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Invasion biology of the Chinese mitten crab *Eriochier sinensis*: A brief review

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ABSTRACT

The Chinese mitten crab *Eriocheir sinensis* is a native of freshwater and estuarine habitats along the east coast of Asia. Invasive populations have existed in northern Europe since the early 20th century, and more recently a breeding population has become established in the San Francisco Bay system along the west coast of North America. Ballast water is the most probable vector for both invasions, although there is also potential for escape from ethnic markets and from the ornamental aquarium industry. Invasive populations of mitten crabs have caused millions of dollars in economic and ecological damage. Economic impacts center largely on the burrowing activity of the crabs, which damages stream banks and levees, and the annual spawning migration, which interferes with fishing activities and irrigation projects. Chinese mitten crabs have recently appeared in the Chesapeake and Delaware Bays on the east coast of the USA, and there are confirmed reports of breeding females in both estuaries. The potential for large populations of mitten crabs in these estuaries has not been determined. This paper presents a review of the biology and ecology of native and invasive populations of the species and provides recommendations for research relevant to the prediction of future mitten crab invasions.

Contents

1. Introduction

Many studies have documented the impact of invasive species in freshwater and marine ecosystems (see Carlton, 1996). Freshwater forms such as the zebra mussel, *Driessena polymorpha*, and the Asian clam, *Corbicula fluminea*, have had large effects in rivers and lakes in

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North America and Europe (Carlton, 1996; Johnson and Carlton, 1996). These effects include displacement of native species, disruption of power-plant cooling systems, and clogging of irrigation and drainage facilities. Economic cost from freshwater bioinvasions tallies in the hundreds of millions of dollars. Likewise, invasive marine species have caused substantial ecological and economic damage including the collapse of entire fisheries in areas such as the Black Sea (Vinogradov et al., 1989; Harbison and Volovik, 1994) and have facilitated ecological regime shifts in estuaries like San Francisco Bay (Carlton, 1996; Grosholz, 2002).

Moreover, the pace of introduction of aquatic species has increased in recent years (Carlton, 2003). Expansion of transoceanic shipping has resulted in larger and faster vessels which have augmented the number of introductions associated with release of ballast water (Carlton, 1996, 2003). Among the many species that are transported in ballast water are a number of brachyuran crabs including the Chinese mitten crab, *Eriocheir sinensis*. Because of its unique life history, *E. sinensis* is one of few invasive species that impact both freshwater and marine ecosystems.

E. sinensis is a native of eastern Asia and first appeared in Europe in the early 20th century. More recently, the species has become established on the west coast of North America (Rudnick et al., 2000, 2003, 2005a). Documented impacts include weakening of levees and stream banks due to the burrowing behavior of the crab (Panning, 1939; Ingle, 1986; Dutton and Conroy, 1998; Rudnick et al., 2005b). In addition, the feeding activities of the crab have caused declines in natural vegetation, and the crabs have hindered fishing activities by consuming bait and clogging fishing gear (Panning, 1939; Veldhuizen and Stanish, 1999). Economic damage in German waters alone totals approximately 80 million Euros since 1912 (Gollasch, 2006). Financial impacts from California populations of *E. sinensis* are on the order of millions of dollars per year (White et al., 2000).

E. sinensis has very recently appeared on the east coast of the USA (Ruiz et al., 2006). Available evidence is mostly anecdotal, but Chinese mitten crabs unquestionably occur in Chesapeake and Delaware Bays, and there are confirmed reports of brooding females in both estuaries (SERC, 2007). The potential for large populations of mitten crabs in these estuaries has not been determined. But two other invasive crabs (*Carcinus maenas*, *Hemigrapsus sanguineus*) are well established on the east coast, and each has had negative effects on populations of native crab species (Grosholz et al., 2000; Jensen et al., 2002; Lohrer and Whitlatch, 2002; MacDonald et al., 2007).

