takahashi et al. 1985; Fukui 1988; Lohrer et al. 2000). During this investigation, *H. sanguineus* was never observed among marsh grasses in the absence of cobbles and boulders. However, when cobbles and boulders were scattered among plant shoots, marsh areas were occasionally occupied (e.g., BP sites 5 and 14, Appendix 1). Lower densities of *H. sanguineus* were recorded in areas where heavy sedimentary burial of loose stones occurred (Appendix 1) and *H. sanguineus* was never found in excavated burrows (personal observations). Protected areas generally had more sedimentary burial, smaller sediment grain size, and were often influenced by freshwater inputs (Appendix 1). While *H. sanguineus* has been reported to occasionally extend into shallow subtidal habitats (Takahashi et al. 1985; M. Syslo, pers. comm.; T. Furota, pers. comm.), no crabs were found below the level of maximum low tide in either TB or LIS during the study period.

Use of 3 rocky sites by crabs in
the invaded habitat

In June and August 1997, *H. sanguineus* was common at all 3 LIS sites, comprising > 40% of the total crabs collected during 5 of the 6 sampling dates (Figure 3(B) and (C)). *C. maenas* and *E. depressus* were only common at one site each. Species-specific differences in habitat utilization patterns were apparent, as each species had maximum densities at different

sites (*E. depressus* exhibited its highest densities at NH, *C. maenas* at MS, and *H. sanguineus* at PJ). *H. sanguineus* was distributed more evenly throughout these 3 sites than the other species were, reflecting relatively broad utilization of different intertidal cobble and boulder habitats. These results were consistent with previous studies (Lohrer and Whitlatch 1997).

Habitat use by co-occurring crabs within sites:
a finer spatial scale

H. sanguineus was found throughout the intertidal zone in both native and invaded habitats (Figure 4). Furthermore, it exhibited a more even distribution across the 4 tidal heights than any of the other species in either region. The uppermost tidal height generally had the fewest *H. sanguineus*, but densities were roughly equal
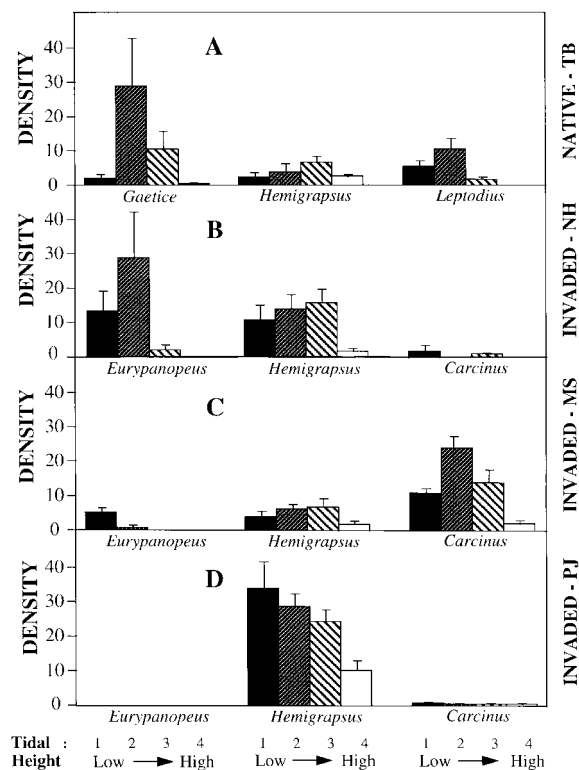

Figure 4. Vertical distributions of crabs at 1 native and 3 invaded sites were characterized by estimating mean densities (# crabs m^{-2}, + 1 S.E.) at 4 different tidal heights per site. The tidal heights 1–4 span from the lower to upper intertidal zone (tidal heights 1 and 2 were below the mid-tide level whereas 3 and 4 were above it). Panel A = Torinosu, March 1998; B = NH, June 1997; C = MS Point, June 1997; D = PJ, June 1997.

in the lower 3 heights; density differences among the lower 3 tidal heights were significant on just one occasion (Tukey HSD tests, $P < 0.05$, 1 of 7 sampling dates). Two small grapsids (*Cyclograpsus intermedius* and *Acmaeopleura parvula*) inhabited the upper intertidal in TB, but this zone was relatively underutilized by other crabs in LIS.

Sizes of H. sanguineus *and co-occurring crabs in native and invaded regions*

H. sanguineus reportedly reaches maximum CW of roughly 40 mm (Fukui 1988). In general, *H. sanguineus* was as large or larger than other co-occurring crabs in both habitats (Figure 5). In TB, where *H. sanguineus* exhibited a relatively even distribution among size-classes, other species were more restricted in size. For example, *G. depressus* and *A. parvula* were always less than 25 mm CW, and *L. exaratus* was generally grouped into larger size classes (i.e., 15–40 mm CW). In invaded habitats,
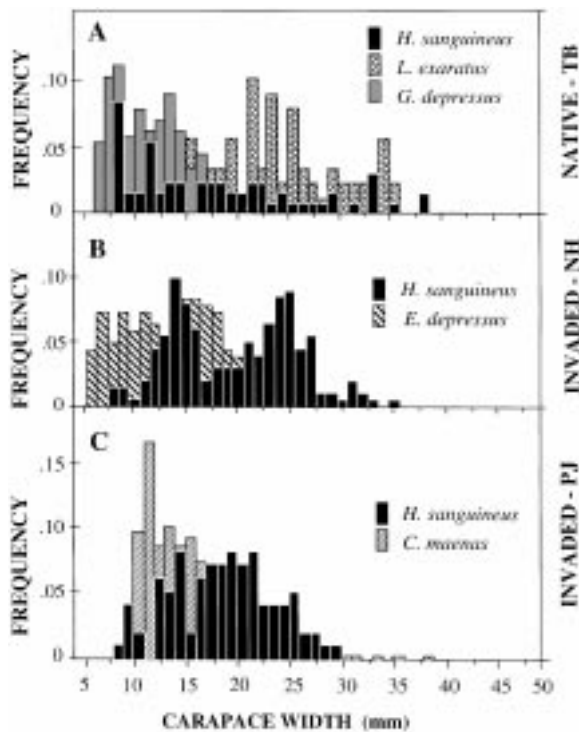

