



Invasion biology of the Asian shore crab *Hemigrapsus sanguineus*: A review

Charles E. Epifanio *

School of Marine Science and Policy, University of Delaware, 700 Pilottown Road, Lewes, DE 19958, USA

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ABSTRACT

The Asian shore crab, *Hemigrapsus sanguineus*, is native to coastal and estuarine habitat along the east coast of Asia. The species was first observed in North America near Delaware Bay (39°N, 75°W) in 1988, and a variety of evidence suggests initial introduction via ballast water early in that decade. The crab spread rapidly after its discovery, and breeding populations currently extend from North Carolina to Maine (35°–45°N). *H. sanguineus* is now the dominant crab in rocky intertidal habitat along much of the northeast coast of the USA and has displaced resident crab species throughout this region. The Asian shore crab also occurs on the Atlantic coast of Europe and was first reported from Le Havre, France (49°N, 0°E) in 1999. Invasive populations now extend along 1000 km of coastline from the Cotentin Peninsula in France to Lower Saxony in Germany (48°–53°N). Success of the Asian shore crab in alien habitats has been ascribed to factors such as high fecundity, superior competition for space and food, release from parasitism, and direct predation on co-occurring crab species. Laboratory and field observations indicate that *H. sanguineus* is a generalist predator with potential for substantial effects on sympatric populations of mollusks and crustaceans. However, broad ecosystem effects and actual economic impact are unclear. The literature on *H. sanguineus* is limited in comparison to better known invasive species like the European green crab (*Carcinus maenas*) and the Chinese mitten crab (*Eriocheir sinensis*). Nevertheless, there are substantial bodies of work on larval biology, trophic ecology, and interspecies competition. This paper presents a review of the biology and ecology of invasive populations of the Asian shore crab *H. sanguineus* in North American and European habitats.

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* Tel.: +1 302 645 4272; fax: +1 302 645 4007.

E-mail address: epi@udel.edu.

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1. Introduction

Alien crab species occur in coastal environments worldwide (Galil et al., 2011). These introductions are aided by human activities and may involve transport across entire ocean basins (Ng et al., 2008; Williams, 1984). For example, the green crab *Carcinus maenas* is native to Europe, but has been common in the western Atlantic since the 19th Century and now occurs in widely divergent areas throughout the Atlantic and Pacific basins (Edgell and Hollander, 2011). Likewise, the mitten crab *Eriocheir sinensis* is indigenous to the temperate shores of Asia, but was introduced in the river systems of western Germany in the early 20th Century (Panning, 1939). The crab is now established in Europe from the Baltic Sea to the Bay of Biscay (Christiansen, 1982; Herborg et al., 2005) and also occurs some 10,000 km away on the Pacific coast of North America (Dittel and Epifanio, 2009; Rudnick et al., 2000; Rudnick et al., 2003).

Exotic populations of large crabs like *C. maenas* and *E. sinensis* have obvious impacts on local habitats, and effects on ecosystems and human economies are well documented (e.g., Brockerhoff and McLay, 2011; Edgell and Hollander, 2011; Rudnick et al., 2003). However, smaller species have received more cursory study, probably because their economic impact is less evident (Griffen, 2011; Soors et al., 2010). One case in point is the Asian shore crab, *Hemigrapsus sanguineus* (De Haan, 1835), which is native to rocky habitat along the east coast of Asia and was first observed in North America near Delaware Bay in 1988 (Ai-yun and Yang, 1991; McDermott, 1991; Williams and McDermott, 1990). The Delaware estuary hosts the fifth largest port complex in the USA (Kim and Johnson, 1998), and release of ballast water by ocean-going vessels is the likely vector for introduction of Asian shore crabs into the Delaware region (Carlton and Geller, 1993). Alternatively the crab may have been part of the fouling community on sea chests or other parts of ships entering the estuary. The species spread rapidly in the initial 15 years after its discovery, but new colonization has slowed since that time. Nevertheless, *H. sanguineus* is now the dominant crab in rocky intertidal habitat along much of the northeast coast of the USA (Ahl and Moss, 1999; Griffen, 2011; Kraemer et al., 2007). Moreover, *H. sanguineus* has displaced native mud crabs and the previously invasive green crab at many locations in its North American range (Bourdeau and O'Connor, 2003; Grosholz et al., 2000; Lohrer et al., 2000a, 2000b). The Asian shore crab also occurs on the Atlantic coast of Europe and was first observed in Le Havre, France in 1999 (Breton et al., 2002). Invasive populations now extend from the English Channel to the North Sea and have caused displacement of native crab species throughout the invasive range (Dauvin et al., 2009).

The success of Asian shore crabs in North American habitats has been ascribed to factors such as extended spawning season and high fecundity (McDermott, 1998a; Park et al., 2005), superior competition for space and food (MacDonald et al., 2007; Steinberg and Epifanio, 2011), release from parasitism (McDermott, 2011; Takahashi et al., 1997), and direct predation on co-occurring crab species (Lohrer and Whitlatch, 2002a). Laboratory and field observations indicate that *H. sanguineus* is a generalist predator that can affect sympatric populations of mollusks and crustaceans (Brousseau and Baglivo, 2005; Griffen and Byers, 2009; Lohrer and Whitlatch, 2002b). However, broad ecosystem effects and actual economic impact remain unclear.

The purpose of this review is to update existing information about the ecology and biology of invasive populations of the Asian shore crab. The literature on *H. sanguineus* is limited compared to better known species like *C. maenas* and *E. sinensis*. Nevertheless, there are substantial bodies of work on larval biology, trophic ecology, inter-species competition, and community interactions. The remainder of this paper is divided into eight sections that cover various aspects of the systematics, distribution, life history, physiology, and ecology of *H. sanguineus*. These are followed by a final section that provides summary and conclusions. The review encompasses the traditional peer-reviewed literature, but also includes recent information available online (Table 1).

2. Systematics and taxonomy

Crabs in the genus *Hemigrapsus* are assigned to the Varunidae, which is one of six families in the superfamily Grapsoidea (Kitaura et al., 2002; Martin and Davis, 2001; Schubart et al., 2000). Grapsoide crabs are classified in the infraorder Brachyura (true crabs) and are further distinguished in the section Eubrachyura and subsection Thoracotremata, which also includes the superfamilies, Cryptochiroidea, Ocypodoidea, and Pinnotheroidea. The monophyletic status of the family Varunidae has been confirmed by recent molecular analysis (Schubart et al., 2006). The full taxonomic lineage of *H. sanguineus* can be found at websites listed in Table 1.

Varunid crabs occur worldwide in semi-terrestrial, freshwater, and coastal marine habitats. The genus *Hemigrapsus* inhabits intertidal and shallow subtidal environments and was first described by Dana in 1851 (Sakai, 1976). The genus contains 15 species, but is undergoing revision with probable relocation of some species to other genera (McDermott, 2011; Ng et al., 2008). Only one of the extant species, *Hemigrapsus affinis*, has native range outside the Pacific basin (Davie and Türkay, 2012). However, the Pacific species of *Hemigrapsus* are widely distributed, and the genus occurs on the east coast of Asia, the west coasts of North and South America, and New Zealand.

Table 1

Selected information concerning the Asian shore crab *Hemigrapsus sanguineus* available on the World Wide Web.

Subject	Website
Systematics	http://animaldiversity.ummz.umich.edu/site/accounts/classification/Hemigrapsus.html http://www.marinespecies.org/aphia.php?p=taxdetails&id=439140 http://www.marinespecies.org/aphia.php?p=taxdetails&id=106964 http://www.marinespecies.org/aphia.php?p=taxdetails&id=158417
Taxonomy	http://species-identification.org/species.php?species_group=crabs_of_japan&id=528&menuentry=groepen http://species-identification.org/species.php?species_group=crabs_of_japan&id=1699&menuentry=soorten
Fact sheets	http://www.issg.org/database/species/ecology.asp?si=756&fr=1&sts http://nas.er.usgs.gov/queries/FactSheet.aspx?speciesID=183 http://www.brc.ac.uk/gbnn_admin/index.php?q=node/220
Maps	http://nas2.er.usgs.gov/viewer/omap.aspx?SpeciesID=183

H. sanguineus has several distinguishing characteristics (Dai and Yang, 1991; Fukui et al., 1989; Sakai, 1939). Adults and juveniles have a square-shaped carapace with three distinct teeth on either side of the anterior margin. Color is typically dark and ranges through a variety of hues spanning orange, green, and purple. Chelipeds are marked with red spots, and walking legs have a distinct pattern of alternating light and dark bands. Male crabs possess a fleshy knob at the dactyl base of each cheliped, as well as relatively larger claws than females (Ledesma and O'Connor, 2001). As with most brachyurans, the abdomen of mature females is wider than that of male crabs (McDermott, 1998a). Males are generally larger than females and reach maximum carapace width >40 mm; females rarely exceed 35 mm (Benson, 2005). Additional morphological details are presented at a number of websites (Table 1).

Molecular approaches to the systematics of *H. sanguineus* are limited to a pair of studies of mitochondrial DNA sequences in crabs from native Asian habitat. In one investigation, Yoon et al. (2011) analyzed a nucleotide sequence of mitochondrial COI¹ from a number of Korean and Japanese populations. Overall, the populations had high haplotype diversity and low nucleotide diversity, which may have resulted from recent expansion of a small ancestral population (see below). Additional analysis showed substantial gene flow among all of the populations except those on the Yellow Sea coast of Korea and the Pacific coast of Japan. The authors attributed the diminished gene flow to hydrographic separation of the respective populations.

In a somewhat different tactic, Hong et al. (2012) investigated six local populations of *H. sanguineus* from three spatially discrete coastlines in Korea and analyzed mtDNA sequences of the cytb gene.² Findings were similar to those for mitochondrial COI and showed high haplotype diversity and low nucleotide diversity among the populations. The authors ascribed the results to high gene flow among five of the six populations and recent expansion from low population densities that occurred during Pleistocene glaciation.