The successful invasion of west coast habitats by *E. sinensis* has led to extensive work on the distribution, growth, and reproduction of the species (Rudnick et al., 2000, 2003, 2005a). Most studies have focused on the juvenile and adult stages, and little is known about the early life history of the species. Duration of larval development has been examined under laboratory conditions, and dispersal scenarios have been proposed based on these results (Anger, 1991). However, there have been no direct studies of larval transport in the species, and there is no information on relevant larval behavior in the laboratory or field.

In the present review, we focus mainly on the Chinese mitten crab *E. sinensis,* the most commercially and ecologically important species of the genus *Eriocheir*. However, we also draw comparisons with its

Table 1
Selected information on the Chinese mitten crab (*Eriocheir sinensis*) from the non-refereed literature.

Source	Title	Website/publication information
Canadian Food Inspection Agency, 2006	Guide to Canadian regulatory requirements and examination procedures for imported fish	http://www.inspection.gc.ca/english/anima/fispoi/import/guidee.shtml
Center for Aquatic Resource Studies, Biological Resource Division, U.S. Geological Survey, 2005	*Eriocheir sinensis*. Chinese Mitten Crab. Specimen ID 4249	http://nas.er.usgs.gov/queries/specimenviewer.asp?SpecimenID=4249
CMCWG - Chinese Mitten Crab Working Group, 2003	National management plan for the genus *Eriocheir* (mitten crabs). Aquatic Nuisance Species Task Force	http://www.anstaskforce.gov/Species%20plans/national %20mgmt%20plan%20for%20mitten%20crab.pdf
Gollasch (2006)	Invasive Alien Species Fact Sheet – *Eriocheir sinensis*	Online Database of the North European and Baltic Network on Invasive Alien Species, NOBANIS http://www.nobanis.org/
Hanson, E., Sytsma, M., 2005	The potential for mitten crab colonization of estuaries on the west coast of North America	Prepared for the Pacific States Marine Fisheries Commission and Alaska Department of Fish and Game
MarLIN (Marine Life Information) Network for Britain and Ireland)	Chinese mitten crab-*Eriocheir sinensis*	http://www.marlin.ac.uk/marine_aliens/species.asp?SpID=19
National Biological Information Infrastructure (NBII)	Chinese Mitten Crab	http://nbii.gov/portal/server.pt?open=512&objID=798&&PageID=2259&mode=2&in_hi_userid=2&cached=true
Online Database 2005	ITIS (Integrated Taxonomic Information System), *Eriocheir sinensis*	http://www.cbif.gc.ca/pls/itisca/taxastep?king=every&p_action=containing&taxa=Eriocheir+sinensis&p_format=&p_ifx=plglt&p_lang=
Owen, J., 2003	Eat the Invading Alien Crabs, Urge U.K. Scientists National Geographic News	http://news.nationalgeographic.com/news/2003/11/1113_031113_mittencrabs.html
Pacific States Marine Fisheries Commission (PSMFC)	The aquatic species nuisance fact sheet: Chinese Mitten Crab	http://www.aquaticnuisance.org/chmitcrab.php
Prince William Sound Regional Citizens' Advisory Council Updated 2004	Non-Indigenous Aquatic Species of Concern for Alaska-Fact Sheet 2-Chinese Mitten Crab *Eriocheir sinensis*	http://www.pwsrcac.org/docs/d0015200.pdf
Rogers (2000)	The Feeding Ecology of the Invasive Chinese Mitten Crab, *Eriocheir sinensis*: Implications for California's Freshwater Communities	Senior Research Seminar, Environmental Science Group Major. University of California at Berkeley, Berkeley, CA.
Rudnick et al. (2000)	Distribution, ecology and potential impacts of the Chinese mitten crab (*Eriocheir sinensis*) in San Francisco Bay. University of California, Berkeley, Water Resources Center, Contribution 26. pp 74	http://www.waterresources.ucr.edu
SERC, 2006	Chinese Mitten Crab Caught in Chesapeake Waters. Marine Invasions Research Lab	http://www.serc.si.edu/labs/marine_invasions/news/mitten_crab.jsp
St Lawrence Centre, 2004	Presence of the Chinese Mitten Crab in the St. Lawrence River	http://www.qc.ec.gc.ca/csl/inf/inf003_007_e.html
Veilleux and Lafontaine, 2007	Biological Synopsis of the Chinese Mitten Crab (*Eriocheir Sinensis*)	Fisheries and Oceans Canada Science Branch, Pacific Region Pacific Biological Station Nanaimo, BC V9T 6N7 Canadian Manuscript Report of Fisheries and Aquatic Sciences 2812
White et al. (2000)	Evaluation of the mitten crab exclusion technology during 1999 at the Tracy Fish Collection Facility, California, Sacramento (CA)	Bureau of Reclamation, Tracy Fish Collection Facility Studies 14:43p

