# Possible temperature limits to range expansion of non-native Asian shore crabs in Maine

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## ARTICLE INFO

## ABSTRACT

The intertidal Asian shore crab, Hemigrapsus sanguineus (De Haan, 1835), recently (2001) appeared in very low densities along the southern Maine (USA) coast. Indigenous to Russia and Japan, this species arrived in New Jersey around 1988 and rapidly expanded south to the Carolinas and north to southern New England (CT, RI, MA) by the early 1990s. We examined the characteristics of a non-native species invasion by surveying over 30 intertidal sites in Maine from 2002 to 2005. We found relatively low population densities, slow rates of geographic expansion and virtually no colonization northeast of Penobscot Bay on the central coast of Maine. We hypothesized that further geographic expansion of sustaining populations of H. sanguineus in Maine may be limited by coastal temperatures colder than in its native range. To examine this, we deployed recording thermistors at 11 strategic sites and integrated those data with three oceanographic observation buoys and with satellite thermal images of the coastal zone for the period between 2003 and 2005. We found that Maine's H. sanguineus population densities in the intertidal peaked during the warmest months (July–September) and were lowest during the coldest months (January–March) when the crabs retreated to the subtidal zone. Densities were also greater in warmer localities (southern Maine) than in cooler localities (central and eastern Maine). In fact, populations were absent from areas with mean summer temperatures cooler than 13 °C. In southern Maine, seasonal population densities and reproductive periodicity corresponded to periods with mean temperatures warmer than 15° and 12 °C, respectively. There are many physical and biological factors that could limit this invasion. However, our temperature and demographic data are consistent with the thesis that the H. sanguineus invasion has stalled at the terminus of the Gulf of Maine's cold, Eastern Maine Coastal Current. We compared published mean summer and winter SST data for coastal waters in the western North Atlantic and in the native Asian range of H. sanguineus, and we quantified and compared H. sanguineus abundance in Maine with thermal microenvironments at these sites. From this, we speculate that future distribution of this crab may be limited to the warmer areas of the Maine coast (south and west of Penobscot Bay) and up estuaries that warm every summer. Thus, it may be possible for managers to gauge future risks of marine species invasion from vectors such as ships based on the thermal biogeographic match or mismatch between their ports of origin and their destinations. Such information could be useful for focused monitoring and enforcement of existing laws designed to prevent future introductions of non-native marine species. As coastal waters warm, invasion opportunities could increase from cold-limited species.

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## 1. Introduction

Non-native species represent a threat to marine biodiversity (Simberloff, 1999). However, we know much more about how non-native species arrive to a new region (Carlton and Geller, 1993) than we do about how their populations become established there. When non-native species proliferate in and impact the environment of their new habitat, they are considered to be invasive. There are practical and theoretical reasons to study the epidemiology of invasive species.

Invasive species can change the structure and functioning of marine ecosystems (Grosholz, 2002, Steneck and Carlton, 2000), they can threaten economically important species (Pimentel et al., 2000) and they can trigger costly but often ineffective remediation efforts (Lodge et al., 2006). However, not all non-native species are "invasive." For example, some non-native species intentionally introduced failed to persist, expand or become abundant, such as the American lobster in California (Herrick, 1909) and fungid corals in the Caribbean (LeJeunesse et al., 2005). Why are some species invasive, while others are not, and why are some communities invaded while others remain invader-free? Range expansions of non-native marine species are often, large-scale, natural biogeography experiments. By studying rates of range expansion and population growth of non-native species

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into different physically-defined habitats we can better identify the characteristics of the species, its habitats and processes such as reproduction, dispersal and recruitment that could affect invasibility.

Biogeographic provinces persist because of barriers to dispersal and because species are limited to environments to which they have adapted. Physical or oceanographic barriers to invasion have persisted for over thousands of years. However, in recent centuries and decades these barriers have been breached by modern shipping and other human activities that transport non-native species among geographic areas (Carlton and Geller, 1993). This prompts the question, "What limits range expansions now that the former, natural barriers have been breached?" Answers to this question allow us to identify and evaluate the strong drivers of biogeographic patterns. However, more importantly, these answers may help us better understand what contributes to the success of an invasive species and what limits its invasibility. A biogeographic approach could be useful in developing a general theory about match or mismatches among potential invaders.

Our study quantifies the recent spread of the Asian shore crab (*Hemigrapsus sanguineus*) in Maine and considers whether ocean temperatures, thought to maintain biogeographic patterns, could also constrain range expansion of invasive species. Specifically, by studying the expansion rate and population growth of species in previously unoccupied regions, we can draw conclusions about links between the physical regime of the new habitat and the population dynamics of the invader species.

There are many factors that could affect the success of an invasion in a given area, such as direction and speed of ocean currents as well as distance from points of introduction. In this study we focused on the links between ocean temperature and the population dynamics of *H. sanguineus*. Specifically, we are looking at mean winter and mean summer temperatures. A recent biogeographic study found a high percentage of the world's shallow biogeographic provinces correspond to geographic patterns in winter and summer temperatures integrated over geological time (Adey and Steneck, 2001). Thus we consider if these temperature patterns may also delimit non-native species ranges and thus give us insight into the biogeography of an invasion.

The coast of Maine, USA hosts at least 33 non-native marine species (Carlton, 2004). Several of these have come to dominate Maine's coastal ecosystems over the past century, such as the European green crab, *Carcinus maenas* (L.) or the green alga *Codium fragile* subsp. *tomentosoides* (van Goor) Silva. We chose to document and analyze a recent invasion of the Maine coast by the Asian shore crab, *H. sanguineus*, which was detected in Maine in 2001. This species was first found in North America in the state of New Jersey in 1988 (Williams and McDermott, 1990) and spread from there to its current range between North Carolina and Maine.

In its native range, *H. sanguineus* primarily inhabits rocky intertidal shores (Fukui, 1988, Lohrer et al., 2000). In its invaded range in North America, *H. sanguineus* has been found in the rocky intertidal zone

habitats, including marshes and mudflats in New England (Dobroski, 2005; Lohrer et al., 2000; Seeley, personal observation). In Maine, this crab has been found primarily among and underneath cobblestones, an abundant substrate in Maine's intertidal zone. Wherever *H. sanguineus* is found in Maine, it generally shares habitat with *C. maenas* throughout the intertidal zone (Stephenson, personal observation).

We also focus on ecological processes that may regulate colonization by non-native species. A high reproductive rate (Fukui, 1988) and dispersal potential (Hwang et al., 1993) likely contribute to the success of *H. sanguineus* where it has invaded. However, its breeding season may be shorter in the Gulf of Maine and development times longer in colder temperatures (O'Connor et al., 2007). This, along with ocean currents flowing counter to the direction of spread could limit the dispersal and northward expansion of this species (Byers and Pringle, 2006). Therefore, temperature may limit the success of this invader in colder regions, such as the northern Gulf of Maine.

We investigated the role of temperature as a possible constraint on the invasion of *H. sanguineus* in Maine by a) documenting patterns of distribution and abundance in Maine, USA, b) comparing patterns of distribution in its native Asian and invaded U.S. habitats, relative to temperatures in those regions, c) quantifying population densities and reproductive timing in the intertidal zone on a southern Maine shore to determine if they are correlated with seasonal temperature changes, and d) identifying temporal patterns in recruitment in southern Maine through size frequency analysis.

## 2. Methods

### 2.1. Coast-wide patterns of distribution and abundance in Maine

Surveys were conducted in the summers of 2002–2005 at sites along the Maine coast. Each site was visited at least once per year. We conducted two types of surveys: a) timed searches, and b) quadrat surveys.

#### 2.1.1. Vertical timed searches

We conducted searches for crabs at low tide along a transect perpendicular to the shoreline and from the low to the high tide line. During these surveys, one searcher lifted rocks and seaweed fronds to expose crabs, and collected them for 15 minute periods. We targeted the preferred habitat of *H. sanguineus*, i.e. areas of high density cobble, (Fukui, 1988; Lohrer et al., 2000) and avoided bare gravel and ledge. We conducted four adjacent transects at each site for a total of 1 h of one person survey time. After the four transects were completed, we recorded the sex, carapace width (CW) and presence/absence of eggs for individuals collected in each transect before returning the crabs to the intertidal zone.

