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

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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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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, interspecies 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). Grapsoid 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