Figure 5. Size frequency distributions of *H. sanguineus* and other co-occurring brachyurans are overlayed at 1 native and 2 invaded sites. A = Torinosu, March 1998; B = NH, June 1997; C = MS, June 1997.

the most informative comparisons were *Hemigrapsus–Carcinus* at MS and *Hemigrapsus–Eurypanopeus* at NH because of low abundances of 1 or both of these other species at certain sites. While *C. maenas* can reportedly reach 65–80 mm CW at its maximum adult size in New England (Ropes 1968; Grosholz and Ruiz 1996), with few exceptions, only recruit and juvenile green crabs were found in the intertidal study sites (Figure 5; see also Elner 1981; Berrill 1982; Reise 1985)

Food utilization of H. sanguineus *in native and invaded habitats*

In both native and invaded habitats, *H. sanguineus* consumed turf-forming red algae, green sheet-like algae, mytilid bivalves, small herbivorous snails, small crustaceans, and polychaete worms (Figure 6). Both male and female *H. sanguineus* generally consumed calcified prey items that were small in size (e.g., snails <4 mm shell height, mussels <10 cm shell length). One notable difference in the diet of *H. sanguineus* was the consumption of barnacles (*Semibalanus balanoides*) in the invaded habitat only (Figure 6). While barnacles (*Balanus albicostatus*, *Chthamalus challengeri*) were fairly common in TB, they were never observed in *H. sanguineus* guts collected there.

Plant material (green, brown, and red algae; vascular plant debris) made up the largest portion of the overall diet of *H. sanguineus* in both native and invaded habitats (Figure 6). Also, most of the unidentified items ('detritus') were probably of plant origin. It was not possible to assess how much plant material was attached and actively grazed by *H. sanguineus*; at least some portion drifted into the intertidal zone where it was encountered by *H. sanguineus* (e.g., *Zostera marina*). While there was considerable variability in diet at the 3 sites in each region, diets of *H. sanguineus* in native and introduced habitats were similar. Animal food items made up roughly 40% of the overall diets in TB and LIS, and in both regions, prey availability and consumption appeared to be linked (Figure 6). For example, NH and Sakata both had elevated polychaete densities and *H. sanguineus* consumed proportionately more polychaetes at these sites. NH also had the highest density barnacle population of the 3 invaded sites, and barnacles were taken by *H. sanguineus* in greater proportions at this site. No mytilid bivalves were observed at NH, and none were found in the guts
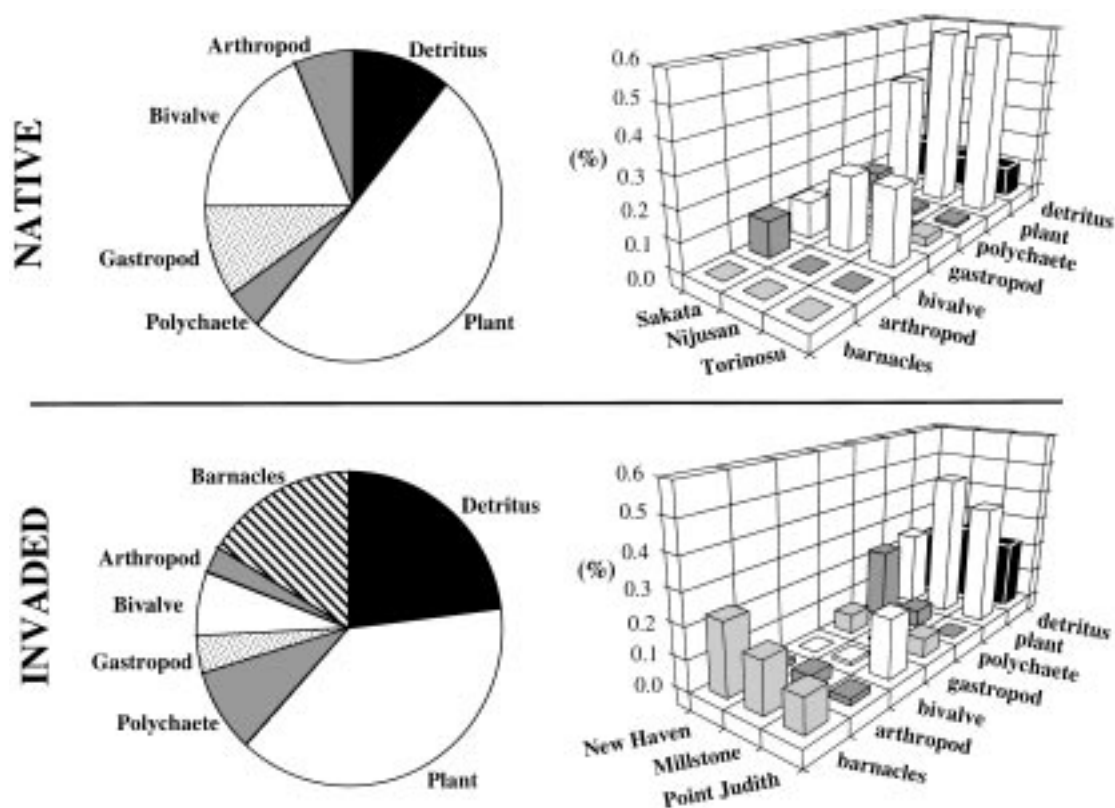
Figure 6. Overall food use of *H. sanguineus* (pie diagrams) and food use at 3 sites in the native and invaded ranges of this species (bar charts). The proportional use of only 7 broad food categories is depicted for clarity.

of *H. sanguineus*. Arthropods (amphipods, isopods, insect larvae, ostracods, and harpacticoid copepods) were 3–4 times more abundant at Sakata relative to Nijusan or Torinosu; arthropods made up a significant proportion of *H. sanguineus* diet at Sakata, but not at the other TB sites mentioned.