3. Geographic distribution

3.1. Asian range

Native populations of *H. sanguineus* are very widely distributed on the east coast of Asia and extend northward more than 3000 km (20°–50°N) from Hong Kong all the way to Sakhalin Island, Russia (e.g., Hwang et al., 1993; Sakai, 1976; Shen, 1932; Takahashi et al., 1985). Asian habitat often includes the middle and upper intertidal zones on rocky shorelines (Fukui, 1988; Kikuchi et al., 1981; Sakai, 1976), although some studies have reported common occurrence in the lower intertidal as well (Saigusa and Kawagoye, 1997). The extent of penetration into estuaries by *H. sanguineus* is limited to euhaline regions, presumably an effect of restricted tolerance of low salinity (Epifanio et al., 1998; Gerard et al., 1999; McDermott, 1998b).

H. sanguineus co-occurs with two congeners (*H. penicillatus* and *H. takanoi*) through much of its Asian range. This sympatry is facilitated by partition of habitat wherein *H. penicillatus* and *H. takanoi* are more common in low-energy, fine-sediment areas, while *H. sanguineus* is prevalent in moderate-energy, coarse-sediment habitat (Asakura and Watanabe, 2005; Dauvin et al., 2009). The arrangement is similar to the sympatric distribution of two species of *Hemigrapsus* on the Pacific coast of North America where *H. oregonensis* inhabits low-energy habitat and *H. nudus* is more abundant in moderate-energy areas (Hiatt, 1948; Knudsen, 1964; Willason, 1981).

3.2. North American range

The first report of Asian shore crabs in North America was a single ovigerous female collected at Townsend Inlet near the mouth of Delaware Bay in 1988 (Williams and McDermott, 1990). Subsequent collections at the same site in 1990 provided clear evidence of a breeding population and showed the occurrence of adult males, additional ovigerous females, and young-of-the-year juveniles (McDermott, 1991). Using a variety of evidence, including the estimated age of the first ovigerous female, McDermott (1998b) proposed an initial introduction of *H. sanguineus* via ballast water in the early 1980's.

McDermott recognized the opportunity to observe a nascent bioinvasive event and established a monitoring program in 1990 to document the spread of Asian shore crabs along the Atlantic coast of the USA (McDermott, 1991). Results showed rapid extension both northward and southward. By 1993, specimens had been collected at sites ranging from Cape Charles at the mouth of Chesapeake Bay all the way to Woods Hole, Massachusetts (McDermott, 1995). Two years later the range extended from Oregon Inlet, North Carolina to Cape Ann, Massachusetts (McDermott, 1998b), and by the year 2000 very dense populations existed in Long Island Sound and southern New England (Bourdeau and O'Connor, 2003; Lohrer et al., 2000a, 2000b). The species has continued to spread slowly since that time, and individuals have been collected as far north as the Schoodic Peninsula in Maine (Delaney and Sperling, 2008). However, further expansion into Canadian waters may be blocked by cold ambient temperatures (Stephenson et al., 2009). Likewise, there has been no movement southward beyond Cape Hatteras since the initial discovery near that location in 1995 (Table 1). This is puzzling because *H. sanguineus* is common as far south as Hong Kong (~20°N) in its native Asian range, which is at the same latitude as Cuba in the western Atlantic (Fig. 1). Moreover, ocean waters along the east coasts of Asia and North America are highly influenced by western boundary currents (i.e., Kuroshio Current and Gulf Stream) and have similar temperature regimes at comparable latitudes (Mann and Lazier, 2006).

The lack of natural rocky substratum south of Cape Hatteras is one factor that could limit colonization beyond that point. However, the amount of anthropogenic rocky shoreline along the southeast coast of the USA is comparable to the Middle Atlantic Bight where *H. sanguineus* has been established since the early 1990's (McDermott, 1998b). Likewise, the mean current field in the Middle Atlantic Bight does not favor transport of larval forms southward beyond Cape Hatteras, but event-scale processes are more than sufficient to provide gene flow between populations of species that occur on both sides of the cape (Byers and Pringle, 2006; Epifanio and Garvine, 2001). Thus, the truncated southward range of *H. sanguineus* remains unexplained as of this writing.

3.3. European range

Invasive populations of *H. sanguineus* also occur on the Atlantic coast of Europe (Fig. 2). The species was first reported at Le Havre, France in 1999 along with an invasive congener initially identified as *H. penicillatus* (Breton et al., 2002; Noël et al., 1997). However, European populations of the latter taxon were assigned to a new species (*H. takanoi*) in 2005, and this name is used in the subsequent literature (Asakura and Watanabe, 2005; Yamasaki et al., 2011).

Available evidence suggests that *H. sanguineus* and *H. takanoi* were first introduced along the Dutch and Belgium coasts of the North Sea via ballast water and then spread northward into Germany and westward along the English Channel (Dauvin et al., 2009; Gollasch, 1999; Obert et al., 2007). A number of studies have documented the two species in the Netherlands (e.g., d'Udekem d'Acoz 2006; Nijland and Beekman, 2000; Nijland and Faasse, 2005), in Belgium (Breton et al., 2002; Kerckhof et al., 2007), and in northern France (Dauvin, 2009). Breeding populations of both species now extend from Lower Saxony in Germany to the Cotentin Peninsula in France (54°–49°N), and

¹ Mitochondrial cytochrome c oxidase subunit I gene.

² Mitochondrial DNA of the cytochrome b gene.

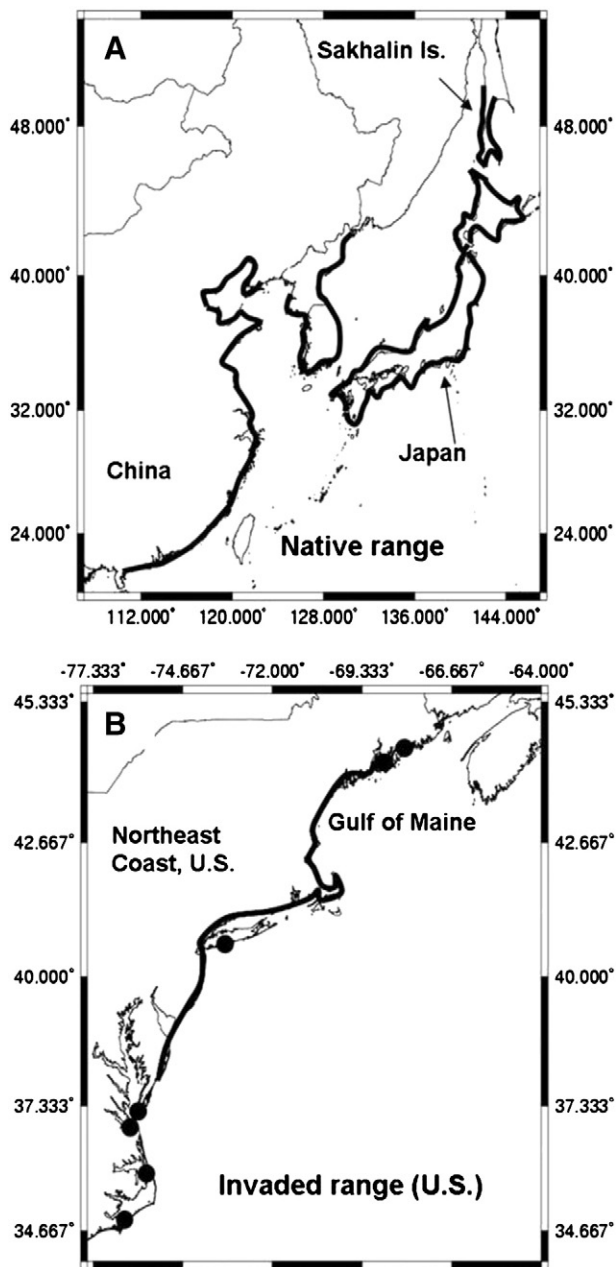


Fig. 1. Comparison of geographic range of the Asian shore crab (*Hemigrapsus sanguineus*) in native Asian and alien American habitats. Modified from Stephenson et al. (2009).

populations of *H. takanoi* also occur along the Spanish and French coasts of the Bay of Biscay (Noël and Gruet, 2008). *H. sanguineus* has likewise been reported from Istra Peninsula in the northern Adriatic Sea and from Constanta, Romania in the Black Sea. But there is no evidence that breeding populations have been established at these locations (Micu et al., 2010; Schubart, 2003). However, there are no climatic or physiological barriers restricting additional southward movement, and the species may eventually extend to the Mediterranean and the Atlantic coast of North Africa (Dauvin et al., 2009). Spread of both species along the southern coast of Britain also seems likely and may have already occurred (Dauvin et al., 2009). Further expansion into the North Sea, perhaps as far as 60°N is also possible, given the relatively warm European climate compared to similar latitudes on the east coasts of Asia and North America (e.g., Seager et al., 2002).

4. Reproductive biology

4.1. Ovarian development and reproductive period

Length of reproductive season varies with latitude and with winter temperature in native populations of *H. sanguineus*. For example, the reproductive period of Japanese populations ranges from 3 months at Oshoro Bay (43°N; <5 °C) in western Hokkaido to 8 months at Tanabe Bay (34°N; 14 °C) in southern Honshu (Fukui, 1988; Kurata, 1968; Takahashi et al., 1985). Analogous latitudes in the western Atlantic stretch from southern Maine to North Carolina and encompass much of the invasive American range of *H. sanguineus* (Griffen, 2011). McDermott (1998a) observed a reproductive period of 5 months for Asian shore crabs along the coast of New Jersey (39–40°N; 5°–7 °C), which is coherent with data from Japanese populations. McDermott also monitored gonadal development in the New Jersey populations and found that 70% of adult females had mature ovaries immediately prior to initiation of the spawning season in May. In contrast, no females showed extensive ovarian development at the end of the season in October. Epifanio et al. (1998) reported similar results for an invasive population farther south in Delaware Bay where the proportion of ovigerous females ranged from 35 to 70% during the period June through September and dropped to zero in October.