Sources are in the form of reports and newsletters, as well as miscellaneous publications available on the World Wide Web.

Table 2
Distribution of mitten crab species *Eriocheir sensu lato* in native and invasive ranges.

Species	Common name	Native range	Invasive range
Eriocheir sinensis H. Milne Edwards, 1835	Chinese mitten crab	eastern and northern China	Europe, North America, western Asia
Eriocheir japonica de Haan, 1835	Japanese mitten crab	East Coast of Korea and Japan, Taiwan	X
Eriocheir hepuensis Dai, 1991		Northern China and Korea	X
Eriocheir formosa Chan et al. (1995)		Taiwan	X
Neoeriocheir leptognathus Rathbun, 1913		Northern China	X

X indicates that a species is not found outside its native range. There are no English-language common names for *E. hepuensis*, *E. formosa*, or *N. leptognathus*.

close relative the Japanese mitten crab *Eriocheir japonica*, which has not become widely established outside its native range (Jensen and Armstrong, 2004). Considerable information about *E. japonica* has become available in the past 15 years (Kobayashi and Matsuura, 1991, 1995a,b, 1999; Kobayashi, 2003), and comparison with *E. sinensis* may help to answer questions as to why certain species are successful invaders, while others fail to establish non-indigenous populations.

The purpose of this paper is to update existing information about the ecology and biology of native and invasive populations of the Chinese mitten crab. An understanding of the requisite conditions for successful invasions will aid in assessing the potential threat that this species poses to newly invaded ecosystems such as the Chesapeake and Delaware bays. Much of the remainder of this paper is divided into seven sections that cover various aspects of the systematics, life history, physiology, and ecology of *E. sinensis*. These are followed by single sections that respectively address economic impacts and risk assessment and a final section that provides a summary and conclusions. Our review encompasses the traditional peer-reviewed literature, but also includes citations of recent information in the form of reports, newsletters, and miscellaneous publications available on the World Wide Web (Table 1).

2. Systematics and distribution

Brachyuran crabs in the genus *Eriocheir* are assigned to the Varunidae, which is one of six families in the superfamily Grapsoidea (Schubart et al., 2000; Martin and Davis, 2001; Kitaura et al., 2002). Grapsoid crabs are distributed worldwide and are adapted to a wide variety of semi-terrestrial, freshwater, and marine habitats. Until recently, the genus *Eriocheir* included four species: *E. japonica, E. sinensis*, *E. hepuensis*, and *E. leptognathus*. The latter species has now been assigned to the genus *Neoeriocheir* (Sakai, 1983), but there is still controversy about this revision and about the taxonomy of mitten crabs in general (Chan et al., 1995; Cohen and Carlton, 1997; Guo et al., 1997; Ng et al., 1999; Tang et al. 2003).