Comparisons of co-occurring crab diets in native and invaded sites

Of the 3 brachyuran species collected from Torinosu, *H. sanguineus* consumed the most animal matter and had the broadest diet (Figure 7). While all 3 crab species consumed significant amounts of plant matter, the particular algal species eaten differed among them. For example, *H. sanguineus* primarily consumed *Caulacanthus okamurai* (30% of the diet), an abundant turf-forming red alga found throughout the middle and lower rocky intertidal zone. In contrast, *L. exaratus* consumed *Caulacanthus* (35%) and a crustose red alga, *Lithophyllum* sp. (37%), which grew on hard substrates

in the lower intertidal zone. However, these two algal species taken together made only a 20% proportional contribution to the diet of *G. depressus*.

Crabs collected from LIS tended to have more animal matter in their diets compared to crabs collected in TB (Figure 7). Green crabs, reported to be primarily carnivorous (Ropes 1968, 1989; Elner 1981), readily consumed molluscs, barnacles, and polychaetes (Figure 7). At NH, mud crabs (*E. depressus*) consumed polychaetes and barnacles, but plant material and detritus made up roughly 68% of *E. depressus* diet. As in TB, a number of the same food items were consumed by *H. sanguineus* and other co-occurring species in LIS.

Comparison of niche metrics (breadth and overlap) in native and invaded regions

H. sanguineus was collected from (and therefore utilized) all portions of the intertidal zone (Figure 4) and calculations depicting the breadth in use of this resource (i.e., space/shelter) were relatively
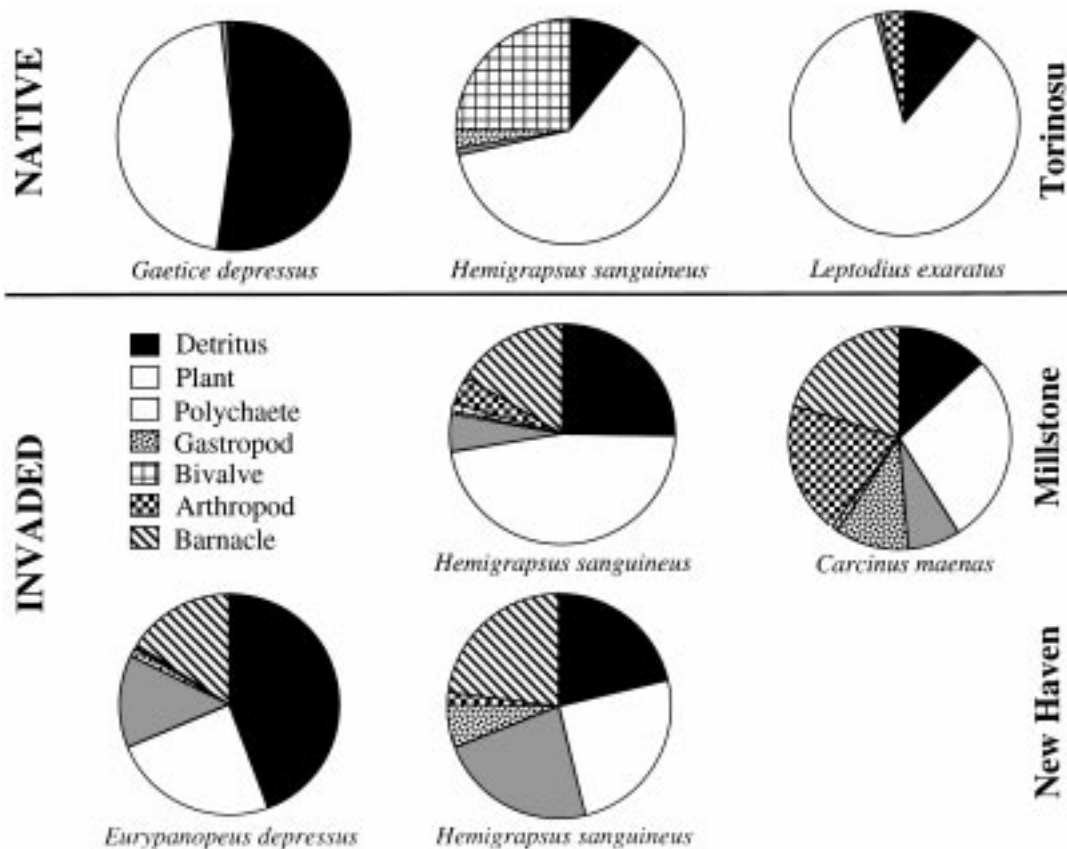
50

Figure 7. Graphical comparison of food use among *H. sanguineus* and other co-occurring crabs in native and invaded habtats. The proportional use of 7 broad food categories is presented (see legend on figure). Diets of *G. depressus*, *H. sanguineus*, and *L. exaratus* were compared at the Torinosu site in TB. Diets of *C. maenas* and *H. sanguineus* were compared at MS Point, CT. Diets of *E. depressus* and *H. sanguineus* were compared at NH, CT.

large compared to calculations for the other co-occurring species (Figure 8). Furthermore, for this resource dimension, breadth values were similar for *H. sanguineus* in native and invaded habitats (3.26 and 3.16 ± 0.30, respectively; mean ± 1 S.E.). Moderately high levels of overlap in the vertical distributions of crabs were observed in both regions. In TB, the spatial overlap value between *H. sanguineus* and 'all other' crabs was 0.63, and in LIS, the average spatial overlap value was 0.67 ± 0.19 (± 1 S.E.). *E. depressus* mostly utilized the lower 2 tidal heights, and therefore, *H. sanguineus* overlapped more with *C. maenas* in invaded sites. In the native habitat, *H. sanguineus* had the most spatial overlap with *G. depressus*, followed by *L. exaratus*, and *A. parvula*.