4.2. Mating behavior

Patterns of courtship and copulation vary greatly among brachyuran crabs. Visual signals often initiate courtship in semi-terrestrial taxa (Christy and Salmon, 1984; Yamaguchi, 2001), while chemical cues serve the same purpose in subtidal crabs (Bamber and Naylor, 1996; Gleeson, 1980; Herborg et al., 2006). In many intertidal forms, mating requires both visual and chemical stimuli (Abele et al., 1986; Broukerhoff and McLay, 2005a,c; Fukui, 1993). In some families, mating is restricted to a certain molt stage or life stage (Broukerhoff and McLay, 2005b; Wolcott et al., 2005), but in others mating occurs at any point in the molt cycle, as long as the crabs are sexually mature (Schubart et al., 2002). The frequency of copulation also varies among taxa, and in many species the females are able to store sperm from a single mating for periods ranging from weeks to months (Wolcott et al., 2005). Size ratio of copulating males to females is also important for many brachyuran taxa. Generally, the male is larger than the female, perhaps the result of competition for access to females (Comeau et al., 1998; Styrrishave et al., 2004).

Broukerhoff and McLay (2005a) have summarized five typical mating behaviors for the genus *Hemigrapsus*. These include: a) absence of courtship; b) initiation of mating by males; c) short duration of copulation (<10 min); d) post-copulatory guarding by males; and e) polygamous mating by females after an initial copulation. Mating in *H. sanguineus* follows this general pattern, but differs in several important details (Table 2). As with other species in the genus, there is no apparent courtship behavior in *H. sanguineus*, and it is not clear how males determine the receptivity of females (Anderson and Epifanio, 2010a). Moreover, copulation is always initiated by the male, and both male and female are in calcified intermolt stage at the time of copulation. In most cases, the male is larger than the female.

However, copulation in *H. sanguineus* is comparatively long, averaging about 30 min and sometimes exceeding 60 min (Anderson and Epifanio, 2010a, 2010b). In contrast to other species of *Hemigrapsus*, guarding behavior by males is rare, and post-copulatory females do not mate with additional males. Likewise, the mating position in *H. sanguineus* is unique in the genus and consists of an orientation perpendicular to the substratum with the male and female facing each other. Other species of *Hemigrapsus* have horizontal mating positions with the male on the bottom and the dorsal surface of the male in contact with the substratum, which limits movement

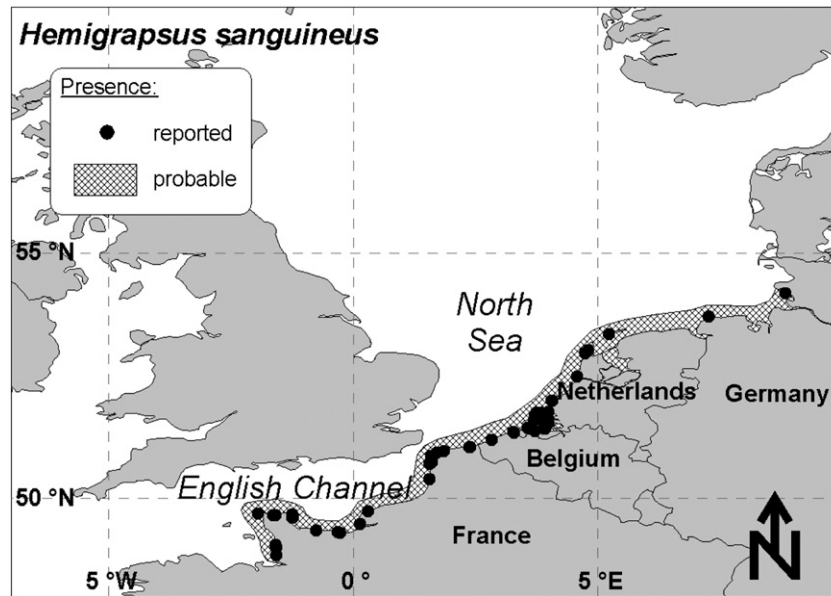


Fig. 2. Geographic range of invasive populations of the Asian shore crab (*Hemigrapsus sanguineus*) in European habitats. From Dauvin et al. (2009).

by the copulating pair (Brockerhoff and McLay, 2005a; Knudsen, 1964). Unlike other species of *Hemigrapsus* that seek shelter while mating, *H. sanguineus* pairs are less secretive (at least under laboratory conditions) and copulate in open areas during both diurnal and nocturnal hours. However, the upright mating position of *H. sanguineus* allows the female to move the couple away from disturbances, and the chelae of the male are available to defend the pair (Anderson and Epifanio, 2010a, 2010b).

4.3. Brooding, hatching and fecundity

Brooding in *H. sanguineus* follows the typical pattern for brachyuran crabs (e.g., Jivoff et al., 2007). Copulation allows deposition and storage of sperm packets in the seminal receptacles of the female for eventual fertilization of eggs (Lee and Yamazaki, 1990). Inseminated eggs are then extruded from the genital ducts and deposited on abdominal appendages (pleopods) where they are brooded until hatching. Laboratory observations show that a single copulation in *H. sanguineus* provides viable sperm for at least two broods of eggs. Moreover, females are available for mating shortly after spawning and appear to copulate multiple times during the reproductive season (Anderson and Epifanio, 2010a; McDermott, 1998a). Time from copulation to extrusion of eggs is typically <24 h. Incubation time varies with temperature and ranges from 16 days at 25 °C to 22 days at 20 °C

(Anderson and Epifanio, 2010a; Epifanio et al., 1998; McDermott, 1998a). A second batch of eggs is often extruded a few days after hatching of the initial brood.

Results of field and laboratory investigations indicate that hatching in *H. sanguineus* always occurs near the time of nocturnal high tide (Park et al., 2005). Hatching takes place throughout the spawning season, and there is no clear indication of lunar or spring/neap periodicity (Epifanio et al., 1998; Park et al., 2005; Saigusa and Kawagoye, 1997). Hatching near nocturnal high tide has been reported for a number of crab species and may reduce predation on females, as well as on newly hatched larvae (Morgan and Christy, 1996). Release of larvae near the time of high tide also allows transport away from intertidal habitats (see Section 6.2) where conditions may not be optimum for larval development (Epifanio and Garvine, 2001).

Female *H. sanguineus* achieve sexual maturity in about a year post-hatching when they have reached a carapace width of approximately 15 mm (Takahashi and Matsuura, 1994; Takahashi et al., 1985). The crabs may live another 2 years, eventually exceeding 30 mm in width (Fukui, 1988). Fecundity is a function of size, with small females producing <500 eggs per brood, and the very largest individuals releasing >50,000 larvae per spawning event (Fukui, 1988; McDermott, 1998a). Thus, a 3-year old female that has extruded 2–3 broods per year may have produced several hundred thousand larvae in a life time.

5. Early life history

5.1. Larval forms

Development of Asian shore crabs includes five zoeal stages and a megalopal stage (Epifanio et al., 1998; Hwang et al., 1993; Hwang and Kim, 1995). Larval morphology is similar to other species in the family Varunidae. However, differences in several characters allow discrimination of *H. sanguineus* from other species of *Hemigrapsus* (Kim and Hwang, 1995; Montu et al., 1996; Ng et al., 1998; Shy and Yu, 1992). Morphological features commonly used in distinguishing zoeal stages include setation on antennules, maxillae, and maxillipeds, while megalopal stages are often differentiated by examining maxillipeds and antennae (Dittel and Epifanio, 2009). Kim and Hwang (1995) have developed a taxonomic key to the first

Table 2

Asian shore crab *Hemigrapsus sanguineus*. Summary of mating parameters.

Mating parameter	Characteristic
Duration	6 to 60 min
Position	Upright
Initiator	Male
Time of day	Night & day
Shelter usage	No
Post-copulatory guarding	Rare
Frequent female mating	No
Easily disturbed	No
Time to extrusion	<24 h
Extrusion to hatching	16 d
Broods from single mating	At least 2

zoeal stage of several Asian species in the family Varunidae, and recent work has provided relevant keys to brachyuran zoeae in San Francisco Bay (Rice and Tsukimura, 2007) and the Sea of Japan (Kornienko and Korn, 2008). Discrimination of closely related varunid species may be of particular value in areas of Europe where invasive populations of *H. sanguineus*, *H. takanoi* and *E. sinensis* already co-occur and on the west coast of the USA where *E. sinensis* overlaps with native populations of *H. nudus* and *H. oregonensis* (Dauvin et al., 2009; Dittel and Epifanio, 2009; Gilbey et al., 2008; Tilburg et al., 2011).

5.2. Effects of temperature and salinity

Larval duration in *H. sanguineus* is strongly dependent on temperature. Kurata (1968) worked with larvae from native Asian populations and reported 34 days from hatching to the megalopa stage at room temperature (~22 °C), while Hwang et al. (1993) found a mean time to megalopa of 18 days at 25 °C. In more extensive work, Epifanio et al. (1998) investigated effects of salinity and temperature on larvae from an invasive population along the Middle Atlantic coast of the USA. In that research, duration from hatching to megalopa was 16 days under optimum conditions and increased to about 23 days at lower values of salinity and temperature (Table 3). Maximum survival always occurred at high salinity and temperature, and survival at reduced salinity was modulated by temperature (Table 4). This interaction between effects of temperature and salinity has been documented for zoea larvae of other coastal and estuarine crabs, including native species that co-occur with *H. sanguineus* in the Middle Atlantic region (e.g., Costlow et al., 1960, 1962, 1966; Epifanio et al., 1988) and along the Atlantic coast of Europe (e.g., Anger et al., 1998; Dawirs et al., 1986; deRivera et al., 2007).