**Table 1**
Locations and abbreviations for intertidal recording thermistors.

| Site | Abbrev. | Latitude/longitude (decimal degrees) | Approx. tidal elev. (m) | Period when thermistor was collecting data |
|---|---|---|---|---|
| Seapoint Beach, Kittery | KIT | 43.0909 N 70.6602 W | 2.30 | 7/15/03–9/30/2005 |
| Biddeford Pool | BDPL | 43.44019 N 70.34294 W | 1.10 | 8/19/03–9/30/05 |
| Lands End, Bailey Island | BLY | 43.71753 N 70.00314 W | 1.90 | 8/10/03–9/30/05 |
| Pemaquid Point | PEM | 43.83533 N 69.50733 W | 0.80 | 10/25/03–4/20/05 |
| Darling Marine Ctr. Walpole* | DMC | 43.93667 N 69.58167 W | 1.90 | 8/08/03–9/30/05 |
| Dodge Pt. State Park* | DGPT | 43.98451 N 69.5637 W | 2.20 | 8/02/03–9/30/05 |
| Crescent Beach, Owls Head | OWL | 44.06500 N 69.06611 W | 2.20 | 8/18/03–9/30/05 |
| Sears Island, Searsport* | SRS | 44.46112 N 68.88512 W | 2.10 | 7/12/04–9/30/05 |
| Bass Harbor, Mount Desert Island | MDI | 44.23350 N 68.34810 W | 2.20 | 8/04/03–9/30/05 |
| Jonesport Campground, Jonesport | JSPT | 44.52972 N 67.58864 W | 1.40 | 8/14/03–9/30/05 |
| Carrying Place Cove, Eastport* | ESPT | 44.92306 N 67.01778 W | 4.80 | 8/17/03–9/30/04 |

Estuarine sites are denoted by a *.
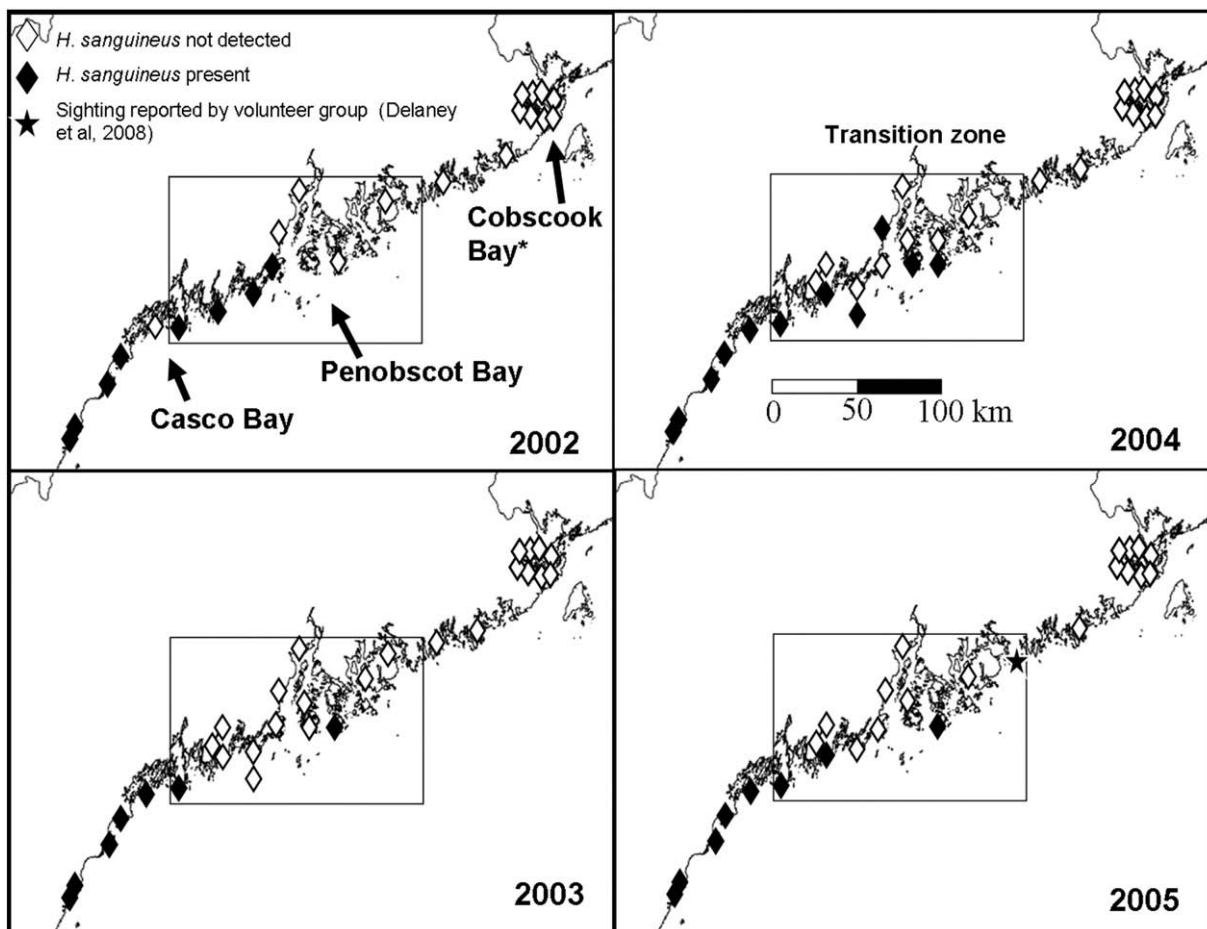
**Fig. 1.** Distribution of *H. sanguineus* in Maine based on surveys. The box outlines a transition zone between areas that have established populations of *H. sanguineus* and areas where none of these crabs have been detected. *All 15 sites surveyed in Cobscook Bay are not shown here due to space limitations.

### 2.1.2. Horizontal timed searches (by tidal height)

We also conducted timed surveys along transects parallel to the shoreline at four different tidal elevations high, high-middle, low-middle and low intertidal zone. These elevations corresponded to the following: a) high zone: area above the limit of macroalgae on the shore; b) high middle zone: area of fucoid algae, usually *Ascophyllum nodosum ((L.) Le Jolis),* highest on the shore; c) low middle zone: area of fucoid algae lowest on the shore; d) low zone: lowest area of intertidal algae on shore (*Chondrus crispus (Stackhouse)*). A fifteen minute timed survey was conducted at each of these tidal elevations.

### 2.1.3. Quadrat surveys

A quadrat survey was conducted in an area adjacent to the timed survey at the tidal elevation in which the highest numbers of *H. sanguineus* were detected in the timed survey.

During the quadrat survey, we surveyed between 20 and 30 replicate 1 m$^2$ quadrats along the chosen tidal elevation. Each quadrat was placed in a location that would maximize the percent cover of cobble habitat within the quadrat (i.e. non-random placement). We searched for crabs by combing through the seaweed, displacing all moveable boulders, cobbles, and pebbles, and scraping the underlying sediment in each quadrat. Sex, CW and the presence of eggs were recorded for each crab. For each quadrat, we also recorded the percent cover of suitable cobble habitat. Cobbles that were entirely embedded in the substrate and provided no room to shelter crabs were not included as suitable habitat.

To adjust crab abundance data by the abundance of suitable cobble habitat, we divided *H. sanguineus* abundance in each quadrat by the percent cover of cobble in that quadrat.