Large crabs, particularly portunids > 40 mm CW, have been reported to migrate into intertidal areas during high water and leave as the tide recedes (Elner 1981; Warman et al. 1993). While snorkeling surveys and the deployment of crab traps at high water suggested that this was not widespread (Lohrer 2000), the low tide sampling regime would not have effectively sampled large crabs. Calculations describing the amount of overlap in size were only done for crabs sampled at low tide (Figure 5) and the overlap values were probably inflated because of this. This was satisfactory based on a desire to provide maximum estimates of overlap (i.e., to be conservative): *H. sanguineus* had substantial size-overlap with other dominant crabs in TB (0.86) whereas the size overlap between *H. sanguineus* and potential competitors was lower in LIS (0.59 ± 0.04, mean ± 1 S.E.).

H. sanguineus utilized a wide variety of food types in both habitats and diet breadth values were similar in TB

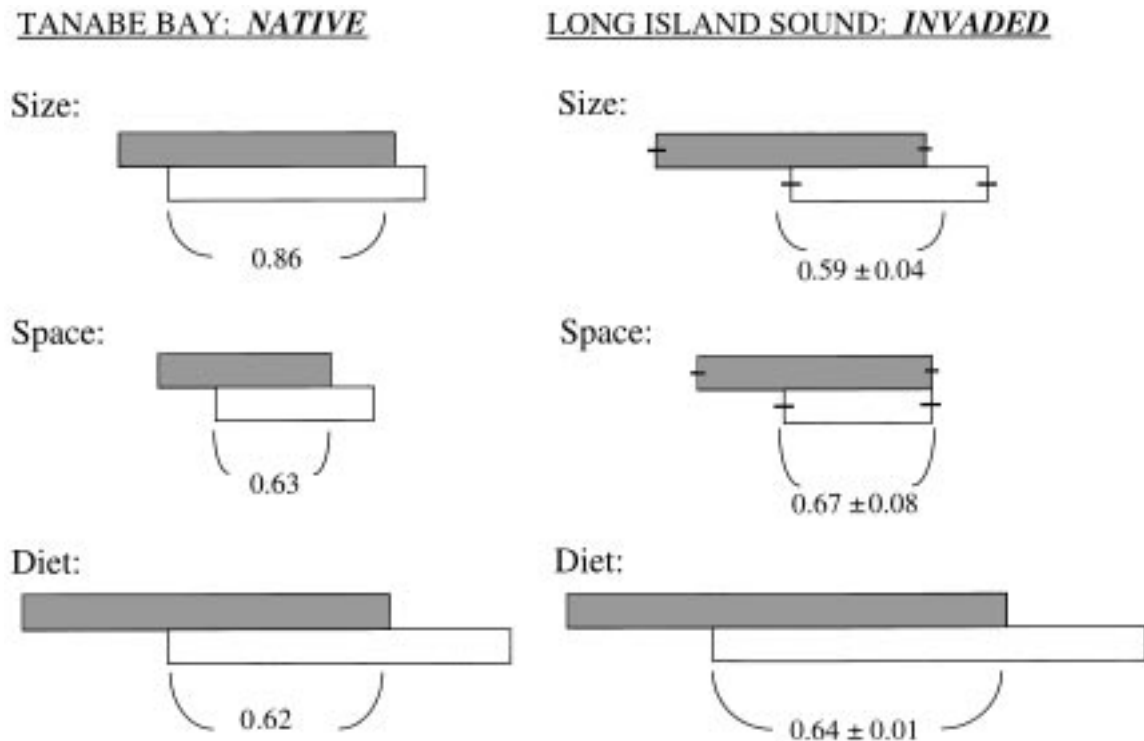TANABE BAY: *NATIVE*   LONG ISLAND SOUND: *INVADED*

Figure 8. Niche ovelap values between *H. sanguineus* and 'all other' co-occurring crab species were compared along 3 dimensions of the niche in both native and invaded habitats. Niche breadths of *H. sanguineus* (filled bars) and 'all others' (empty bars) were drawn roughly to scale.

(6.85 ± 0.77) and LIS (6.32 ± 1.44) (means $\pm$ 1 S.E.). Only *C. maenas* had larger dietary breadth values than *H. sanguineus*. As with the spatial niche dimension, the amount of dietary overlap between *H. sanguineus* and 'all other' crabs was similar in native and invaded habitats (Figure 8).

Discussion

H. sanguineus was reportedly an 'upper intertidal', herbivorous crab species (Kikuchi et al. 1981; Fukui and Wada 1983; Depledge 1984; Takada and Kikuchi 1991; Lafferty and Kuris 1996; McDermott 1992, 1998b). Recent studies, however, have indicated that the crab consumes a significant amount of animal matter and that *H. sanguineus* is predominantly found in middle and lower intertidal zones throughout LIS (Lohrer and Whitlatch 1997; Gerard et al. 1999; Lohrer 2000). These contradicting descriptions of diet and vertical distribution suggested a possible niche shift upon establishment in the invaded habitat. The main goal of this study was to compare habitat and food utilization by *H. sanguineus* in native and invaded ranges, and data analysis was framed to test how resource use by the crabs varied among sites and between regions.