In contrast to the wide tolerance frequently seen in zoea larvae, the megalopal stage may have a more restricted set of requirements. For example, megalopae of *H. sanguineus* failed to develop to the juvenile crab stage at salinities below 25‰ and temperatures below 20 °C (Epifanio et al., 1998). The limited tolerance of megalopae to low salinity provides an explanation for the absence of *H. sanguineus* in mesohaline and oligohaline regions of estuaries. However, laboratory data concerning tolerance of low temperature by megalopae are at odds with the observed northward distribution of the species in both native and invasive habitat where summer water temperatures are often below 20 °C (see Section 3 above). Reasons for this discrepancy are not clear, but it is important to recognize that laboratory studies are unable to mimic many characteristics of the natural environment that may have concomitant effects on survival, development, and growth (Christiansen and Costlow, 1975; Epifanio et al., 1994; MacKenzie et al., 1990; Welch and Epifanio, 1995). Moreover, the Epifanio et al. (1998) study used larvae from a Middle Atlantic population, and there have been no studies of low temperature effects on larvae from more northern populations where there may have been selection for wider tolerance.

Table 3

Early life history of the Asian shore crab *Hemigrapsus sanguineus*. Mean duration in days from hatching to the megalopa stage at different combinations of temperature and salinity. Values were rounded to the nearest whole day. Dashes indicate that no larvae survived to the megalopa stage. Minimum duration is in bold font. Modified from Epifanio et al. (1998).

Salinity (‰)	Temperature		
	15°	20°	25°
10	—	—	—
15	—	—	22
20	—	23	16
25	55	22	16
30	53	21	16

Table 4

Early life history of the Asian shore crab *Hemigrapsus sanguineus*. Mean percentage survival from hatching to the megalopa stage at different combinations of temperature and salinity. Values were rounded to the nearest integer. High survival is in bold font. Modified from Epifanio et al. (1998).

Salinity (‰)	Temperature		
	15°	20°	25°
10	0.0	0.0	0.0
15	0.0	0.0	8.0
20	0.0	23.0	60.0
25	3.0	60.0	50.0
30	5.0	60.0	47.0

6. Larval dispersal, settlement, and metamorphosis

6.1. Behavior

The motion of water in estuaries and on the continental shelf is subject to vertical shear in velocity (Epifanio and Garvine, 2001). For example, the speed of tidal currents is higher at the surface and lower deep in the water column because of frictional drag exerted by the bottom. Likewise, flow at subtidal frequency varies with depth and may involve changes in both speed and direction. For instance, gravitational circulation at the mouth of large estuaries is usually seaward near the surface and landward closer to bottom (Epifanio, 1988; Epifanio and Garvine, 2001; Pape and Garvine, 1982). While swimming speed of crab larvae is slow compared to the ambient current field (Epifanio, 2007), the larvae often exhibit behaviors that regulate vertical position in the water column (Forward and Tankersley, 2001; Sulkin, 1984). Because of shear in velocity, these behaviors ultimately control the horizontal transport of larvae.

Park et al. (2004) studied the response of *H. sanguineus* to gravity and hydrostatic pressure in order to predict changes in vertical distribution during larval development. Results showed a suite of behaviors that would facilitate export of newly hatched larvae from estuarine habitats to the adjacent coastal ocean. As expected, larvae were negatively buoyant, and sinking speed increased with advancing larval stage. Additional experiments showed that early-stage zoeae are negatively geotactic (upward orientation in the water column) and that exposure to increasing hydrostatic pressure elicits a rise in swimming activity (positive barokinesis). The combination of negative geotaxis and positive barokinesis would result in enhanced upward swimming as larvae sink in the water column and experience increasing hydrostatic pressure. This response would keep early-stage larvae in surface waters where they would undergo net seaward transport out of estuaries. However, advanced-stage zoeae showed a different set of behaviors that would result in return of larvae to coastal and estuarine habitat. Advanced larvae were positively geotactic (downward orientation) and showed low sensitivity to increases in hydrostatic pressure. These responses would keep larvae deep in the water column where subtidal flow associated with estuaries is landward. The clear ontogenetic difference in behavior of *H. sanguineus* larvae supports an export-and-return model of larval transport wherein early development occurs in the coastal ocean and advanced stages are transported back to the estuary (Arana and Sulkin, 1993; Epifanio, 1988; Sulkin and Van Heukelem, 1982; Wheeler and Epifanio, 1978). However, it is important to keep in mind that geotactic and barokinetic responses occur in the context of a photic environment in nature, and there are no published studies of the response of Asian shore crab larvae to light.

6.2. Field distribution of larvae

There have been very few studies concerning the field distribution of larvae from native or introduced populations of *H. sanguineus*. Jancaitis (2003) used satellite tracking techniques to follow patches of early-stage larvae near the mouth of Delaware Bay along the east

coast of the USA. Maximum densities approached 80 zoeae m^{-3} and generally declined over the 48-hour duration of tracking, probably due to predation and mixing. Park et al. (2005) worked in the same geographical area and documented the presence of newly hatched zoeae at the expected time of larval release near nocturnal high tide (see Section 4.3 above). High concentrations of larvae occurred in the local water column for an hour after each spawning event, but declined rapidly thereafter—probably reflecting tidal transport away from the hatching site. In related work, Park (2005) conducted hourly sampling over two tidal cycles at a station about 5 km seaward of the spawning site and found early-stage zoeae during the nocturnal ebb phase. Park also monitored larval abundance in the adjacent coastal ocean and collected zoeae as far as 25 km offshore of the bay mouth. These results indicate that newly hatched *H. sanguineus* are carried seaward by ebb tidal currents and are subsequently influenced by circulation on the continental shelf where long distance transport is possible (Epifanio and Garvine, 2001). In more recent work, Delaney et al. (2012) modeled transport of *Hemigrapsus* larvae on the continental shelf and compared model results to field observations of juvenile occurrence along the coast of New England. The authors attributed inconsistent results to the crude simulation of larval behavior in the model.

6.3. Settlement and metamorphosis in response to chemical cues

Eventual return of larvae to coastal and estuarine habitat is accomplished via gravitational circulation (see Section 6.1 above) or through onshore transport associated with wind events (Epifanio and Garvine, 2001; Garvine et al., 1997; Jones and Epifanio, 1995). In many species, settlement and metamorphosis in estuarine habitat are facilitated by the response of megalopae to chemical or physical cues. Chemical cues often involve water-soluble metabolites (exudates) produced by conspecific adults or by other species that typify a certain benthic environment (Forward et al., 2001). Some chemical cues are explicit for a particular species, while others evoke settlement responses in a variety of taxa (Rodriguez and Epifanio, 2000; Weber and Epifanio, 1996). Physical cues typically involve characteristics of the substratum. These may include grain size or surface roughness (O'Connor, 2007; Steinberg et al., 2008).

Andrews et al. (2001) studied cues that stimulate settlement of a native mud crab (*Panopeus herbstii*) along the Middle Atlantic coast of the USA. As expected, results showed accelerated metamorphosis of megalopae in response to exudates produced by conspecific adults (Rodriguez and Epifanio, 2000; Weber and Epifanio, 1996). However, megalopae also responded to exudate from Asian shore crabs, which was surprising because the two species are not closely related and had only a few decades of sympatric history. Kopin et al. (2001) conducted an inverse set of experiments wherein *H. sanguineus* megalopae were exposed to exudates produced by adult Asian shore crabs and by two species of native mud crabs (*P. herbstii* and *Dyspanopeus sayi*). As anticipated, results showed a strong effect of conspecific exudate on metamorphosis of *H. sanguineus*. However, there was no response whatsoever when *H. sanguineus* megalopae were exposed to exudate from either mud crab.

Additional work by O'Connor (2007) again found strong response of *H. sanguineus* megalopae to conspecific adults, but also to exudate produced by the green crab, *C. maenas*. The latter result was in contrast to Kopin et al. (2001) and was notable because the two species are not closely related and have little sympatric history. However, further studies by Steinberg et al. (2007) investigated the response of Asian shore crabs to exudates produced by four congeneric species and by several sympatric taxa from Asia and North America. Results were coherent with Kopin et al. in that megalopae again responded strongly to exudate from conspecific adults. Moreover, the cue was highly specific, and *H. sanguineus* did not respond to exudates from other species, regardless of taxonomic affinity. Corollary studies by

Anderson et al. (2010) provided similar results and showed positive response to cues produced by juvenile *H. sanguineus* as well as adults. The consensus result of these experiments is that *H. sanguineus* responds to a very narrow range of chemical metamorphic cues, which is contrary to expectations for a species that has been very successful in colonizing new habitat in the absence of adult conspecifics.

Further studies have investigated the chemical nature of the cue produced by adult *H. sanguineus* (Anderson et al., 2010; Steinberg et al., 2007). Results indicate a small molecule (<12 kDa) that behaves like a very small protein or peptide (Anderson et al., 2010). For example, the cue was rendered inactive when all protein was precipitated from solution with trichloroacetic acid or when proteins were cleaved with enzymes like the serine proteases, trypsin and proteinase K. Quantitative analysis of protein in the exudate indicated a sensory threshold between 0.1 and 0.01 μg of protein ml^{-1} of sea water. However, the calculated range refers to total protein, and not the specific metamorphic molecule. Accordingly, the actual cue is probably detected by megalopae at even lower concentrations.

Measurement of response to water-soluble cues under field situations presents a different set of challenges. Welch et al. (1997) were among the first to attempt this type of study with brachyuran crabs. These authors determined the effect of potential cue sources on settlement of wild blue crab megalopae under natural conditions. Welch et al. concluded that blue crab megalopae can distinguish among natural benthic substrata—avoiding sites with odors from potential predators and settling in sites with odors from seagrass. In a different approach, O'Connor and Judge (1999, 2004) deployed mesh cages containing laboratory-reared, fiddler crab megalopae in different field environments and measured the proportion undergoing metamorphosis in a set period of time. Results indicated that metamorphosis in fiddler crab larvae is strongly habitat-specific. Cages deployed immediately adjacent to a salt marsh showed high levels of metamorphosis with significant decline within 15 m of adult habitat.