### 2.2. Temperature patterns

### 2.2.1. Regional sea surface temperature patterns: northeast U.S. and Asia

We used NOAA-CIRES (National Oceanic and Atmospheric Administration – Cooperative Institute for Research in Environmental Sciences) Climate Diagnostics Center maps depicting contours of mean monthly sea surface temperature (SST) to determine annual
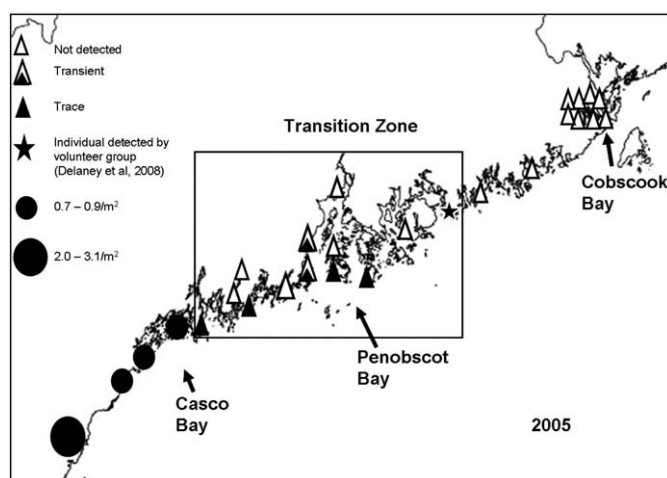


**Fig. 2.** Regional patterns of abundance in Maine based on 2005 surveys. "Transient" = not detected in 2005 survey but detected in previous years; "Trace" = 1 to 3 individuals detected in a 1 h survey.
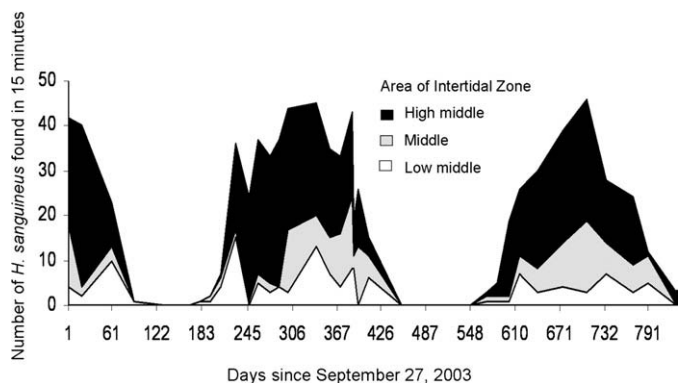
**Fig. 3.** Area graph showing relative abundance of *H. sanguineus* at three tidal elevations at Seapoint Beach in Kittery.

summer and winter means in the native Asian and invaded U.S. range of *H. sanguineus*. The annual summer mean was defined as the average of July, August and September temperatures and the annual winter mean as the average of January, February and March temperatures (Adey and Steneck, 2001) averaged over the years 2003 through 2005. We recorded temperature data at regular intervals, at every 0.5 to 1 degree of latitude along coastlines inhabited by *H. sanguineus*. We also recorded temperature data points from areas just outside the crab's native and invaded ranges.

We used Gulf of Maine Ocean Observing System (GoMOOS) buoys to obtain data on the average cumulative number of days ≥ 15 °C for the years 2003–2005. We chose 15 °C, as this was reported by Epifanio et al.

(1998) as the temperature at which *H. sanguineus* megalopae experienced 100% mortality in the laboratory, regardless of salinity.

### 2.2.2. Intertidal temperature patterns in Maine

We placed a HoboTemps (Onset Computer Corporation) recording thermistor inside an approximately 10 cm long × 3 cm diameter white PVC pipe. We secured the pipe to a rock in the intertidal zone at selected sites along the Maine coast (Table 1). We measured the tidal elevation of the thermistors using a sighting level. We were unable to place the thermistors at the same tidal elevations at all sites because we could not always find suitable substrate to which we could attach the thermistor at the same elevation at each site. The thermistors recorded temperatures every 30 min and were left in the intertidal zone between August 2003 and September 2005. Storms and theft resulted in some sites missing temperature data for some periods between August 2003 and September 2005 (Table 1).

After downloading the thermistor data, we sorted air from water temperature readings by using tables showing changes in tidal elevation at 30 minute intervals. By using these tables and knowing the elevation of the thermistor, we were able to determine when the thermistor was submerged, and record those periods as water temperature. We then averaged the water temperatures from July, August and September of 2003–2005 to obtain summer means and January, February and March for the same years to obtain winter means.

To check for correspondence between intertidal and sea surface temperatures, we obtained fine scale contour maps of the Maine coast
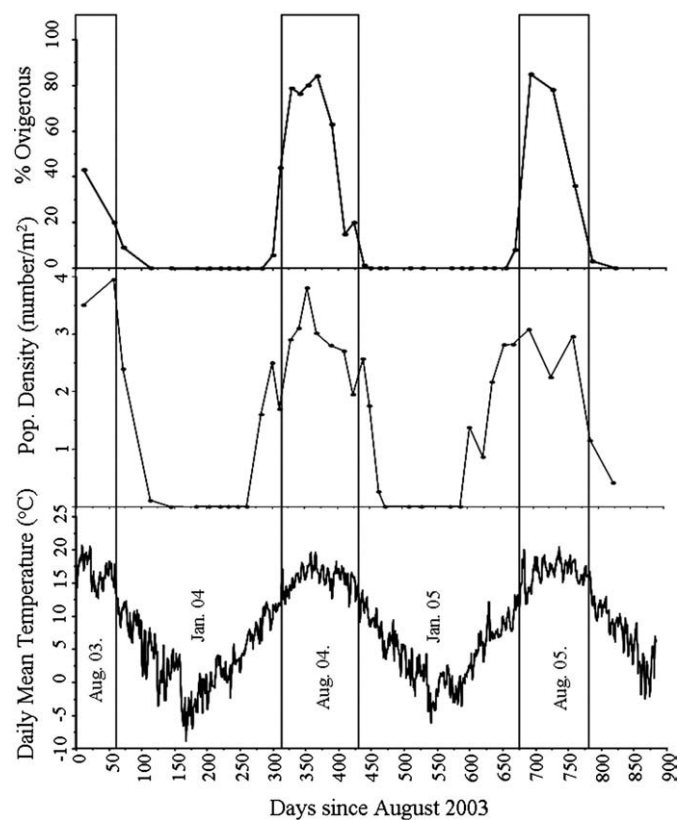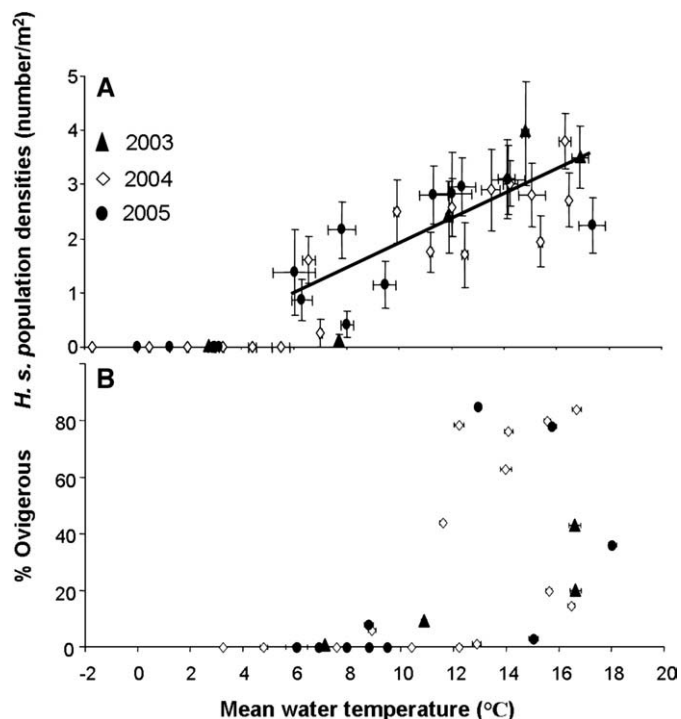


**Fig. 4.** Seasonal patterns in temperature, population density and ovigery from August 2003 to December 2005 in the high middle intertidal zone at Seapoint Beach in Kittery. Daily mean temperature is an average of air and water temperatures collected by the thermistor placed at approximately 2.3 m above MLW. Boxes outline periods equaling or exceeding 15 °C. Population density is adjusted to show mean number of individuals per m² of suitable habitat.