Eriocheir japonica is the most widely distributed species of *Eriocheir* in Asian habitats, with populations ranging from Japan to the southern coast of China, including Taiwan and Hong Kong (Chan et al., 1995). *Eriocheir japonica* is the dominant mitten crab in southern China. The Asian distribution of *E. sinensis* is more restricted and extends from the Yellow Sea of Korea throughout the northern and central coastal regions of China where it is the most common species of mitten crab (Panning, 1939; Sakai, 1976; Hymanson et al., 1999). While these two species have similar life-history characteristics, (Kobayashi and Matsuura, 1995a,b, 1999; Kobayashi, 2003), *E. japonica* has not invaded habitats outside Asia (Guo et al., 1997). In contrast, *E. sinensis* has been established in Europe for nearly a century and has recently invaded estuarine systems on the west coast of North America. The remaining species, *E. hepuensis* and *N. leptognathus*, have limited Asian ranges and do not occur outside

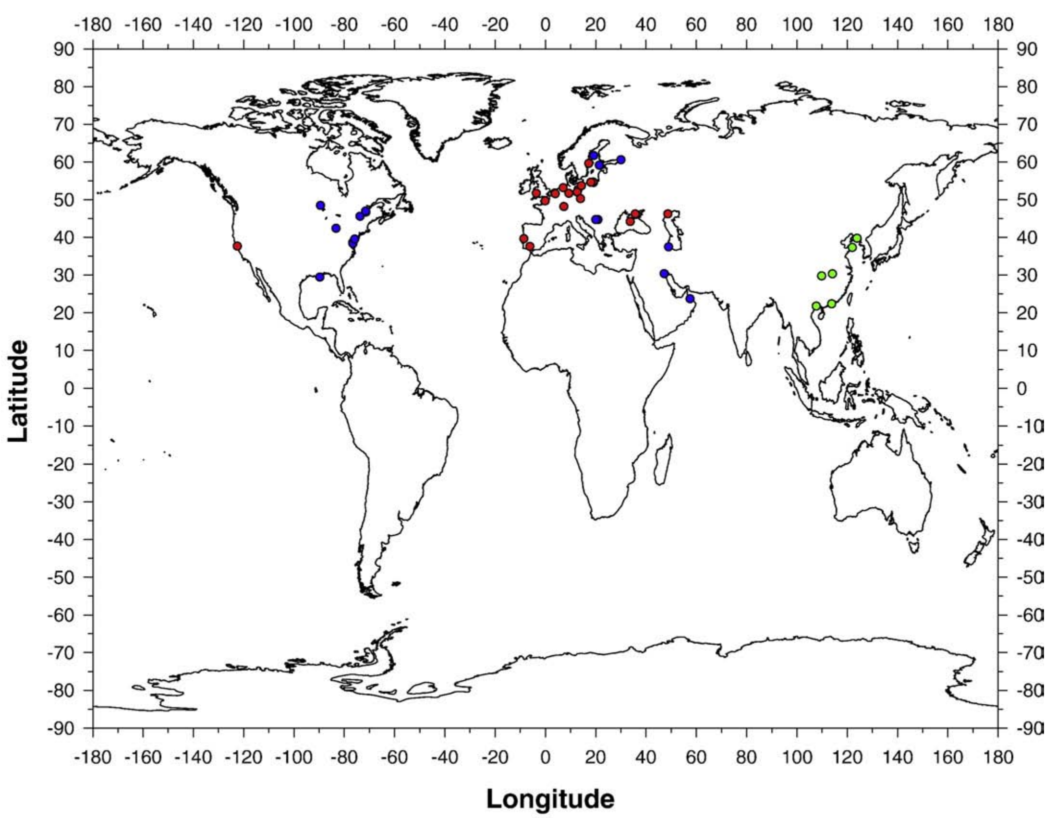

Fig. 1. General distribution of mitten crab *Eriocheir sinensis* populations in their native and invasive ranges. Circles correspond to established (●) and non established populations (●) in non-native range; (●) indicates distribution in the native range.

their respective native habitats (Sakai, 1939, 1976; Chu et al., 2003) (Table 2).

E. sinensis spends most of its adult phase in freshwater habitat with abundant submerged aquatic vegetation (Jin et al., 2001). Panning (1939) conducted early studies of *E. sinensis* populations in its native Asian range, as well as in invaded habitats in Western Europe. Panning reported that Chinese mitten crabs may migrate as much as 1400 km up large rivers such as the Yangtze, but generally prefer the low-lying regions near the coast. According to the author, mitten crabs in native Asian habitat are commonly found in coastal rice fields, but also occur in riverine habitats in inland areas.