Resource overlap is low among crabs inhabiting LIS

In LIS and throughout the invaded range of *H. sanguineus*, crab diversity is relatively low and the resident crabs are distantly related to this alien species. These facts suggested a limited potential for niche overlap between *H. sanguineus* and other crabs in the region. Measurements of shared resource use by crabs in LIS supported this hypothesis. All 3 estimates of overlap from the invaded habitat were < 0.7 (on a scale from 0 to 1; Figure 8). When all 3 dimensions of the niche were considered simultaneously (i.e., when a 3-dimensional volumetric niche space was created), values of overlap in resource utilization fell between 0.25 and 0.63. The 25% value was derived after assuming that the 3 niche dimensions were completely

independent from each other (and values obtained for each dimension were multiplied together). In contrast, the 63% value was calculated after assuming the 3 niche dimensions were completely correlated (and the 3 values were averaged). The answer likely lies somewhere in between these extreme cases (perhaps closer to the lower value, since conservative calculation methods definitely over-estimated the 3 component values). In summary, other co-occurring crab species did not appear to heavily utilize the resources that *H. sanguineus* used in the invaded habitat, and may not have offered much competitive interference or resistance to the establishment and maintenance of *H. sanguineus* populations along the northeastern coast of North America.

Patterns of resource use were not shifted following the invasion

When native and introduced populations of *H. sanguineus* were compared, no demonstrable shift in the pattern of habitat use was detected. *H. sanguineus* was predominantly found in moderately exposed rocky intertidal areas in both locations (Figures 1 and 2). Within such habitats, there was no appreciable change in the amount of spatial overlap (i.e., vertical partitioning) between *H. sanguineus* and other common crabs when comparing native and invaded sites, and vertical distribution patterns of *H. sanguineus* were similar in both regions (Figure 4). Variation in the vertical zonation of this mobile species is probably mostly explained by seasonality (Lohrer and Whitlatch 1997; Gerard et al. 1999) and by the distribution of available shelter (Lohrer et al. 2000); it does not appear to be a fundamental population-level difference in resource utilization between native and invaded habitats.

Food utilization by *H. sanguineus* was similar in native and invaded sites. There were some taxonomically-based differences in prey species between native and invaded regions. However, the number ($n_{invaded} = 20$, $n_{native} = 17$) and types (e.g., amphipods, mytilid bivalves, gastropods) of food categories identified in the guts were consistent between native and invaded regions. Niche metrics revealed that diet breadth was similar in both regions, and that the amount of dietary overlap between *H. sanguineus* and other common crabs was comparable as well (Figure 8). Measurements of shell strength of several molluscan prey in native and invaded habitats showed that small snails and mussels were similar in strength, or perhaps

weaker, in the invaded habitat (unpublished data on 5 native range and 4 invaded range species). Barnacles were commonly consumed by *H. sanguineus* in LIS, but did not contribute to the diet of this crab in TB. Modes of substrate attachment and shell profile differ for the dominant intertidal barnacle species in LIS and TB, providing a possible mechanism for this finding. For example, *S. balanoides* uses a membranous attachment mechanism (Weiss 1995) and has a moderately angled profile (Anderson 1994). The dominant species in TB either has a calcareous basis (*B. albicostatus*) or a flattened profile (*C. challengeri*); both characters make it more difficult for crabs to pry barnacles from the substrate (Anderson 1994). Furthermore, some of the barnacles in Japan are significantly more robust in appearance than *S. balanoides* (e.g., *Balanus* spp., *Tetraclita* sp., AM Lohrer, pers. obs.) and their strong tests may make them difficult to open.

Collectively, *H. sanguineus* appeared 'pre-adapted' for success along the northeast coast of North America. *H. sanguineus* used space and food resources in LIS in much same way it did in TB, and none of the ecological parameters measured reflected a dramatic niche shift following its establishment in LIS. The likelihood of invasion success is probably greatest in situations where an alien is not forced to substantially constrict its niche or deal with elevated physical/biological stresses. *H. sanguineus*, transported from the northwestern Pacific to the northwestern Atlantic, seems to follow this scenario. While there are likely several more contributing factors that were not addressed during this investigation, this comparative approach provided some ecological insights that were not previously available.

Concluding remarks

Given the broad latitudinal range of *H. sanguineus* in the western Pacific Ocean, what can be learned by examining one population of *H. sanguineus* in Japan? Firstly, in the native range of *H. sanguineus*, there was very little ecological information available on its patterns of resource use and its interactions with other crab species. For example, crab densities and vertical distributions in the rocky intertidal zone were not well characterized for any of the Asian species discussed here. Diets of wild-caught crabs had also not been described for any of the Asian species. The Asian literature that was available, however, was largely consistent with the observations made during this investigation (e.g., with

respect to broad patterns of habitat use, size data, life histories, reports of temperature and osmotic tolerances). Secondly, since data were collected in a similar manner in the invaded range of *H. sanguineus* (e.g., in LIS, USA), comparisons could be made with first hand knowledge of 2 systems studied.

During this investigation, several types of resources used by *H. sanguineus* were identified and quantified. Assuming that the TB population of *H. sanguineus* was fairly representative of other populations in the native range and assuming that *H. sanguineus* had reproductive success when associated with the resource states which were quantified in TB, hypotheses can be made about the resource requirements of this species. The probability of invasion success may have been increased, to some degree, because *H. sanguineus* was introduced to a habitat where the resources it requires were available/underutilized. This study also provided information about the invasive potential of *H. sanguineus* as it spreads to the north (where the resources normally associated with *H. sanguineus* are widely available) and south (where the scarcity of suitable habitat may inhibit the success of *H. sanguineus*).