**Fig. 5.** *H. sanguineus* ovigery and density data versus mean water temperatures in Kittery. A) *H. sanguineus* density versus mean water temperature for surveys done in the high middle intertidal zone at Seapoint Beach in Kittery, ME. Each data point represents quadrats averaged for each survey date and adjusted to show mean number of individuals per m² of suitable habitat. Mean temperatures for each survey were calculated by averaging water temperature from the recording thermistor at 2.3 m above MLW elevation for the 48 h prior to each survey. B) Percent of females (≥ 12 mm CW) that were ovigerous during each survey, includes crabs found throughout the intertidal zone. Mean temperature for each survey was calculated by averaging water temperatures from the thermistor at 2.3 m above MLW for the week prior to each survey.
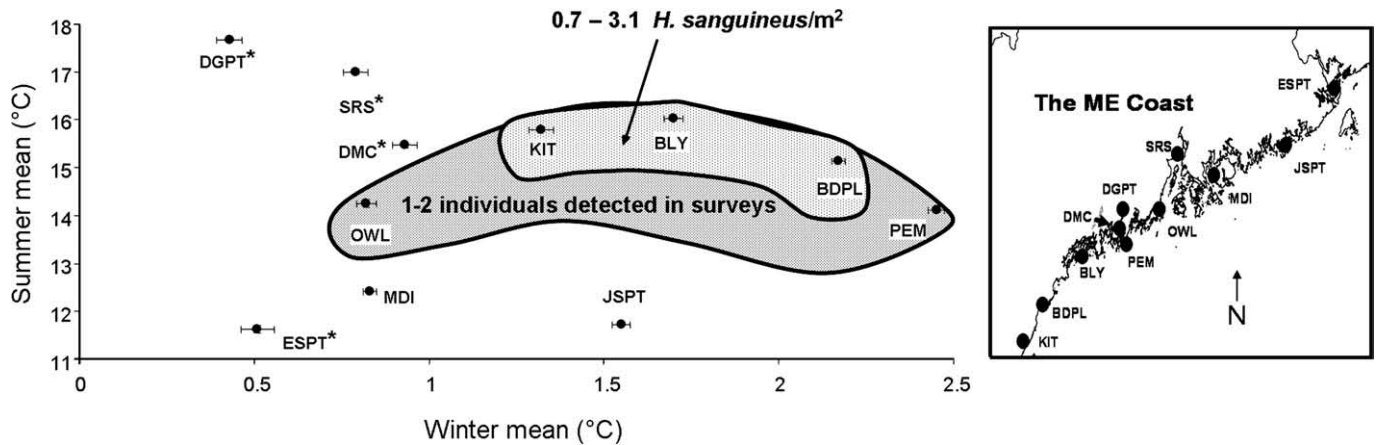
**Fig. 6.** *Hemigrapsus sanguineus* abundance and regional thermogeography. Winter and summer means from recording thermistors with *H. sanguineus* abundance (see Table 1 for site details and abbreviations). Areas shaded in grey in the graph represent sites at which *H. sanguineus* was detected. Locations of thermistors (and their abbreviations) are represented in map to the right. Estuarine sites are denoted with a *.

from the Satellite Oceanography Data Lab at the University of Maine and compared them to the thermistor data.

### 2.3. Local temperature patterns and crab abundance at Kittery, Maine

#### 2.3.1. Collection of temperature data

We collected and analyzed temperature data as above except that at this site, the thermistors were placed at four elevations in the intertidal zone at approximately 0.2, 0.8, 1.5, and 2.2 m above mean low water. Tidal range at Seapoint beach is approximately 3.2 m. When analyzing patterns of ovigery and changes in intertidal population density, we used mean water temperatures taken from thermistors for 48 hours prior.

#### 2.3.2. H. sanguineus surveys

Timed and quadrat surveys were conducted at least once a month at Seapoint Beach in Kittery between August 2003 and December 2005.

We conducted 15 minute timed searches as described above parallel to the shoreline in the high middle, middle and low middle zone. These surveys were conducted at least monthly. We also performed timed

surveys at elevations below MLW during 5 surveys over the study period when spring tides made this area accessible. We conducted surveys of the high zone once per summer during the study period.

Quadrat surveys as described above were conducted on a transect parallel to the shoreline at the tidal elevation indicated by the results of the timed surveys having the highest densities of *H. sanguineus*.

For both timed and quadrat surveys, the CW, sex and presence of eggs were recorded for each individual collected. To calculate percent ovigerous females, we divided the number of ovigerous females by the total number of females that were mature (12 mm CW).

### 2.4. Identifying local recruitment patterns

During surveys at Seapoint Beach, we recorded CW in mm of each *H. sanguineus* we encountered during the timed and quadrat surveys. We used this data to generate size frequency histograms for each survey date. We also constructed size frequency histograms using data we collected from Long Beach in York, Maine and Odiorne Point, New Hampshire in August 2005.
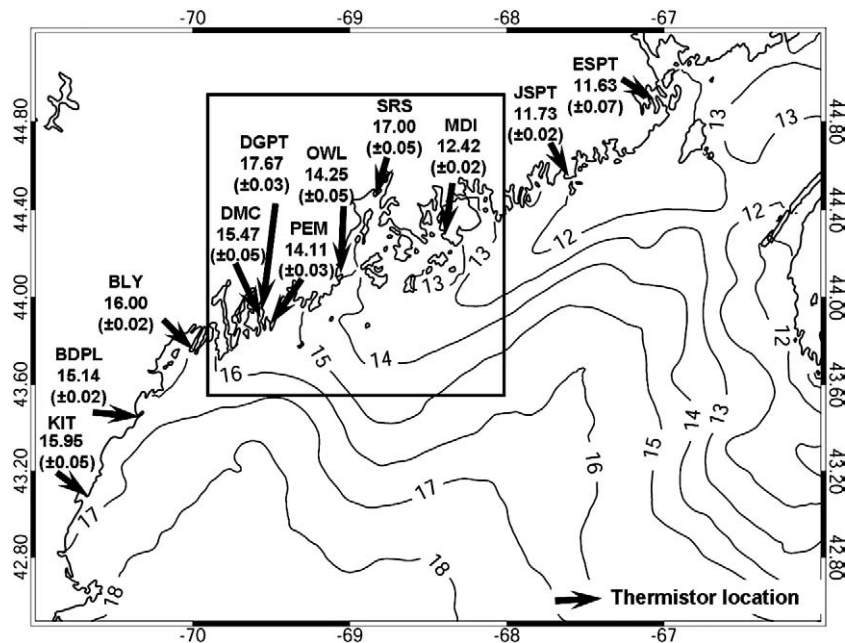


**Fig. 7.** Comparison of mean summer sea surface temperatures (2003–2005) calculated from satellite data (contours) and mean summer intertidal temperatures from thermistors (2003–2005). Square shows *H. sanguineus* transition zone (Figs. 1 and 2). Contour map generated by the University of Maine Satellite Oceanography Data Lab.

Finally, during one survey in Kittery, we recorded CWs for all European green crabs found during the quadrat survey and compared them to the size frequencies recorded for *H. sanguineus* during the same survey. We defined the size of *H. sanguineus* recruits as ≤8 mm CW (as per Lohrer and Whitlatch, 2002).

## 3. Results

### 3.1. Patterns of distribution and abundance in Maine

From 2002 though 2005, *H. sanguineus* was found consistently in southwestern Maine, sporadically in mid-coast Maine (greater Penobscot Bay) and was absent on the northeastern Maine coast (Fig. 1). In 2005, highest densities of *H. sanguineus* were in the southwestern Maine region (Fig. 2) specifically in Kittery and York. Isolated individuals were occasionally detected at locations north and east of Casco Bay and south of Schoodic Point (in the transition zone, Figs. 1, 2 and 7). A single crab found at Schoodic Point at the eastern end of the transition zone (Delaney et al., 2008) represents the current (as of 2007) northernmost limit for *H. sanguineus* on the east coast of North America.

*H. sanguineus* abundance in the intertidal zone at Seapoint Beach, Kittery, Maine fluctuated seasonally. Highest densities occurred during the summer or early fall with the greatest densities in the high middle intertidal zone (Fig. 3). Quadrat sampling recorded annual peak densities of $3.95/m^2$ ($\pm0.95$, $n=20$ quadrats) in late September 2003, $3.8/m^2$ ($\pm0.51$, $n=30$ quadrats) in late July 2004 and $3.08/m^2$ ($\pm0.64$, $n=20$ quadrats) in late July 2005 (Fig. 4). No Asian shore crabs were detected in the intertidal zone from December through February.

### 3.2. Demographic variations with temperature

Seasonal patterns of abundance in *H. sanguineus* corresponded with temperature in the intertidal zone (Fig. 4). Peak population densities generally occurred during periods of warmest air and sea temperatures (except for August 2003). The greatest proportion of ovigerous females were also found during periods of warmest air and water temperatures. The percentage of ovigerous females increased from 6% to 79% between early and late June, 2004 and from 8% to 85% between late May and late June, 2005.