However, studies have shown that wild populations of *E. sinensis* have declined considerably in Asia due to a combination of factors including fishing, water pollution, and dams and floodgates that prevent migration to breeding grounds (Hymanson et al., 1999). But at the same time, a large aquaculture initiative for *E. sinensis* has been developed in China, especially in the Yangtze Basin (Jin et al., 2001; Wang et al., 2006). According to recent reports, this industry supplies local and international markets with live crabs year-round and is valued at $1.25 billion per year (Hymanson et al., 1999; Herborg et al., 2005; Wang et al., 2006). In addition to their food value, mitten crabs also have been used as bait for eel fishing, to produce fish meal and cosmetic products, and as agricultural fertilizer (Herborg et al., 2005).

2.1. Invasive range

Mitten crabs were first introduced to Europe almost a century ago, most likely via the release of ballast water (Panning, 1939). The first invasion was documented in Germany in 1912, and the species spread rapidly throughout northern Europe. By the 1940s, the mitten crab had been reported in Denmark, Sweden, Finland, Poland, the Netherlands, Belgium, France and the UK (Panning, 1939; Herborg et al., 2003, 2005). Forty years later, the European range of Chinese mitten crabs stretched from the Bay of Biscay to the Baltic Sea (Christiansen, 1982). By the 1990s, the invasion had reached Spain and Portugal (Cabral and Costa, 1999; Cuesta et al., 2004) and Eastern Europe. Crabs were reported from the Volga River delta (Slynko et al., 2002), the Serbian part of the Danube River (Paunovic et al., 2004), and Lake Ladoga in Russia (Panov, 2006). Other recent reports include two different areas in western Asia—the River Tazeh Bekandeh in Northern Iran (Robbins et al., 2006) and the Shatt Al-Basrah Canal in Iraq (Clark et al., 2006) (Fig. 1).