While biological invasions represent a global threat to biodiversity, the factors affecting invasion success remain in question despite more than 40 years of study (Elton 1958; Williamson 1996; Wiser et al. 1998). In specific cases, however, the problem becomes more tractable. Furthermore, since invasions by individual species ultimately become the data points used to make broader generalizations, accuracy and predictability in the field of invasion ecology depends on sound conclusions from individual case studies. Home and away comparisons (i.e., systematic comparisons of species in their native and invaded ranges) may be important as tools for understanding how individual species successfully invade new habitats. Even in cases where this approach fails, the data will be valuable for assessing ecological and economic impacts and may provide baselines for future investigations.

Acknowledgements

Appendix 1. Relative abundance of *H. sanguineus* in various habitat types in both its invaded and native ranges. Site number refers to numerals displayed on the maps of TB and LIS study location.

Habitat description	Abundance stones	Burial of type	Sediment	Salinity number	Site
Bluff Point, CT, USA					
Marsh edge, below S. alternaflora stands, under *Ascophyllum*-covered cobbles	Absent	High	Thick mud	Seawater	6
Rock fill on a river bank under bridge	Absent	High	mud	Brackish	1
Solid rock substrate meets water's edge; *Spartina, Fucus*, boulders	Absent	High	Muddy sand	Seawater	16
Rock fill under train bridge, square artifical rocks	Absent	Moderate	mud	Brackish	2
Tidal creek, entrance to inner embayment, protected by barrier beach	Absent	Moderate	mud	Seawater	8
Backside (river side) of jetty	Absent	Moderate	Muddy sand	Brackish	3a
Marsh creek drainage, some *Spartina*	Absent	Moderate	Sand	Brackish	15
Inside a bed of *Spartina*	Absent	Low	Muddy sand	Seawater	4
Tidal creek in *Spartina* marsh, heavily silted cobbles	Absent	Low	Muddy sand	Seawater	7
Stones scattered in amongst *Spartina, Fucus*-covered cobbles in front	Common	Moderate	Muddy sand	Seawater	14
Front (ocean side) of jetty	Common	Moderate	Sand	Seawater	3b
Very small cove, next to rocky shore on exposed point	Common	Moderate	Sandy gravel	Seawater	12
Small rocks fairly uniformly distributed on a Sandy shore	Common	Low	Sand	Seawater	13
Marsh edge, below S. *alternaflora* stands, under *Ascophyllum*-covered cobbles	Abundant	High	Thick mud	Seawater	5
Rocky intertidal site, loose stones	Very abundant	Low	gravel	Seawater	10
Rocky point at end of barrier beach, connecting to an island	Very abundant	Low	Sandy gravel	Seawater	9
Solid rock base with scattered boulders, exposed rocky headland	Very abundant	none	None	Seawater	11
Tanabe Bay, Japan					
Inner protected embayment, anoxic mud, oyster shellhash	Absent	High	Thick mud	Brackish	4
Inner protected embayment, anoxic muds	Absent	High	Thick mud	Brackish	5a
Protected, Muddy habitat with oysters common on stones	Absent	High	Thick mud	Seawater	10b
Brackish pond anoxic muds, marsh reeds	Absent	High	Thick mud	Brackish	18a
Very protected mudflat, crab burrows, oyster-covered rocks present	Absent	High	Thick mud	Seawater	19
Large inlet to protected bay, strong tidal currents, buried jetty stones	Absent	High	Thick mud	Seawater	20

Description	Abundance	Height	Substrate	Water	Site
Sloping mudflat with oyster encrusted rocks, protected	Absent	High	Thick mud	Seawater	6
Very protected bay, seawall at edge of mud flat	Absent	High	Mud	Seawater	9a
Jetty stones at base of seawall, no crevices	Absent	High	Mud	Seawater	9b
Stagnant, Muddy flat area with a lot of *Ulva*, occasional rocks	Absent	High	Mud	Seawater	11
Inlet to brackish pond, large cobbles in a human-made dike	Absent	High	Mud	Brackish	18b
Edge of broad mudflat, oysters common of scattered stones	Absent	High	Muddy sand	Seawater	7b
Edge of a protected embayment, few scattered stones next to a wall	Absent	Moderate	Mud	Seawater	21
Course sand flat facing perpendicular to waves, biogenic structures	Absent	Moderate	Sand	Seawater	13
Back of embayment, facing ocean	Very rare	High	Thick mud	Seawater	17
Jetty stones with oyster shells and red algal mat, a few loose stones	Very rare	High	Mud	Seawater	5b
Edge of broad mudflat, rocks clumps against a seawall	Very rare	Moderate	Muddy sand	Brackish	7a
Inner bay, next to sea wall	Very rare	Moderate	Muddy sand	Seawater	15
Protected, Muddy habitat with oyesters common on stones	Very rare	Low	Mud	Brackish	10a
Small rocks on a Muddy beach, protected shore	Very rare	Low	Muddy sand	Seawater	8
Solid rocks reef flat, no loose stones	Very rare	None	None	Seawater	1
Edge of embayment, scattered stones next to a seawall	Rare	Moderate	Muddy sand	Seawater	22
Behind island, scattered stones next to a seawall	Rare	Moderate	Sand	Seawater	14b
Sand flat adjacent to solid rock reef flat, stones patchily distributed	Rare	Moderate	Sand	Seawater	24b
Behind island, scattered stones next to seawall	Common	Moderate	Sand	Seawater	14a
Scattered stones near a seawall, edge of solid rock reef flat	Common	Moderate	Sand	Seawater	14c
Inner part of exposed embayment	Common	Low	Sand	Seawater	26
Exposed cobble shore, heavy human disturbance	Common	Low	Shellhash	Seawater	2b
Exposed solid rock reef flat, loose stones patchily distributed	Common	None	None	Seawater	24a
Exposed solid rock reef flat, loose stones patchily distributed	Common	None	None	Seawater	27
Base of seawall, many large boulders	Abundant	Moderate	Sand	Seawater	3
Small cobble beach on exposed shore of Fujishima Island	Abundant	Low	Sand	Seawater	12
Exposed cobble shore	Abundant	Low	Sand	Seawater	16
Exposed cobble shore	Abundant	Low	Sand	Seawater	25a,b,c
End of Torinosu Point, rocky shore	Abundant	Low	Gravel	Seawater	23
Rocky cove, exposed cobble shore	Abundant	None	None	Seawater	2a