At water temperatures greater than 6 °C crab densities increased linearly with increasing mean sea temperatures (thermistor data, pooling all years 2003–2005, Fig. 5a). Crabs were not detected during surveys when mean water temperatures in the intertidal zone were below 6 °C. Similarly, ovigerous females were not detected at mean water temperatures below about 9 °C. The density of egg-bearing crabs showed a positive but more abrupt increase in abundance at mean water temperatures exceeding 11.5 °C (Fig. 5b).

From 2003 to 2005, population densities were greatest in Maine where mean intertidal winter water temperatures ranged between 1.3 °C and 2.2 °C and mean intertidal summer temperatures ranged between 15.2 °C and 16 °C, (thermistor data, pooling all years 2003–2005) (Fig. 6). Trace populations having one or two individuals were found in more thermally variable habitats in the transition zone that were slightly cooler in the summer. No crabs were detected at locations where thermistors recorded mean intertidal summer water temperatures below about 13 °C or winter temperatures below 0.75 °C. Winter temperatures at Pemaquid Point (PEM) in the transition zone and in Jonesport (JSPT) in eastern Maine were warmer than winter temperatures in Kittery where crabs were most abundant. Crabs were not detected at estuarine sites (ESPT, DGPT, DMC and SRS, see Table 1 for abbreviations) despite the fact that the latter three sites had some of the warmest mean summer temperatures recorded.

Intertidal recording thermistor temperature data generally corresponded with satellite interpreted temperature data for the three summer months during the three years of temperature data collection

for this study (2003–2005) (Fig. 7). The two southwestern-most intertidal sites (KIT and BDPL) were slightly cooler than the offshore, satellite-based isotherms suggested.

The duration of warm summer periods (≥15 °C) was greatest in southwestern Maine, the region of the state where *H. sanguineus* densities are the highest. The GoMOOS buoy (WMS) and the intertidal thermistor (KIT) in this region recorded an average of 89 and 17 cumulative days, respectively, where summer water temperatures reached at least 15 °C (averaged over 2003–2005) (Fig. 8). The offshore GoMOOS buoy (EMS) at the eastern end of the transition zone (where crabs were rare) recorded 1 cumulative day where summer water temperatures reached 15 °C. The intertidal thermistor (JSPT) in eastern Maine (where crabs are absent) recorded 0 cumulative days where summer water temperatures were 15 °C or higher (averaged over 2003–2005).
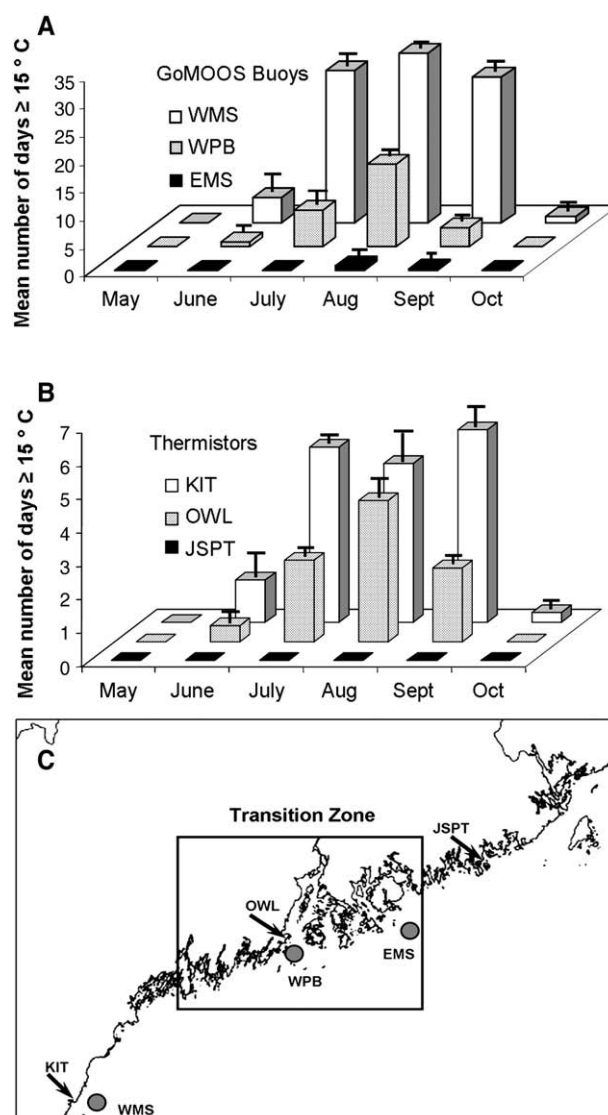


**Fig. 8.** Mean number of cumulative days when water temperature ≥15 °C, averaged over the summers of 2003–2005. White, gray and black bars represent abundant, transition and absent zones respectively. A) Data obtained from GoMOOS data buoys in the western Maine Shelf, "WMS", western Penobscot Bay, "WPB", and eastern Maine Shelf "EMS." B) Data taken from recording thermistors in the intertidal zone. C) Map of locations of thermistors and GoMOOS buoys. Square shows *H. sanguineus* transition zone (Figs. 1 and 2).
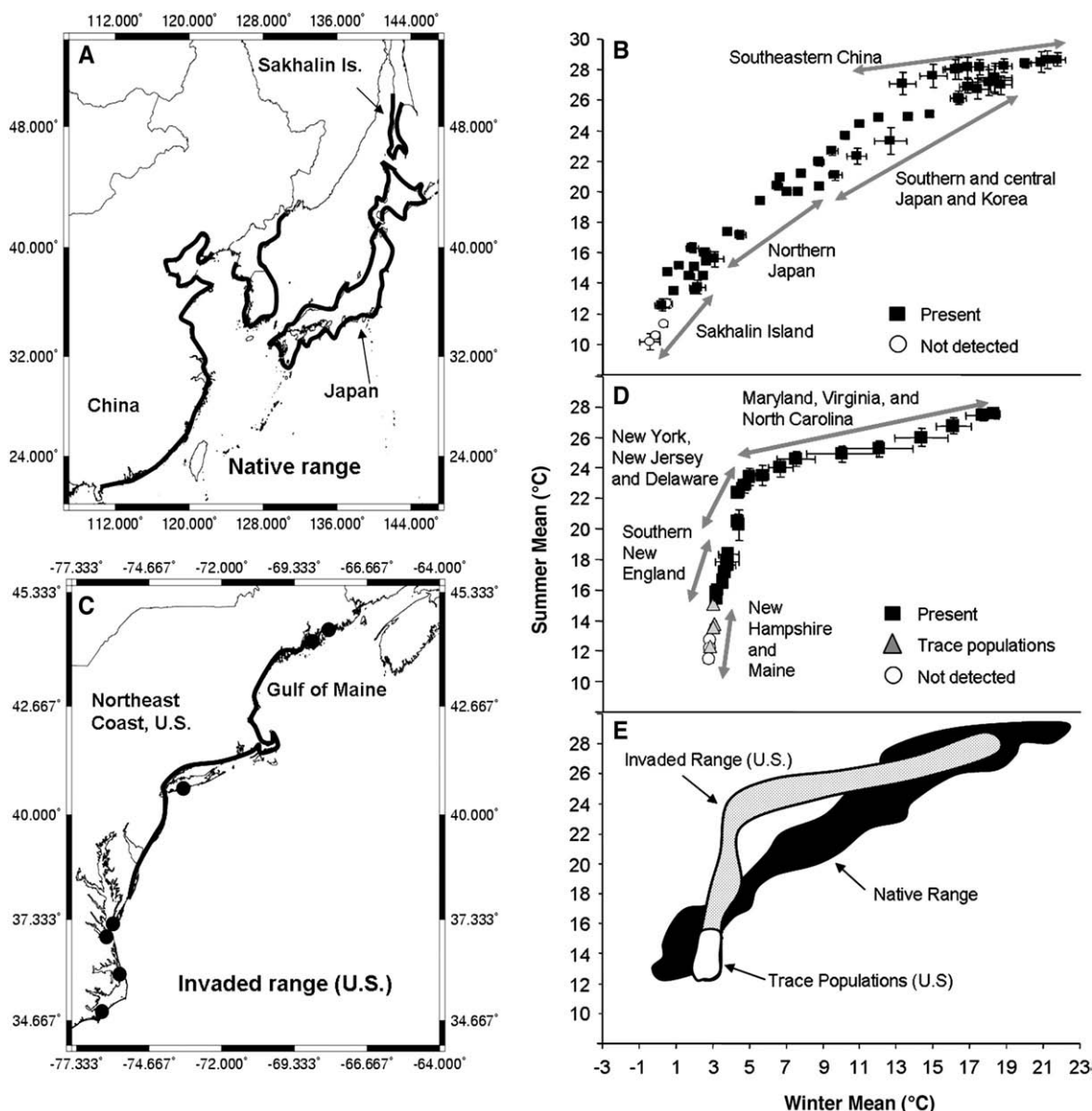
**Fig. 9.** Thermogeography (from satellite data) and maps of native and invaded ranges of *H. sanguineus*. A) Native range of *H. sanguineus*; B) Winter and summer SST means in native range of *H. sanguineus* based on satellite data; C) Invaded range of *H. sanguineus* on the east coast of the United States; D) Winter and summer SST means in invaded range of *H. sanguineus* on east coast of the United States. E) Comparison of summer and winter SST means in native range and range on the east coast of the U.S.