O'Connor and Judge (2010) used similar techniques to investigate effects of metamorphic cues on *H. sanguineus* megalopae in field settings. Results showed high response in cages moored near rocky habitat with an established adult population, but metamorphosis was also stimulated in cages deployed in marsh environments with few adult *H. sanguineus*. The authors concluded that broad response to habitat cues may have facilitated the invasion of American and European habitats by *H. sanguineus*. Anderson and Epifanio (2010b) also used caging techniques to determine response of *H. sanguineus* megalopae to natural water-borne cues near adjacent rocky and marsh habitats. Like the above study, the percentage of megalopae undergoing metamorphosis was greatest in cages that were closest to the adult population. However, results differed from O'Connor and Judge and showed reduced metamorphosis in cages adjacent to the salt marsh. While reasons for disparate findings are not clear, both studies demonstrate that *H. sanguineus* megalopae respond strongly to water-soluble cues under field conditions, and both investigations provide real-world support for the existing body of laboratory work on settlement and metamorphosis.

6.4. Settlement and metamorphosis in response to substratum cues

Early work with brachyuran crabs showed that metamorphosis can also be stimulated by biofilm associated with benthic habitat and sometimes by physical features of the substratum in the absence of biofilm. For example, Weber and Epifanio (1996) found that pebbles from adult habitat induced metamorphosis of mud crabs (*P. herbstii*) when covered with natural biofilm, while abiotic mimics of the pebbles were inactive. Andrews et al. (2001) continued this line of investigation with *P. herbstii* and determined that water-soluble chemicals emanating from natural biofilms were effective inducers of metamorphosis, even after biofilms themselves were removed from the experimental containers. Rodriguez and

Epifanio (2000) conducted similar experiments that compared biofilms from different locations. Results showed that water-soluble cues originating from biofilm in adult habitat stimulated metamorphosis in *P. herbstii*, while biofilm from nearby sand flats was inactive—even when the physical substrata were identical. The obvious conclusion was that *P. herbstii* megalopae are able to discriminate among potential habitats based on differences in biofilm. These workers also quantified the proportions of algae and bacteria in the biofilm and conducted light/dark experiments to determine that bacteria were the source of the cue. O'Connor and Judge (1997) took a slightly different approach to the problem that included field deployment of caged fiddler crab megalopae. Results showed enhanced metamorphosis in the presence of natural and abiotic (combusted) marsh sediment, and the authors concluded that *U. pugnax* megalopae responded to both water-soluble and tactile cues associated with the sediment.

Kopin et al. (2001) were the first to investigate the role of substratum cues in the metamorphosis of *H. sanguineus*. Their experiments showed significant response of megalopae to natural pebbles from adult habitat, but did not distinguish between the water-soluble and tactile nature of the cue. In more recent work, Steinberg et al. (2008) facilitated the growth of natural biofilm on artificial surfaces and showed significant induction of metamorphosis in *H. sanguineus* megalopae. Moreover, these authors used microscopic techniques to confirm and quantify the presence of bacteria in the biofilm. Related studies by Anderson and Epifanio (2009) again showed that *H. sanguineus* megalopae respond to biofilm associated with rocky intertidal habitat. But in contrast to results from *P. herbstii*, the cue did not appear to be water-soluble, and exposure to exudate from otherwise active biofilm did not elicit a response.

O'Connor (2007) studied the combined effects of biofilm and substratum on metamorphosis of Asian shore crabs. Results indicated that megalopae generally reacted to complexity of substratum. Molting was accelerated by small pebbles (with or without biofilm) and by nylon mesh with pore sizes ranging from 500 to 5000 μm . Steinberg et al. (2008) determined a similar broad response of *H. sanguineus* to tactile cues wherein texture of substratum had strong effects on metamorphosis. Megalopae responded to abiotic nylon mesh of medium texture (100 and 1000 μm), but there was no significant effect of 10 μm or 2000 μm mesh treatments. These results suggest lower and upper thresholds of roughness, below and above which the substratum loses attractiveness. Likewise, there was significant effect of different types of abiotic pebbles (slate, sandstone, marble, and concrete) on metamorphosis, and the magnitude of response was augmented with increasing roughness. This general effect of abiotic pebbles from natural habitat was confirmed by Anderson and Epifanio (2009). In a separate experiment, Steinberg et al. (2008) again showed that clean nylon mesh (1000 μm) facilitated metamorphosis, but also revealed an amplified effect when that mesh was covered with natural biofilm. This result is particularly interesting because there was no response to the same biofilm when established on a smooth plastic surface. Thus, the augmented effect depends on both the biochemical character of the biofilm and the textural character of the substratum.

The overall results of these investigations confirm the importance of substratum-based cues in accelerating the metamorphosis of *H. sanguineus* and point to the critical role that suitable habitat plays in the survival and success of juvenile *H. sanguineus*. But within this broad response to physical texture, there is a narrower range of preferred settlement cues, which implies an optimal bottom texture that provides shelter for megalopae as they metamorphose to the juvenile stage. Moreover, the ability to detect multiple substratum cues for settlement and metamorphosis is a clear advantage for range extension of bioinvasive species like *H. sanguineus*. Likewise, the strong response to water-soluble cues produced by conspecific adults is an advantage in recruiting megalopae to invasive populations that have already been established.

7. Growth of larvae and juveniles

7.1. Zoeal and megalopal stages

Epifanio et al. (1998) investigated growth of larval *H. sanguineus* under varying conditions of salinity and temperature (Table 5). Mean duration from hatching to metamorphosis was 25 days at optimum conditions, and dry-weight growth of zoea larvae fit an exponential model. Specific growth rates ranged from 0.19 d^{-1} to 0.23 d^{-1} at high salinities and temperatures; these respective values are roughly equivalent to dry-weight increases of 19% to 23% d^{-1} . Newly hatched zoea larvae had a mean dry weight of 11.4 μg . Under optimum conditions, zoeae reached dry weights as great as 210 μg before molting to the megalopa stage. In turn, the dry weights of megalopae reached values as high as 475 μg shortly before metamorphosis.

Growth rates of *H. sanguineus* were similar to published values for native mud crab species (Epifanio et al., 1994). However, newly hatched *H. sanguineus* were nearly twice as heavy as comparable mud crab zoeae, which at exponential growth rates, yielded widely divergent dry weights at succeeding developmental stages. For example, newly molted *Hemigrapsus* megalopae had grown to approximately 200 μg compared to 75 μg for *P. herbstii* megalopae (Welch and Epifanio, 1995). Thus, the larvae of mud crab species such as *P. herbstii* may be suitable prey for the late developmental stages of the much larger *Hemigrapsus*.

7.2. Early juvenile stages

There have been very few studies of growth of juvenile Asian shore crabs. McDermott (1998a) reared a single field-caught megalopa through three juvenile stages and also collected and measured a few specimens in juvenile stages 1–3. From these data he estimated that female *H. sanguineus* reach sexual maturity in about 10 molts after metamorphosis. Epifanio et al. (1998) also determined growth rates of juvenile *H. sanguineus*, but used larger numbers of crabs that had been reared from hatching under optimum laboratory conditions. Increase in dry weight in this investigation was exponential, and proportional growth was $\sim 8\%$ of body weight d^{-1} . Mean dry weight of stage-1 juvenile crabs was approximately 650 μg . After 35 days of growth, juveniles had a mean dry weight of more than 8000 μg ; this represents a twelve fold increase in weight during a period of slightly more than a month. Newly metamorphosed juveniles underwent four molts in 29 days, and intermolt duration increased at each succeeding stage (Table 6). Average carapace width of stage-1 crabs was 1.6 mm, and growth was linear at 0.06 mm d^{-1} . The authors assumed continued linear growth in carapace width (Dittel et al., 2000; Krinsky and Epifanio, 2010; Van Heukelem et al., 1984) and calculated that female crabs would reach maturity (15 mm) in approximately 7.5 months. Because growth probably ceases during the coldest winter months, the authors concluded that *H. sanguineus* reaches maturity in about one year after metamorphosis in invasive North American populations.

Table 5

Early life history of the Asian shore crab *Hemigrapsus sanguineus*. Parameters of larval growth under laboratory conditions (25 °C, 30‰). Z-1 = zoea stage 1. Z-V = zoea stage 5. Data from Epifanio et al. (1998).

Parameter	Value
Mean zoeal duration	16 days
Mean megalopal duration	9 days
Total larval duration	25 days
Dry weight Z-1	11.4 μg
Dry weight Z-V	210.0 μg
Dry weight megalopa	475.0 μg
Specific growth rate	0.23 d^{-1}

Table 6

Early life history of the Asian shore crab *Hemigrapsus sanguineus*. Parameters of juvenile growth under laboratory conditions (25 °C, 30‰). Mean day of molt was calculated from time of metamorphosis. C-1 is crab stage 1, etc. Growth in carapace width was linear at 0.06 mm d⁻¹. Growth in dry weight was exponential. Specific growth rate was 0.08 d⁻¹. Modified from Epifanio et al. (1998).

Molt Stage	Mean day molt	Mean carapace width (mm)	Mean dry weight (μg)
C-1	5.1	1.6	700
C-2	11.0	1.9	1300
C-3	18.1	2.3	2900
C-4	29.4	2.7	4600
C-5		3.2	8100

8. Ecological impacts

8.1. Competition with native crab species

Invasions of alien habitat by the Asian shore crab have been characterized by rapid geographical expansion and widespread displacement of competing crab species (see Sections 3.2 and 3.3 above). These features imply extensive interaction between invasive *H. sanguineus* and co-occurring native crabs. One aspect of this interaction is the possibility of direct predation. Lohrer and Whitlatch (2002a) conducted a suite of experiments to investigate predator/prey relationships between invasive *H. sanguineus* and the resident green crab *C. maenas* in Long Island Sound along the east coast of the USA. The study included a four-year survey that showed a precipitous decline in green crab abundance coincident with a sharp rise in numbers of Asian shore crabs. Results indicated that yearling *H. sanguineus* consume newly settled green crabs and likely reduce recruitment of *C. maenas* in areas where both species occur. In contrast, the presence of juvenile green crabs does not affect survival of small *H. sanguineus* and apparently does not mediate recruitment—at least in terms of predator/prey relationships.