56

References

Anderson DT (1994) Barnacles. Structure, Function, Development, and Evolution. Chapman & Hall, London, 357 pp

Batie RE (1983) Rhythmic locomotor activity in the intertidal shore-crab *Hemigrapsus oregonensis* (Brachyura, Grapsidae) from the Oregon Coast. Northwest Science 57(1): 49–56

Beck MW (1995) Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. Ecology 76(3): 968–980

Berrill M (1982) The life cycle of the green crab *Carcinus maenas* at the northern end of its range. Journal of Crustacean Biology 2(1): 31–39

Carlton JT (1993) A steady stream of invading organisms creates ecological roulette in New England waters. Estuarine Research Federation Newsletter 19(4): 11

Carlton JT (1995) Forward. In: Balcom N (ed) Proceedings of the Northwest Conference on Non-Indigenous Aquatic Nuisance Species. Connecticut Sea Grant College Program, Groton, Connecticut

Carlton JT (1996) Pattern, process, and prediction in marine invasion ecology. Biological Conservation 78: 97–106

Case TJ (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings of the National Academy of Sciences, USA 87: 9610–9614

Cohen AN, Carlton JT and Fountain MC (1995) Introduction, dispersal, and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Marine Biology 122: 225–237

Colwell RK and Futuyma DJ (1971) On the measurement of niche breadth and overlap. Ecology 52: 567–576

Depledge MH (1984) Cardiac activity in the intertidal crab *Hemigrapsus sanguineus* (de Haan). Asian Marine Biology 1: 115–123

Drake JA, Mooney HA, Di Castri F, Groves RH, Kruger M, Rejmanek M and Williamson M (1989) Biological Invasions: A Global Perspective. John Wiley and Sons, New York

Eggleston DB (1990) Functional responses of blue crabs *Callinectes sapidus* Rathbun feeding on juvenile oysters *Crassostrea virginica* (Gmelin): effects of predator sex and size, and prey size. Journal of Experimental Marine Biology and Ecology 143: 73–90

Eggleston DB, Lipcius RN, Miller DL and Coba-Cetina L (1990) Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. Marine Ecology Progress Series 62: 79–88

Ehrlich PR (1986) Which animal will invade? In: Mooney HA and Drake JA (eds) Ecology of Biological Invasions of North America and Hawaii, pp 79–85. Springer, New York

Ehrlich PR (1989) Attributes of invaders and the invading process: vertebrates. In: Drake JA, Mooney HA, Di Castri F, Groves RH, Kruger M, Rejmánek M and Williamson M (eds) Biological Invasions: A Global Perspective, pp 315–328. John Wiley and Sons, New York

Elner RW (1981) Diet of green crab *Carcinus maenas* (L.) from Port Hebert, southwestern Nova Scotia. Journal of Shellfish Research 1(1): 89–94

Elner RW and Hughes RN (1978) Energy maximization in the diet of the shore crab, *Carcinus maenas*. Journal of Animal Ecology 47: 103–116

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Methuen, London, 181 pp

Fernandez M, Iribarne O and Armstrong D (1993) Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. Marine Ecology Progress Series 92(1–2): 171–177

Fukui Y (1988) Comparative studies on the life history of the grapsid crabs (Crustacea, Brachyura) inhabiting intertidal cobble and boulder shores. Publication of the Seto Marine Biological Laboratory 33(4–6): 121–162

Fukui Y and Wada K (1983) Intertidal anomura and brachyura and their distributions on the south coast of Tanabe Bay. The Nanki Biological Society 25(2): 159–167

Gerard VA, Cerrato RM and Larson AA (1999) Potential impacts of a Western Pacific grapsid crab on intertidal communities of the northwestern Atlantic Ocean. Biological Invasions 1: 353–361

Grosholz ED and Ruiz GM (1996) Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenus*. Biological Conservation 78: 59–66.

Hengefeld R (1989) Dynamic of Biological Invasions. Chapman & Hall, London

Hines AH (1982) Coexistence in a kelp forest: size, population dynamics, and resource partitioning in a guild of spider crabs (Brachyura, Majidae). Ecological Monographs 52(2): 179–198

Hobbs RJ (1989) The nature and effect of disturbance relative to invasions. In: Drake JA, Mooney HA, Di Castri F, Groves RH, Kruger M, Rejmánek M and Williamson M (eds) Biological Invasions: A Global Perspective, pp 389-405. John Wiley and Sons, New York

Hulbert SH (1978) The measurement of niche overlap and some relatives. Ecology 59: 67–77

Hutchinson GE (1957) Concluding remarks. In: Cold Spring Harbor Symposium on Quantitative Biology 22: 415–427

Kikuchi T, Tanaka M, Nojima S and Takahashi T (1981) Ecological studies on the pebble crab, *Gaetice depressus* (de Haan). I. Ecological distribution of the crab and environmental conditions. Publication from the Amakusa Marine Biological Laboratory 6(1): 23–34

Lafferty KD and Kuris AM (1996) Biological control of marine pests. Ecology 77(7): 1989–2000

Lee SY and Seed R (1992) Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. Marine Ecology Progress Series 84: 151–160

Levins R (1968) Evolution in changing environments. In: Monographs in Population Ecology. Volume 2. Princeton University Press, Princeton, New Jersey