### 3.3. Biogeographic and thermogeographic patterns of Asian shore crabs in native Asian and invaded U.S. regions

The native range of *H. sanguineus* spans from southeastern China to Russia's Sakhalin Island (Sakai, 1976) (Fig. 9a). Its geographic distribution spans a considerable range of coastal temperatures (Fig. 9b). Average summer SSTs (satellite data pooled over the years 2003–2005) ranged between 12.6 °C at the northern end and 29 °C at the southern end of its native range. We were unable to find information about population densities of *H. sanguineus* at the northern and southern terminus of their native range.

The non-native range of *H. sanguineus* in North America spans from North Carolina to Maine (Fig. 9c) (McDermott, 1998b and this paper). The average summer and winter sea temperatures differ slightly from those of its native range (Fig. 9c). There is general correspondence in the thermogeographic plots when their native and introduced ranges (Fig. 9b and d) are overlaid on one another, (Fig. 9e). In its native range, *H. sanguineus* has not been reported in locations where summer SST means fall below 12.6 °C. In its invaded

range, trace populations (isolated individuals) have been reported at summer SST means as low as 12.5 °C. However, established populations have not been detected at summer SST means below 15 °C in its invaded range. The coldest winter SST means in the native and invaded ranges of *H. sanguineus* are 0.3 °C and 2.8 °C, respectively.

### 3.4. Recruitment estimates from size frequency distributions

*H. sanguineus* recruitment to the benthos was infrequent and modest (Fig. 10). "Young of the year" recruits (newly settled crabs ≤8 mm CW, Lohrer and Whitlatch, 2002) were observed during only four of the 41 year-round surveys conducted between 2003 and 2005 (Fig. 10). Recruits were detected in late June and early July of 2004 and in late July and August of 2005. This latter, modest recruitment pulse was also observed at Odiorne Point, New Hampshire and in York, Maine, locations which lie in close proximity to Kittery, Maine (Fig. 11). These three sites were also similar in their relative lack of early adult size classes (between 12 and 15 mm CW). We found early adults in Kittery during only 3 out of 6 surveys between May and October 2005 (Fig. 10). This rarity of early
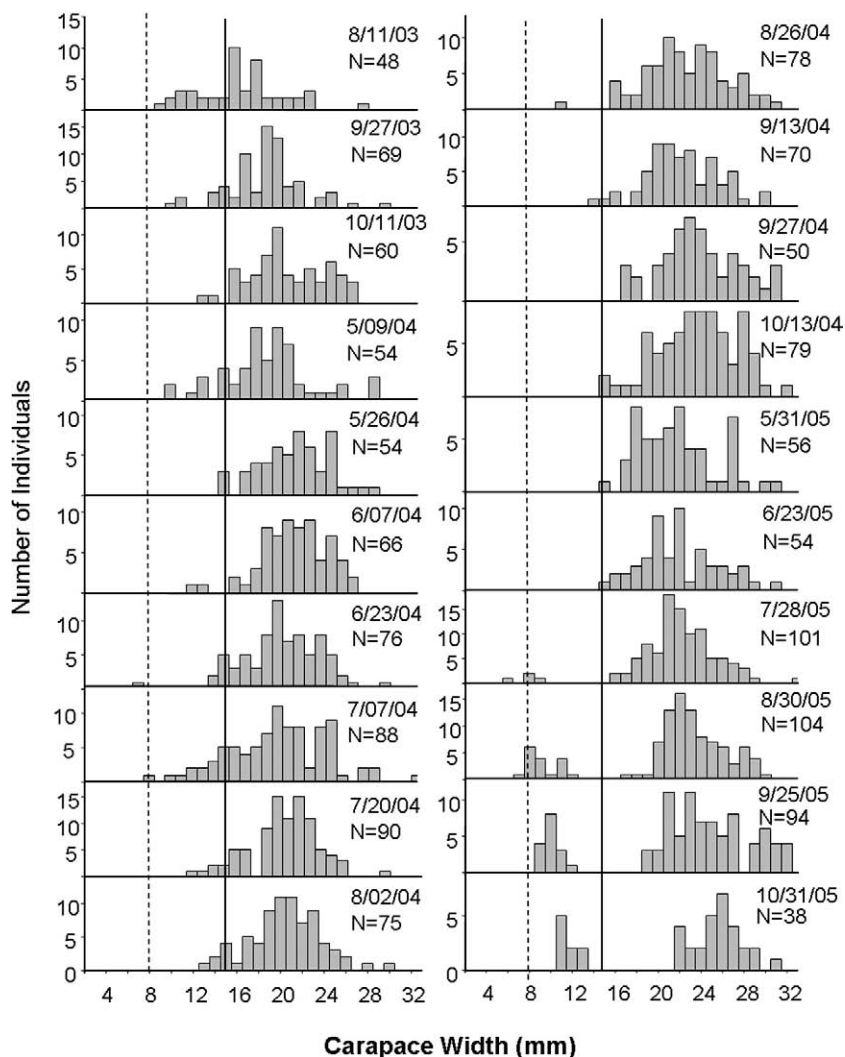
**Fig. 10.** Time series of size frequency histograms for *H. sanguineus* sampled at Seapoint Beach in Kittery, ME. Solid vertical line represents size at which 50% of females were ovigerous. Individuals to the left of the dashed line are defined as recruits.

adults could potentially indicate a weak recruitment of *H. sanguineus* in the previous year. The relative lack of small *H. sanguineus* individuals starkly contrasts the pattern observed for the European green crab, *C. maenas* (Fig. 12). Newly settled green crabs, 3–4 mm in CW, were frequently observed in Kittery during the late summer and early fall of each year (personal observation in 2003 and 2005, data here for 2004). *C. maenas* size frequency distribution (shown for September 13, 2004) is strongly skewed to the left. In contrast, none of the *H. sanguineus* individuals measured were recruits and few were early adults.

## 4. Discussion

We found that geographic, zonal, and seasonal patterns in distribution and abundance as well as patterns of reproductive timing and recruitment for *H. sanguineus* in Maine correspond to water temperature. This is consistent with the hypothesis that cold ocean temperatures limit the invasion of this species in northern New England. There are temperature thresholds to which this species is apparently adapted that control growth rates, reproduction and larval development for this species (Epifanio et al., 1998). These thresholds may not only define biogeographic boundaries but also limit population growth in regions where this crab has been introduced. Here we consider the evidence for temperature limitation along with other factors that may be slowing or halting the range expansion of *H. sanguineus* in Maine.

### 4.1. A case for thermal limits and thresholds

Regional patterns of distribution and abundance of *H. sanguineus* fall into three broad areas that correspond to summer temperature regimes on the Maine coast (Figs. 2 and 7). Established populations of *H. sanguineus* were found only in southwestern Maine (Casco Bay and south) where mean summer intertidal temperatures (from thermistors) and SST (from satellite data) were at least 15 °C and 16 °C, respectively. Isolated individuals were detected in the "transition zone" (from east of Casco Bay to Schoodic Peninsula) where mean summer SST's ranged between 12.5 °C and 16 °C, and intertidal temperatures ranged between 12.4 °C to 14.1 °C on the outer coast. Asian shore crabs were not detected in eastern Maine where mean summer intertidal and sea surface temperatures fell below 13 °C and 12.5 °C respectively. This temperature limit corresponds with that of the crab's native range where *H. sanguineus* is not reported at average summer SST's below 12.6 °C (Fig. 9).