Jensen et al. (2002) investigated competition more directly and implemented a pair of studies to explore interaction between native and invasive crab species on both the east and west coasts of the USA. Each investigation included *C. maenas*, which was considered a native crab on the east coast³ and an invasive species on the west (Carlton and Cohen, 2003). Competing taxa were *H. sanguineus* in the Atlantic and *Hemigrapsus oregonensis* on the Pacific coast. Results of field observations suggested strong dominance of the respective *Hemigrapsus* species in competition with *C. maenas* for rock shelter. Occupancy of shelter by juvenile green crabs was 100% in natural areas devoid of *Hemigrapsus*, but never exceeded 25% in habitat where either species of *Hemigrapsus* occurred. Likewise, *H. oregonensis* and *H. sanguineus* respectively dominated *C. maenas* juveniles in laboratory experiments that allowed one-on-one competition for shelter. However, interaction concerning food showed mixed results with *H. sanguineus* displaying clear supremacy on the east coast, and *C. maenas* dominating *H. oregonensis* on the west coast.

MacDonald et al. (2007) conducted a similar set of experiments to study competition for food among three co-occurring crabs on the Atlantic coast. Results showed that *C. maenas* juveniles respectively dominated adult *H. sanguineus* and juvenile blue crabs (*Callinectes sapidus*) in direct competition for food, while that the latter two species showed equal success when pitted against each other. Moreover, *C. maenas* and *H. sanguineus* each demonstrated high levels of success in agonistic interactions with blue crabs of similar size. But any competitive advantage attendant to *C. maenas* or *H. sanguineus* is restricted to the corresponding juvenile stages because of the much larger size of adult *C. sapidus*. In fact, there is some indication that adult

blue crabs prey on *C. maenas* in areas where the two species overlap (deRivera et al., 2005).

Despite its success on the Atlantic seaboard, *H. sanguineus* is absent from the Pacific coast of North America, which in several ways seems a more probable invasion site. For example, there is extensive rocky habitat over a wide latitudinal range on the west coast, and there is more shipping contact with Asian ports, which provides more ballast-water discharge. However, there are two native species of *Hemigrapsus* on the west coast, which presupposes competition with invading *H. sanguineus*. Steinberg and Epifanio (2011) addressed this issue through a series of video-based experiments concerning the resident species (*H. nudus* and *H. oregonensis*) and the putative invader *H. sanguineus*. As in previous work, *H. sanguineus* exhibited a strong preference for shelter, and adults typically dominated the other two species in direct encounters. However, *H. sanguineus* was out-competed by *H. oregonensis* and *H. nudus* at the juvenile stage, which may explain the absence of Asian shore crabs in areas already occupied by the other two species of *Hemigrapsus*.

8.2. Predation on native species

The Asian shore crab was not considered an important predator in the immediate years following its introduction in the western Atlantic (Lafferty and Kuris, 1996). The species occurs in the upper half of the intertidal in some native Asian habitats (Fukui and Wada, 1983; Takada and Kkuchi, 1991), and initial studies reported a similar distribution on the east coast of North America (McDermott, 1992, 1998b). Furthermore, the available literature indicated an herbivorous diet for grapsoid crabs that occur in the upper intertidal (Hiatt, 1948; Kennish, 1996), and preliminary analysis of fecal pellets supported this view for alien populations of *H. sanguineus* (McDermott, 1992). Thus, predation on other crabs and bivalve mollusks was expected to be minimal.

However, subsequent work showed a broader intertidal distribution in both Asian and American populations of *H. sanguineus* (Ledesma and O'Connor, 2001; Lohrer and Whitlatch, 2002a; Saigusa and Kawagoye, 1997), often with maximum abundance in the lower intertidal and some extension into the subtidal (Gilman and Grace, 2009; McDermott, 1998b; Takahashi et al., 1985). With greater vertical range, the Asian shore crab interacts with a more extensive array of species and has potential for major effects as both predator and prey (Brousseau et al., 2000). For example, McDermott (1998b) listed 13 co-occurring seaweeds and 34 sympatric invertebrates in New Jersey habitats and saw common occurrence of mussel shell in stomach contents and feces. McDermott also conducted laboratory feeding trials and reported efficient predation on small blue mussels (*Mytilus edulis*), balanoid barnacles (*Semibalanus balanoides*), and hyalid amphipods (*Hyale plumulosa*). Likewise, Ledesma and O'Connor (2001) found high frequency of crustaceans in gut contents and concluded that *H. sanguineus* is an eclectic omnivore in southern New England habitats.

Brousseau et al. (2001) carried out more extensive laboratory experiments on prey selection by *H. sanguineus*. Results with three species of commercial bivalve showed that crabs generally preferred small prey (<10 mm shell length) and chose soft clams (*Mya arenaria*) over blue mussels (*M. edulis*) and oysters (*Crassostrea virginica*). These preferences corresponded to differences in shell morphology among the bivalves (Mascaró and Seed, 2000). In the Brousseau et al. study, total consumption of small mussels increased with crab size and reached nearly 13 individuals per day for large *H. sanguineus*. This value is twice the reported rate from earlier work with Asian shore crabs (Gerard et al., 1999) and similar to findings for the co-occurring mud crab *Panopeus herbstii* when feeding on ribbed mussels *Geukensia demissa* (Seed, 1980).

Tyrrell and Harris (2001) conducted analogous work in northern New England and found extensive overlap in diet and food preferences of *H. sanguineus* and juvenile green crabs *C. maenas*. DeGraaf

³ *C. maenas* was introduced to the east coast of the USA from Europe in the 19th Century. The authors considered *C. maenas* to be “native” in the context of their study because of the long history of the species in the western Atlantic.

and Tyrrell (2004) continued this line of inquiry and reported high consumption of small mussels (<5 mm shell length) by both crab species, but more efficient predation by *H. sanguineus* on larger sizes. In yet another laboratory study, Brousseau and Baglivo (2005) compared herbivorous versus carnivorous behavior in *H. sanguineus*. Results showed strong preference for blue mussels or barnacles compared to macroalgae, regardless of gender or life stage of the crabs.

When taken as a whole, the results of laboratory experiments have shown that Asian shore crabs are competent predators of mussels and barnacles, and researchers have predicted substantial impact on recruitment of these taxa throughout the American range of the crab. However, laboratory studies often minimize foraging time and may overestimate actual ingestion under natural conditions where the availability of prey is limited.

Alternative field approaches provide additional perspective on parameters like ingestion or inter-species competition for prey. One example is the work of Lohrer and Whitlatch (2002b), who conducted caging experiments in Long Island Sound. The study compared predatory effects of *H. sanguineus* and *C. maenas* on an intertidal mussel population. Results showed higher consumption by green crabs, although both species ate large numbers of mussels. But the authors calculated a greater population-level effect of *H. sanguineus* predation because of the higher abundance of Asian shore crabs at the study site. In additional field work in Long Island Sound, Brousseau and Goldberg (2007) carried out a number of caging experiments to determine effects of predation on the sympatric barnacle *Semibalanus balanoides*. The 3-year investigation included an array of enclosure cages, exclosure cages, and open areas.⁴ Results showed that *H. sanguineus* readily consumed settling larvae and juvenile barnacles. However, additional settlement compensated for predation during the reproductive period of the barnacles, and there was no net effect on abundance. In contrast, there was a significant impact of crab predation during the post-reproductive period, but differences among treatments were short-lived because of barnacle mortality from other sources. The authors concluded that invasive populations of *H. sanguineus* consume large numbers of juvenile *S. balanoides* in Long Island Sound, but do not have an effect on annual recruitment in native barnacle populations.

Tyrrell et al. (2006) conducted similar work in northern New England and examined predation by *H. sanguineus* and *C. maenas* in field-deployed mesocosms. The crabs exhibited comparable patterns of consumption that caused declines in barnacles, mussels, polychaetes, and macroalgae; and the authors expected measurable impact in natural habitat as Asian shore crabs become more common in the Gulf of Maine.

8.3. Predation by native species

In addition to their role as predators, invasive crab species may serve as prey for native taxa, and this can mitigate the impact on alien environments (Carlsson et al., 2009). However, predation on *H. sanguineus* in North American waters has received little attention, and there is no information whatsoever for European locations. American studies include the laboratory work of Rasch and O'Connor (2012), who investigated megalopal response to odors from fish predators in southern New England. Results showed avoidance of native species that had close Asian relatives, but no response to American fish that lacked Asian analogues. The authors concluded that innate avoidance of certain predators may augment invasive success in alien habitat.

In a different laboratory approach, Heinonen and Auster (2012) compared fish predation on *H. sanguineus* and two resident crab

species in Long Island Sound. Results showed greater predation on Asian shore crabs compared to native crabs of similar size. Reasons for the disparate predation were unclear, but the authors concluded that fish predators may provide an important control on invasive populations of *H. sanguineus* in southern New England.

In yet another tactic, Kim and O'Connor (2007) conducted both laboratory and field investigations to determine consumption of megalopae and juvenile crabs by striped killifish (*Fundulus majalis*). Results showed high levels of predation on megalopae, regardless of fish size or bottom texture. Likewise, there was extensive ingestion of very small juveniles in tanks with smooth bottom. But predation declined when small crabs were provided structured bottom, and there was little consumption of larger juveniles (>3 mm carapace width) under any conditions. While laboratory data showed potential for high levels of fish predation, the field study found no Asian shore crabs in the stomachs of striped killifish collected from natural habitat.

However, additional studies with co-occurring fish have provided contrasting results. For example, Clark et al. (2006) reported Asian shore crabs in guts of juvenile tautog (*Tautoga onitis*) from Long Island Sound, and Brousseau et al. (2008) found small *H. sanguineus* in the stomachs of two species of killifish, *F. majalis* and *F. heteroclitus*. But frequency of occurrence varied greatly among sites and years, and the investigators concluded that fish predation on juvenile Asian shore crabs was low overall, at least for killifish at their study sites. In contrast to the studies above, Brousseau et al. proposed that success of *H. sanguineus* in the western Atlantic is partially explained by low fish predation compared to native Asian habitat (Keane and Crawley, 2002; Pushchina and Panchenko, 2002).