Lindberg WJ (1980) Behavior of the Oregon mud crab, *Hemigrapsus oregonensis* (Dana) (Brachyura, Grapsidae). Crustaceana 39(3): 262–280

Lohrer AM (2000) Mechanisms and consequences of an exotic crab species invasion. Doctoral Dissertation, University of Connecticut, Storrs, Connecticut, 147 pp

Lohrer AM and Whitlatch RB (1997) Ecological studies on the recently introduced Japanese shore crab (*Hemigrapsus sanguineus*), in eastern Long Island Sound. In: Balcom NC (ed) Proceedings of the Second Northeast Conference on Nonindigenous Aquatic Nuisance Species, pp 49–60. Connecticut Sea Grant College Program, Groton, Connecticut

Lohrer AM, Fukui Y, Wada K and Whitlatch RB (2000) Structural complexity and vertical zonation of intertidal crabs, with focus on the habitat requirements of the invasive Asian shore crab, *Hemigrapsus sanguineus* (de Haan). Journal of Experimental Marine Biology and Ecology 244: 203–217

Lützen J and Takahashi T (1997) *Sacculina polygenea*, a new species of rhizocephalan (Cirrepedia: Rhizocephala) from Japan, parasitic on the intertidal crab *Hemigrapsus sanguineus* (De Haan, 1835) (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 (1992) Biology of the Western Pacific crab, *Hemigrapsus sanguineus*, living along the mid-Atlantic coast of the United States. American Zoologist 32(5): 73A

McDermott JJ (1998a) The western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Altlantic coast of the Untied States: reproduction. Journal of Crustacean Biology 18(2): 308–316

McDermott JJ (1998b) The western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Altlantic coast of the Untied States: geographic distribution and ecology. ICES Journal of Marine Science 55(2): 289–298

Moksnes P-O, Pihl L and van Montfrans J (1998) Predation on postlarvae and juveniles of the shorecrab *Carcinus maenas*: importance of shelter, size, and cannibalism. Marine Ecology Progress Series 166: 211–225

O'Connor RJ (1986) Biological characteristics of invaders among bird species in Britain. Philosophical Transactions of the Royal Society of London B, Biological Sciences 314: 583–598

Ohgaki S, Yamanishi R, Nabeshima Y and Wada K (1997) Distribution of intertidal macrobenthos in 1993 around Hatakejima Island, central Japan, compared with 1969 and 1983–84. Benthos Research 52(2): 89–102

Petraitis PS (1979) Likelihood measures of niche breadth and overlap. Ecology 60: 703–710

Pillay KK and Ono Y (1978) The breeding cycles of 2 species of grapsid crabs (Crustacea: Decapoda) from the North Coast of Kyushu, Japan. Marine Biology 45(3): 237–248

Reise K (1985) Tidal Flat Ecology. Springer-Verlag, Berlin, Germany

Rejmánek M and Richardson, DM (1996) What attributes make some plant species more invasive? Ecology 77(6): 1661–1666

Robinson JV and Dickerson JE (1987) Does invasion sequence affect community structure? Ecology 68(3): 587–595

Ropes JW (1968) The feeding habits of the green crab, *Carcinus maenas* (L). US Fish and Wildlife Service, Fisheries Bulletin 67: 183–203

Ropes JW (1989) The food habits of five crab species at Pettaquamscutt River, Rhode Island. US National Marine Fisheries Service, Fisheries Bulletin 87(1): 197–204

Saigusa M and 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

Sakai T (1976) Crabs of Japan and the Adjacent Seas. Kodansha, Tokyo

Say T (1817) An account of the Crustacea of the United States. Journal of the Academy of Natural Sciences of Philadelphia 1: 57–63

Schoener TW (1974) Some methods for calculating competition coefficients from resource-utilization spectra. American Naturalist 108: 332–340

Stachowicz JJ, Whitlatch RB and Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286: 1577–1579

Suarez AV, Tsutsui ND, Holway DA and Case TJ (1999) Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. Biological Invasions 1: 43–53

Takada Y and Kikuchi T (1991) Seasonal and vertical variation of the boulder shore fauna in Amakusa. Publication from the Amakusa Marine Biological Laboratory 11(1): 1–17

Takahashi T and 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: 300–306

Takahashi K, Miyamoto T, Mizutori Y and Ito M (1985) Ecological studies on rocky shore crabs in Oshoro Bay. Scientific Reports of the Hokkaido Fisheries Experimental Station 27: 71–89 [in Japanese with English abstract]

Takahashi T, Iwashige A and Matsuura S (1997) Behavioral manipulation of the shore crab, *Hemigrapsus sanguineus*, by the rhizocephalan barnacle, *Sacculina polygenea*. Crustacean Research 26: 153–161

Tilman (D) (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78: 81–92

Vigh DA and Fingerman M (1985) Molt staging in the fiddler crab *Uca pugilator*. Journal of Crustacean Biology 5(3): 386–396

Warman CG, Reid DG and Naylor E (1993) Variation in the tidal migratory behaviour and rhythmic light reponsiveness in the shore crab, *Carcinus maenas*. Journal of the Marine Biological Association of the United Kingdom 73: 355–364

Weiss HM (1995) Marine animals of southern New England and New York. State Geological and Natural History Survey of Connecticut. Department of Environmental Protection Publications

Willason W (1981) Factors influencing the distribution and coexistence of *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* (Decapoda: Grapsidae) in a California Salt Marsh. Marine Biology 64: 125–133

Williams AB (1984) Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC

Williams AB and 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(1): 108–109

Williamson M (1996) Biological Invasions. Chapman & Hall, London, 244 pp

Williamson M and Fitter A (1996) The characteristics of successful invaders. Biological Conservation 78: 163–170

Wiser SK, Allen RB, Clinton PW and Platt KH (1998) Community structure and forest invasion by an exotic herb over 23 years. Ecology 79(6): 2071–2081