Maine's summer temperatures may be most important in determining the distribution and abundance of *H. sanguineus*. At our southernmost site in Kittery, the crabs vacated the intertidal zone in the winter, likely finding a refuge from the bitter cold intertidal air temperatures in the much warmer subtidal zone (McDermott, 1998a,b) (Fig. 3). Additionally, in its native range, *H. sanguineus* is found in locations where mean winter sea surface temperatures are more than 2 °C colder than at its northern limit in Maine (Fig. 9). Thus, it is unlikely that winter
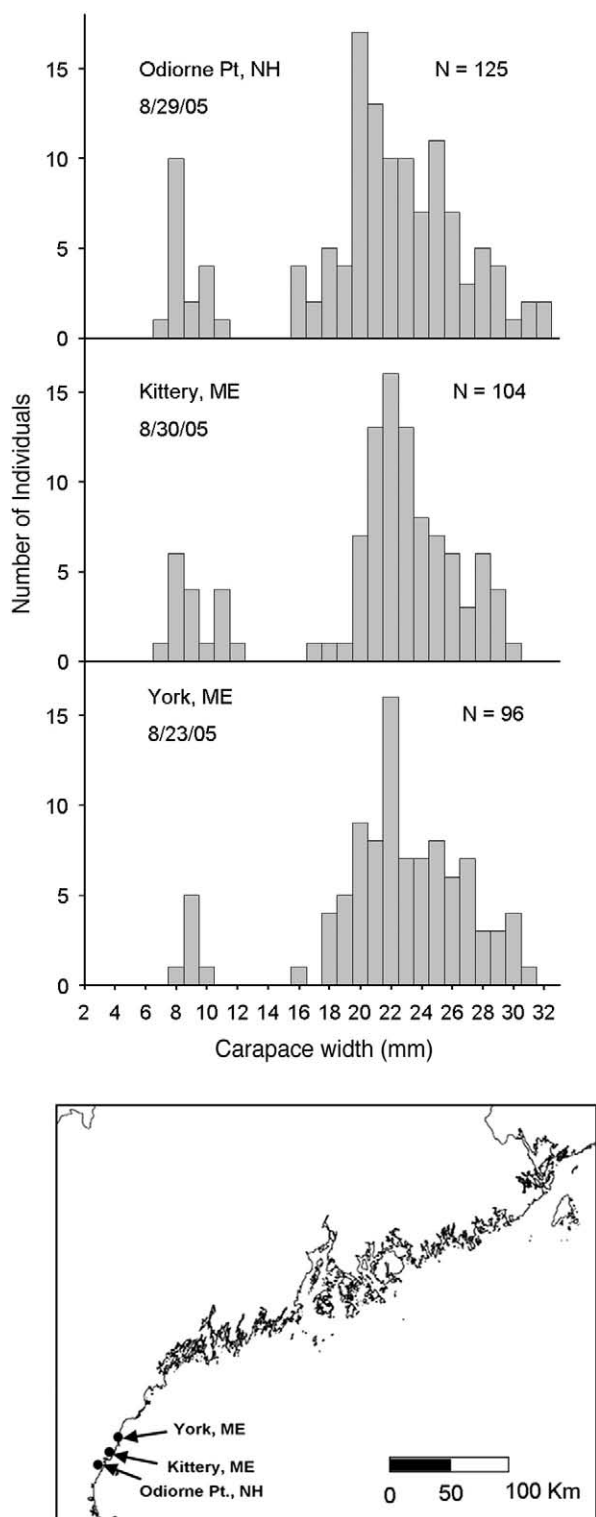
Fig. 11. Size frequency histograms for *H. sanguineus* collected during surveys at three sites in southern Maine and New Hampshire. Map shows locations of three sites.

21 days at 20 °C to 53 days at 15 °C (Epifanio et al., 1998). Larval survival decreases with time spent in the plankton due to increased chances of mortality from predation and other factors (O'Connor et al., 2007). Summer water temperatures in Maine, particularly in the area from the "transition zone" (Figs. 1, 2, 7) east would extend larval stage duration, increase the likelihood of larval mortality and thus inhibit successful settlement. Additionally, laboratory studies show that *H. sanguineus* megalopae exposed to temperatures as low as 15 °C do not survive to crab stage one, regardless of the salinity (Epifanio et al., 1998). Only 3.3% survived at temperatures of 20 °C (and salinities of 30 parts per thousand) (Epifanio et al., 1998). As Epifanio et al. (1998) note, megalopae may have broader tolerances in nature than in the laboratory. However, given the complete mortality observed in the laboratory at 15 °C, this is a useful threshold for comparing the likelihood of successful settlement in the three different regions of the Maine coast. In eastern Maine, for example, intertidal water temperatures never reached 15 °C (Fig. 8). At the far eastern end of the transition zone, there was less than 1 cumulative day in the summer (on average) when sea surface temperatures reached 15 °C. In Penobscot Bay, at the center of the transition zone, the number of days at 15 °C (or greater) rose to 25 and 9 for SST and intertidal temperatures, respectively. Therefore, the isolated individuals found in this region may be able to take advantage of these "windows of opportunity" where temperature conditions meet their survival needs, but the window may not be open long enough to allow for the strong and consistent recruitment necessary for the development of established populations. In southwestern Maine, where the crabs are most abundant, conditions are less hostile to larval survival. Specifically, there were on average 89 and 17 days when SST's and intertidal temperatures, respectively, reached at least 15 °C.
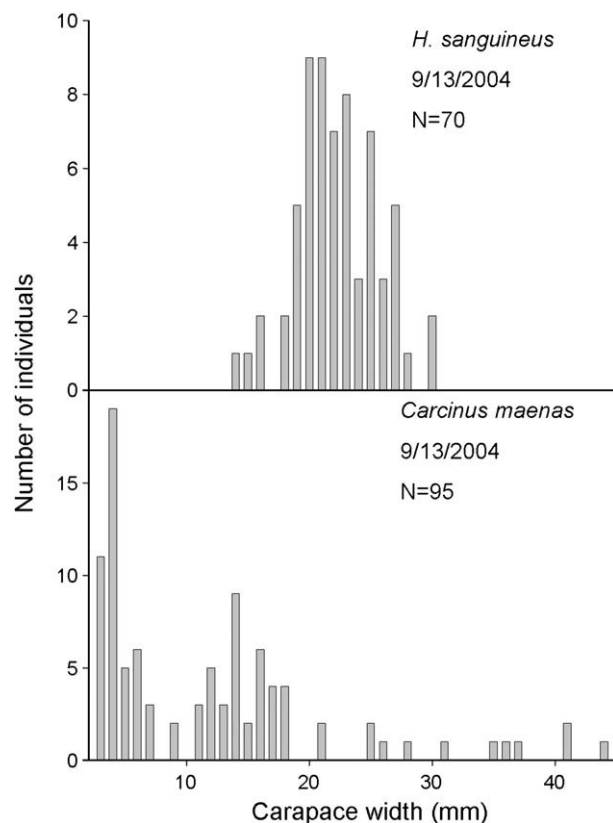


Fig. 12. Size frequency comparisons of *H. sanguineus* and *C. maenas* sampled during a survey at Seapoint Beach in Kittery. Note that the strongly left-skewed size frequency distribution for the European green crab (*C. maenas*) indicates that it recruited frequently.

temperatures on the Maine coast inhibit range expansion and population growth of this species. Instead, it appears that the regions of reduced *H. sanguineus* distribution and abundance may result from reproductive limitations due to the effects of cool summer temperatures on ovigery, larval development and survival.