8.4. Parasitism

The role of alien species in transporting parasites has received scant attention in the marine literature (McDermott, 2011; Torchin et al., 2002). But available data indicate that invasive species are often free of native parasites soon after introduction because many parasites have complex life cycles that are closely tuned to their indigenous environments (e.g., Torchin et al., 2001, 2003). *H. sanguineus* harbors a number of parasites in natural Asian habitats including microsporidian protozoans, trematode flatworms, and rhizocephalan barnacles (Table 7). Rhizocephalans have pathogenic effects on *H. sanguineus* (including feminization of males and ovarian castration of females) and may play a role in the dynamics of Asian populations of the crab (McDermott, 2011; Takahashi et al., 1997). However, *H. sanguineus* is currently devoid of parasites in both North America and Europe (McDermott, 2011), and this may have contributed to rapid growth in alien populations on both sides of the Atlantic (Torchin et al., 2001). But the hypothesis remains untested, and the role of parasites in the invasive success of the Asian shore crab is mostly unknown.

Table 7

Parasites of *Hemigrapsus sanguineus* in native Asian habitat. Invasive populations of *H. sanguineus* in the USA and Europe are devoid of these parasites. X indicates that pathogenicity has been determined or is probable. Dash signifies that pathogenicity is minimal or has not been determined. Modified from McDermott (2011).

Taxon	Species	Pathogenicity
Microsporidia	Unidentified	—
	<i>Maritrema jebuensis</i>	—
Trematode flatworm	<i>Probolocoryphe asadai</i>	—
	<i>Spelotrema capellae</i>	—
Rhizocephalan barnacle	<i>Polyascus polygenea</i>	X
	<i>Sacculina nigra</i>	X
	<i>Sacculina senta</i>	X

⁴ Enclosure cage = crabs and barnacles within cage on natural bottom. Exclosure cage = only barnacles within cage on natural bottom. Open area = natural bottom with no cage.

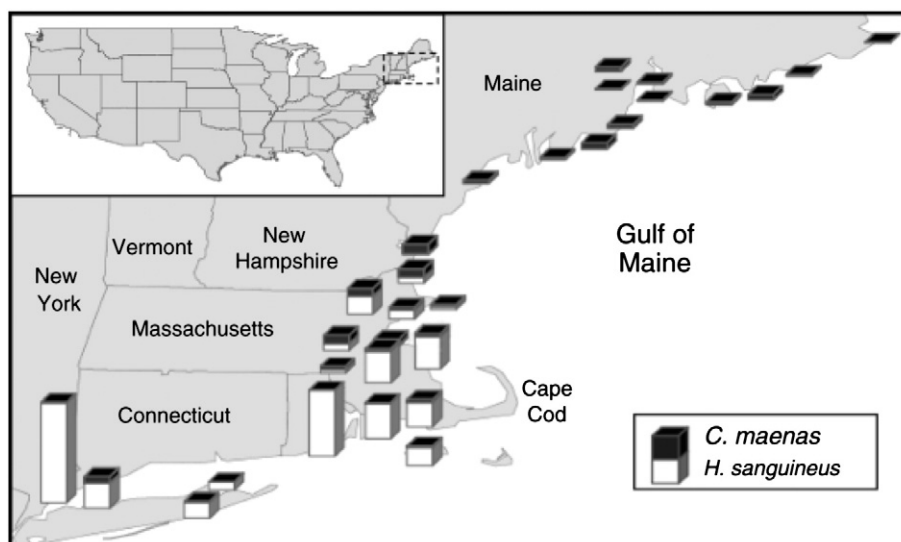


Fig. 3. Relative abundance of *Carcinus maenas* (shaded bars) and *Hemigrapsus sanguineus* (white bars) at several rocky intertidal sites in New England in the summer of 2006. From Griffen (2011).

8.5. Population and community ecology

Interactions at the population and community level occur in the context of the ambient physical environment. In rocky intertidal habitat, this environment includes a number of discrete zones that are located at different heights above sea level and are characterized by particular assemblages of species (e.g., Connell, 1972; Stephenson and Stephenson, 1961; Underwood and Denley, 1984). However, the vertical distribution of *H. sanguineus* within the intertidal has been a matter of controversy for both native and invasive populations (see Section 8.2 above), and this may have important implications concerning competition with other crab species and access to food resources. Lohrer et al. (2000a) addressed this problem in a field experiment that manipulated bottom texture at an intertidal site in Tanabe Bay, Japan. Results showed an increase in abundance of Asian shore crabs consistent with available shelter, regardless of vertical zonation. The authors concluded that structural complexity is more important than zonation in controlling vertical distribution of *H. sanguineus* and that discrepancy in the literature may be explained by differences in available shelter.

In a related study, Lohrer et al. (2000b) included the spatial distribution of *H. sanguineus* in a comparison of ecological niche in Tanabe Bay and in Long Island Sound (USA). Results showed wide vertical range for *H. sanguineus* at all study sites, which the authors again attributed to variation in available shelter and to seasonal changes in ambient physical conditions. Likewise the diets of *H. sanguineus* were broadly similar at all locations and included both plant and animal components. However, the crab assemblages in Tanabe Bay and Long Island Sound were very different. Rocky intertidal areas in Tanabe Bay showed high species richness with 11 co-occurring crab species, including several that were closely related to *H. sanguineus*. In contrast only two crab species were commonly sympatric with Asian shore crabs in Long Island Sound, and these diverged taxonomically at the level of superfamily. Nevertheless, a formal analysis of resource utilization (Hines, 1982) showed similar niche dimensions for native and invasive populations and low to moderate niche overlap among co-habiting crabs. Lohrer et al. concluded that *H. sanguineus* uses space and food resources in much the same way in Asian and American habitats and may in a sense have been pre-adapted for success in the western Atlantic, particularly in areas like Long Island

Sound where competitive interference from native crabs seemed low.⁵

Nevertheless, the spread of Asian shore crabs in alien habitat has invariably caused displacement of resident crab species—and this implies greater niche overlap with native crabs than estimated in the study described above. Griffen (2011) addressed this issue in a summary paper and discussed a number of factors that have contributed to dislocation of green crabs (*C. maenas*) from intertidal habitat in New England (Fig. 3). Previous work by Lohrer and Whitlatch (2002a) had emphasized predation by Asian shore crabs as a major influence in the decline of *C. maenas* (see Section 8.2 above). However, Griffen pointed to high levels of density-dependent cannibalism among juvenile *C. maenas* (Moksnes, 2004; Moksnes et al., 1998) and proposed that additional predation by Asian shore crabs would actually decrease the level of cannibalism by reducing the density of juvenile green crabs. In other words, predation by *H. sanguineus* would represent another source of compensatory mortality within the population of *C. maenas*, and overall mortality of juveniles would remain constant. However, competition with *H. sanguineus* has other effects on *C. maenas* including reduced use of shelter by juveniles (Jensen et al., 2002) and shifts in diet from high-protein animal tissue to low-protein macroalgae (Griffen et al., 2008, 2011). Each of these factors can impact the success of *C. maenas* populations, and it seems that no single factor is sufficient to explain the displacement of *C. maenas* from areas of previous abundance.

Community impacts of Asian shore crabs in areas previously dominated by *C. maenas* have been intensively studied along the coast of New Hampshire in northern New England. For example, Griffen and Byers (2006) found that competitive interference between *H. sanguineus* and *C. maenas* reduced the risk of predation on gammarid amphipods when both crab species were present. However, predatory effects were larger when the crab species were segregated and maintained at equal abundance. In a subsequent investigation, Griffen et al. (2008) reported that green crabs consume fewer mussels in the presence of *H. sanguineus* with consequent reduction in growth rate. And in related work, Griffen and Delaney (2007) argued that

⁵ The term *competitive interference* concerns direct competition for resources where individuals of one species interfere with essential activities of another species. In this case predatory behavior of one species would diminish predatory success of another.

displacement of *C. maenas* by Asian shore crabs has shifted predation from a species with strong predator dependence to one with weak predator dependence.⁶ The outcome of this shift would be higher abundance of *H. sanguineus* compared to previous populations of the displaced green crab and proportionally greater impact on prey populations.

In subsequent work Griffen and Byers (2009) investigated long-term effects of *H. sanguineus* and *C. maenas* on the ambient prey community. In contrast to previous studies (Griffen et al., 2008), competitive interference between the two species had only weak effects on prey abundance. Likewise, the influence of crab density on efficiency of predation was less than reported in earlier investigations (Griffen and Delaney, 2007). The authors attributed these discrepancies to annual variation in recruitment of prey species, which caused large differences in the availability of ambient prey organisms. The study also uncovered a number of indirect effects of the two crab species including reduced predation on barnacles by the snail *Nucella lapillus* and diminished settlement sites for mussels and macroalgae. These impacts were ascribed to predation by the crabs on snails and barnacles. Other indirect effects have been reported in earlier studies where mussels and snails responded to odors from *H. sanguineus* or *C. maenas* by developing thicker shells (Freeman and Byers, 2006; Trussell, 1996; Trussell and Smith, 2000).

Altieri et al. (2010) also investigated indirect community effects, this time in mixed habitat in Narragansett Bay on the southern coast of New England. Results of that study showed higher abundance of *H. sanguineus* in small patches of cordgrass (*Spartina alterniflora*) compared to adjacent cobble beach. The investigators attributed this difference to the influence of key species that provide shade and bottom stability in the grass patches. According to the authors, these direct positive effects were transferred to other members of the cordgrass community in a “facilitation cascade” that led to high densities of *H. sanguineus* along with high diversity of native species. In other words, *H. sanguineus* was in this case the beneficiary, rather than the initiator, of indirect community effects.

The overall body of research on community impacts has been largely couched in the competitive relationship between Asian shore crabs and green crabs in North American habitat. Details of that relationship have been described in this section, often with conflicting results. A more general discussion of community issues appears in the summary below.

9. Summary and conclusions

This paper provides a review of the scientific literature concerning invasive populations of the Asian shore crab *H. sanguineus*. The genus *Hemigrapsus* includes 15 species that are assigned to the family Varunidae and occupy coastal and estuarine environments, mostly in the Pacific basin. *H. sanguineus* is native to rocky intertidal habitat along much of the east coast of Asia (Takahashi et al., 1985).