Larval development time generally increases with decreasing water temperature (O'Connor et al., 2007). Time from hatching to the megalopa stage for *H. sanguineus* in the laboratory increased from

Even though conditions for *H. sanguineus* are more favorable in southwestern Maine, slow population growth rates there suggest that even in the areas of highest relative abundance *H. sanguineus* is on the edge of its thermal limit. *H. sanguineus* population densities in Kittery decreased slightly between 2003 and 2005 (Fig. 3) and at the nearby study site in York between the years 2004 and 2005. This pattern contrasts sharply to early invasion data from southern New England and New York. At sites on the Rhode Island and Massachusetts coasts for example, *H. sanguineus* densities increased from <5/m$^2$ to 30–50/m$^2$ in a two year period (O'Connor, 2001). In Rye, New York, peak *H. sanguineus* densities increased almost eight-fold between 1998 and 2000 (Sellberg and Kraemer, 2002). The stalled growth at southern Maine sites may be due to the lack of regular, strong recruitment classes as was exemplified by size frequency patterns observed in Kittery (Figs. 10–12). The current scarcity of recruits and early adult *H. sanguineus* in Kittery contrasts with the pattern seen in the well established invader, *C. maenas*, in which settling crabs as small as 3–4 mm CW were regularly observed (Fig. 12). In addition, the low number of *H. sanguineus* juveniles seen in Kittery differs from size frequency patterns observed in Massachusetts (Ledesma and O'Connor, 2001), Connecticut (Lohrer and Whitlatch, 2002), Rhode Island (Stephenson personal observation) and in its native range in Japan (Fukui, 1988) in which juvenile size classes were well represented. The lack of strong recruitment in southern Maine may be due to the effects of temperature on recruitment. Although SST's in Kittery are relatively warm compared to other regions of the outer Maine coast, mean summer SST's are likely still cool enough to promote long larval development times, thus subjecting larvae to a higher probability of experiencing mortality prior to settlement (Byers and Pringle 2006, O'Connor et al., 2007). Furthermore, in Kittery, on average, there are only 17 cumulative summer days when intertidal temperatures reach at least 15 °C (Fig. 8). Thus, it is possible that megalopae reaching the intertidal zone just prior to settlement often encounter temperatures that are hostile to their survival (Epifanio et al., 1998).

### 4.2. Thermogeography versus connectivity as prime drivers of invasion

Undoubtedly, multiple factors affect the distribution, abundance and rate of spread of *H. sanguineus*. While we propose that thermogeography may be most important because it limits reproductive success, connectivity may also contribute to the patterns we have documented here.

The lack of Asian shore crab recruitment in warm upper reaches of estuaries is likely the result of lack of connectivity with an effective reproductive population of crabs. Connectivity, or the linkage between reproductive and recruiting populations involves three components; 1) larval availability, 2) propensity to settle and 3) available nursery habitat. Since there is no shortage of intertidal nursery habitat, connectivity for the Asian shore crab likely relates to the first two steps. Mean summer intertidal temperatures at two of the estuarine sites (DGPT and SRS, Fig. 6) in the transition zone were warmer than those found in southern Maine outer coastal sites and thus would likely be more hospitable for megalopae survival and settlement (Figs. 6 and 7). There was ample cobble habitat at these estuarine sites and salinities of these estuaries are within known tolerances of *H. sanguineus* (Jensen et al., 2002; Ledesma and O'Connor, 2001; Epifanio et al., 1998; Field, 1982; Haefner, 1967). However, no *H. sanguineus* were detected in these estuarine environments during repeated annual surveys (Fig. 1). The absence of *H. sanguineus* in these areas may be due to low larval availability effectively severing connectivity with outer coastal larval source areas.

This pattern is consistent with research conducted on the American lobster, *Homarus americanus* and the rock crab, *Cancer irroratus* in these estuaries (Palma et al., 1999). Palma et al. (1999) found a steady decline in settlement from the outer coast to the upper reaches of the estuary although temperature patterns and substrate were ideal for settlement

of those species. Further, reproductive populations of both species were abundant on the outer coast as were their competent larvae. Given the much lower population densities of *H. sanguineus* on the outer coast, as compared to these native decapod species, up estuary recruitment limitation for *H. sanguineus* is not surprising.

Larval behavior governing propensity to settle is influenced by the presence of conspecifics. Specifically, isolated *H. sanguineus* larvae will not metamorphose in the absence of conspecific chemical cues (Steinberg et al., 2007). Small ephemeral populations on the outer coast of Maine might not be a source of conspecific cues strong enough to induce metamorphosis in up-estuary populations.

Connectivity has been proposed to limit the geographic range of *H. sanguineus* populations. Specifically, Byers and Pringle (2006) suggested that ocean currents may be interacting with temperature to create a barrier to range expansion. Given that cool summer temperatures promote long larval duration times (O'Connor et al., 2007), plankton would be expected to remain in the water column longer in Maine than is the case to the south. The longer the larvae spend in the plankton, the higher their mortality (Cowen et al., 2000) and the higher the likelihood they will be carried downstream by the prevailing currents (Byers and Pringle, 2006). Surface currents along the Maine coast generally move in a southwesterly direction (Pettigrew et al., 2005) thus impeding the northeasterly flow of *H. sanguineus* larvae. Additionally, the cool, fast moving surface waters of the Eastern Maine Coastal Current, which runs from eastern Maine to Penobscot Bay (Pettigrew et al., 2005), would promote long development times and inhibit transport of larvae to areas in the transition zone and in eastern Maine. Nevertheless, the other non-native intertidal crab, *C. maenas*, with very similar larval duration to *H. sanguineus* has successfully recruited into eastern Maine (although these populations are ephemeral in some areas) (Dawirs, 1985; Seeley, 1986). Importantly, the average summer temperatures at the northern-most end of the native range of *C. maenas* in Europe are about 2 °C cooler than those at the northern end of the native range of the Asian shore crab (based on satellite SST data from the NOAA-CIRES Climate Diagnostics Center).

### 4.3. Conclusion

In a study on the causes of non-native terrestrial plant invasion in Chile, three factors were found to be necessary for a successful invasion (Figueroa et al., 2004). They include 1) a source of non-native species, 2) a receptive community for the non-native species and 3) physiological life history attributes of the non-native species that allow them to thrive and propagate. Our research suggests that this last criteria maybe limiting *H. sanguineus* from colonizing the entire Gulf of Maine.

We recognize that the history of the *H. sanguineus* invasion in Maine is too brief to conclude what is limiting its range expansion. How the invasion evolves over the next decade should be telling. If the slow rate of invasion throughout the Gulf of Maine is due to low rates of upstream advection coupled with colder temperatures as suggested by Byers and Pringle (2006), then we might expect the eventual establishment of this species throughout the coast of Maine. Alternatively, if thermogeography shaped by a cold summer water temperature thermal threshold is the prime driver, then we expect outer coastal distributions to remain similar to those we see today, provided significant ocean warming does not occur. That is, there will be modest densities with periodic recruitment in the southwest coast, a mid-coast transition zone, and the northeastern coast will remain virtually free of *H. sanguineus.* Estuaries provide another test because they are currently devoid of Asian crabs, but upriver they are warm enough in summers to support recruitment (should larvae arrive there) and subsequent reproduction of Asian crabs (e.g. Figs. 6 and 7). Recent survey data (2007) from the New Meadows River in Casco Bay, Maine, suggests that Hemigrapsus is slowly expanding into estuarine environments there (Seeley, personal observation).

Specific thermal tolerances and limits for many invertebrate species are well documented (e.g. Hummell et al., 1988, 1997). These tolerances are increasingly recognized as delimiting biogeography (e.g. Pörtner, 2002). A study of adaptation of thermal tolerances in three snails of the *Tegula* spp, (Tomanek and Somero, 1999) concluded that "genetically fixed differences … reflect the separate evolutionary histories of these species and may play important roles in setting their thermal tolerance limits and, thereby, their biogeographic distribution patterns" (p 2925). If the relative stability of biogeographic provinces reflects the evolutionary limits to thermal adaptations as suggested by Adey and Steneck (2001), then we may expect those thermogeographic limits to also limit geographic invasion into non-native habitats. Recruitment and population growth of Asian shore crabs into eastern Maine and Canada may remain limited or absent, unless these limits are relaxed by the ever-warming Gulf of Maine.

## Acknowledgements

## Appendix A

Original/unadjusted *H. sanguineus* densities recorded during quadrat surveys in 2004 and 2005.

| Site | Latitude/longitude (decimal degrees) | Original density *H. sanguineus*/m² | |
|---|---|---|---|
| | | 2004 survey | 2005 survey |
| Seapoint Beach, Kittery | 43.0909 N 70.6602 W | 2.5 | 1.75 |
| Biddeford Pool | 43.44019 N 70.34294 W | 0.44 | 0.40 |
| Two Lights State Park Cape Elizabeth | 43.59874 N 70.19900 W | 0.24 | 0.37 |
| Lowell Cove Orr's Island | 43.75940 N 69.97591W | 0.68 | 0.60 |

## Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2009.04.020.

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