A small population of Asian shore crabs was discovered in New Jersey in 1988, and this provided unique opportunity to study a marine invasion from its very inception. The species spread rapidly along the east coast of the USA and now extends from Cape Hatteras northward to the Schoodic Peninsula in Maine (Griffen, 2011). Ballast water is the most likely vector for the initial introduction, and it is not known if subsequent infestations augmented dispersal of the species. There are no published data concerning genetic relationships or geographic origins of invasive *H. sanguineus* in North America. Alien populations of the Asian shore crab also occur on the Atlantic coast of Europe, along with an invasive congener *Hemigrapsus takanoi*. Both crabs were introduced along the Dutch and Belgium coasts of

the North Sea in the mid 1990's (probably via ballast water) and then spread northward into Germany and westward along the English Channel (Dauvin et al., 2009). Breeding assemblages of both species now extend from Lower Saxony in Germany to the Cotentin Peninsula in France (Dauvin et al., 2009).

Much of the research on *H. sanguineus* has focused on invasive North American populations (Table 8). Results of these studies have ascribed success of the Asian shore crab to factors such as high fecundity, superior competition for shelter, release from parasitism, and direct predation on co-occurring crab species. For example, the reproductive season of *H. sanguineus* extends for 5 months along parts of the east coast of the USA compared to 2–3 months for competing native species (McDermott, 1998a). This long reproductive period provides high annual fecundity and also assures that at least one cohort of juvenile *H. sanguineus* is already in place when rival crab species begin to recruit to common habitat. Likewise, the unusual mating behavior of Asian shore crabs provides mobility and defensive prowess to copulating pairs, again conveying some advantage over native crabs (Anderson and Epifanio, 2010a).

Brooding in *H. sanguineus* follows the typical pattern for brachyuran crabs. Eggs are extruded within 24 h of copulation, and incubation time ranges from 16 to 22 days, depending on temperature (Anderson and Epifanio, 2010a; Epifanio et al., 1998). Hatching always occurs near the time of nocturnal high tide (Park et al., 2005), and there is no clear indication of lunar periodicity (Epifanio et al., 1998; Saigusa and Kawagoye, 1997). Fecundity is a function of size, and large females release around 50,000 larvae per spawning event (Fukui, 1988; McDermott, 1998a). Females reach sexual maturity in one year, reproduce for an additional two years, and release two or more broods each year.

Development of *H. sanguineus* includes five zoeal stages and a megalopal stage (Epifanio et al., 1998). Larval duration is dependent on salinity and temperature, and the interval from hatching to the megalopa stage is about 16 days under optimum conditions (Epifanio et al., 1998). The limited tolerance of megalopae to low salinity provides an explanation for the restricted distribution of Asian shore crabs in estuaries. However, laboratory data concerning larval intolerance of low temperature are contrary to the observed northward distribution of the species. Reasons for this discrepancy are not clear.

Zoea larvae of *H. sanguineus* show ontogenetic changes in swimming behavior in response to gravity and hydrostatic pressure (Park et al., 2004). These responses influence horizontal transport of larvae

Table 8

Selected parameters relevant to bioinvasive success. Comparison of three sympatric species in intertidal habitat along Atlantic coast of USA. *Hemigrapsus sanguineus* was introduced from Asia in the 1980's. *Carcinus maenas* was introduced from Europe in the 19th Century. *Panopeus herbstii* is native. X indicates that a parameter has been well studied. Dash indicates substantial gaps in knowledge.

Parameter	<i>H. sanguineus</i>	<i>C. maenas</i>	<i>P. herbstii</i>
Invasive history & vector	X	—	NA
Native range	X	X	X
Invasive range	X	X	NA
Molecular genetics	—	X	—
Systematics	X	X	X
Mating, brooding, fecundity	X	X	X
Larval behavior	—	X	X
Larval distribution & transport	—	X	X
Settlement & metamorphosis	X	—	X
Larval growth	X	—	X
Juvenile growth	X	X	—
Time to maturity	X	X	—
Environmental tolerance	X	X	X
Parasitism	X	X	—
Competitive interactions	X	X	—
Role as predator	X	X	X
Role as prey	—	—	—
Community impacts	—	X	—
Economic impacts	—	X	X

⁶ The term *predator dependence* concerns the dynamics of predation by a single species and refers to an inverse relationship between the abundance of that predator and efficiency of predation.

and suggest that early development occurs in the coastal ocean and that advanced stages are transported back to the estuary (Epifanio, 1988). Field studies generally support this idea, but also show the possibility of long-distance transport along the coast (Park, 2005). Larval settlement and metamorphosis are stimulated by cues associated with juvenile habitat, and this process has augmented the establishment of invasive populations (Anderson and Epifanio, 2009; Steinberg et al., 2008). Juveniles grow rapidly after undergoing metamorphosis, which may insulate young crabs from some forms of predation (Epifanio et al., 1998; Kim and O'Connor, 2007).

Invasions of alien habitat by Asian shore crabs have been characterized by rapid geographical expansion and widespread displacement of resident crab species. These features imply competitive interaction between invasive *H. sanguineus* and co-occurring native crabs. There has been extensive study of the competitive link between Asian shore crabs and the resident green crab *C. maenas*. One aspect of this interaction is direct predation by *H. sanguineus* on newly settled green crabs (Lohrer and Whitlatch, 2002a). In addition, Asian shore crabs are superior competitors for shelter and consistently dominate juvenile green crabs in laboratory and field experiments (Jensen et al., 2002). *H. sanguineus* has also displaced native mud crabs at the southern end of its American range, but there are no published studies of competitive encounters among these species. Despite its success on the east coast, *H. sanguineus* is absent from the Pacific coast of North America. This may be due to competition from two native species of *Hemigrapsus* (Steinberg and Epifanio, 2011).

Results of laboratory experiments show that Asian shore crabs are competent predators of juvenile mussels and barnacles, and researchers have predicted strong impact on recruitment of these taxa throughout the American range of the crab (DeGraaf and Tyrrell, 2004). Field experiments confirm the high level of predation, but (in contrast to predictions) have not demonstrated consistent effects on recruitment (Brousseau and Goldberg, 2007). In addition to their role as predators, alien crab species may serve as prey for native taxa, and this can mitigate the impact of the invading crab (Carlsson et al., 2009). However, predation on Asian shore crabs in North American waters has received little attention, and there is no information whatsoever for European environments. American studies show that a number of fish species prey on larval and juvenile *H. sanguineus* (Brousseau et al., 2008; Clark et al., 2006), but population-scale effects on the crab are unclear (Keane and Crawley, 2002).

H. sanguineus harbors a number of parasites in natural Asian habitats including microsporidian protozoans, trematode flatworms, and rhizocephalan barnacles, but none of these parasites have been identified in alien populations of the crab (McDermott, 2011). This release from parasitism may have contributed to rapid population growth in alien populations of *H. sanguineus* on both sides of the Atlantic (Torchin et al., 2001).

However, community-level impacts of invasive *H. sanguineus* remain unresolved. The obvious and indisputable effect is the displacement of resident crab species—and experimental work has yielded plausible explanation for this occurrence (Griffen, 2011). Additional studies have demonstrated a number of direct and indirect impacts of crab predation on mussels, barnacles, and other members of the ambient community. But these effects are similar for *H. sanguineus* and *C. maenas* (Griffen and Byers, 2009; Trussell and Smith, 2000). So it is possible that displacement of resident crabs is a simple replacement wherein *H. sanguineus* functions like the native crabs in most aspects of community ecology (Griffen, 2011). If this were the case, the only ecological losers would be the displaced crab species, and the rest of the community would function more or less as it had before the invasion. Alternatively, Asian shore crabs may bring new factors into play that will result in substantially different community effects. For example, *H. sanguineus* reaches much higher population densities than *C. maenas* through much of their sympatric range, and additional community-level impacts would seem likely (Griffen and Delaney, 2007). Of course a

final possibility is the resurgence of resident crab populations and establishment of a more stable dynamic between native species and invasive *H. sanguineus*. This scenario has played out a number of times in the past 60 years with invasive populations of the Chinese mitten crab in Europe and North America (Dittel and Epifanio, 2009).

Direct economic impacts of invasive *H. sanguineus* are also difficult to quantify, and there have been no published studies in American or European habitats. Experimental work has shown high predation by Asian shore crabs on juvenile blue mussels in the intertidal, but economic impact on the subtidal dredge fishery or on aquacultural production of mussels has not been established. This is in contrast to green crabs and mud crabs, which are widely regarded as pests in bivalve mariculture and fisheries (Bisker and Castagna, 1987; Glude, 1955; McDermott, 1960). Thus, displacement of native crab species by *H. sanguineus* could in concept have positive effects on commercial production of bivalves. However, green crabs and mud crabs extend widely into the subtidal, and loss of intertidal habitat may have only minor influence on overall population size (Griffen, 2011). Recent years have also seen development of a bait fishery based on invasive Asian shore crabs, but the fishery is artisanal in scale, and there has been no attempt to quantify its positive economic value. Alternatively, the indirect community-level effects of *H. sanguineus* may have negative economic consequences, but analytical tools for determining these indirect impacts are not well developed.

The overall body of research on invasive populations of *H. sanguineus* is both substantial and comprehensive. Scientists recognized the opportunity to study a marine invasion from its inception and carefully mapped the spread of Asian shore crabs on both sides of the Atlantic over a period of more than two decades. Results of extensive laboratory and field experiments have provided plausible explanation for displacement of native crab species and have quantified the potential of *H. sanguineus* as a predator of sympatric taxa such as mussels and barnacles. Early life history of the species is well understood, and there is an extensive body of work concerning settlement and metamorphosis. However, larval transport itself has been only lightly studied, and there are gaps in our knowledge of larval behavior. Likewise, there has been little published work on the population genetics of *H. sanguineus*, and there is no information on the specific Asian origins of American or European populations. Perhaps the largest deficiency concerns the clear demonstration of community-level effects and subsequent translation of these effects into economic impacts.

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