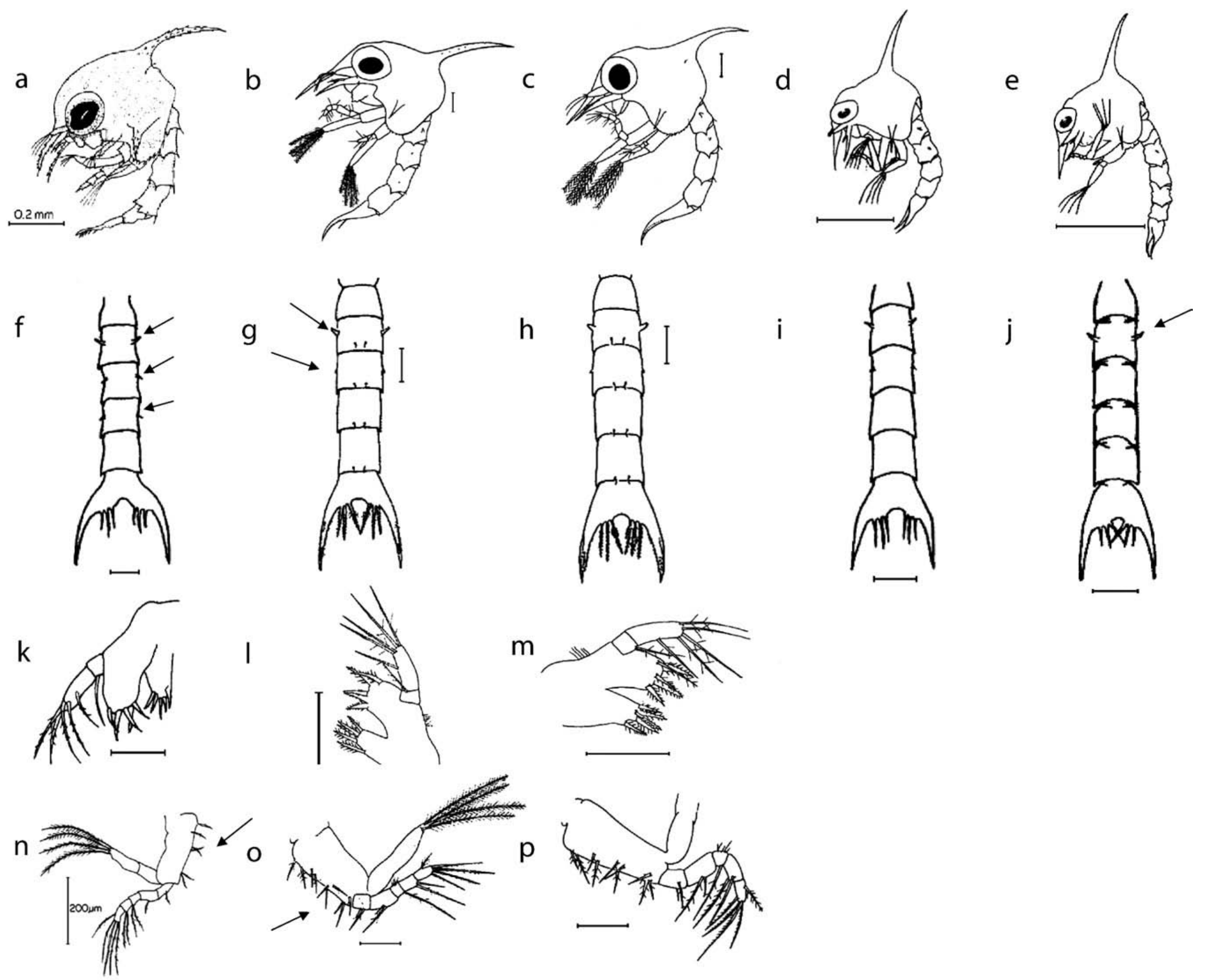

Fig. 2. Comparison of various distinguishing morphological features of first zoeal stage of two species of mitten crabs (*Eriocheir*) and three species of shore crabs (*Hemigrapsus*). a = lateral view of *E. sinensis*. b = lateral view of *E. japonica*. c = lateral view of *H. sanguineus*. d = lateral view of *H. nudus*. e = lateral view of *H oregonensis*. f = dorsal view of telson *E. sinensis*. g = dorsal view of telson *E. japonica*. h = dorsal view of telson *H. sanguineus*. i = dorsal view of telson *H. nudus*. j = dorsal view of telson *H oregonensis*. k = maxillule *E. sinensis*. l = maxillule *E. japonica*. m = maxillule *H. sanguineus*. n = 1st maxilliped *E. sinensis*. o = 1st maxilliped *E. japonica*. p = 1st maxilliped *H. sanguineus* Scale bars for *E. japonica* and *H sanguineus* = 0.1 mm.; Scale bars for d and e = 40 µm; f, i, j = 10 µm; k = 100 µm (Taken from Kim and Hwang, 1990; Hwang et al., 1993; Montu et al., 1996; Rice and Tsukimura 2007).

The Chinese mitten crab was first observed in North America in 1965 near Ontario, Canada, and a few specimens were collected from Lake Superior and Lake Erie between 1973 and 1994 (Nepszy and Leach, 1973). More recently, a female was reported from the St. Lawrence River, near Lévis, Quebec (de Lafontaine, 2005). A single adult crab also has been reported from the Mississippi River (Cohen and Carlton, 1995). However, no breeding populations exist in these locations due to lack of access to higher salinity waters required for spawning (Rudnick et al., 2000). These isolated occurrences are probably the result of escape from ethnic markets or from the aquarium pet trade.

On the west coast of North America, mitten crabs have spread rapidly since they were first reported in the San Francisco Bay drainage in 1992. Currently, a breeding population is well established throughout the bay system, including the Sacramento–San Joaquin delta and the main stems of the tributaries that flow into the estuary (Rudnick et al., 2000, 2003). Ecological and economic impacts of this invasion are well documented (Rudnick et al., 2003).

Very recently, Chinese mitten crabs have been collected from several locations in both Chesapeake and Delaware Bays (Ruiz et al., 2006). Because of the profound economic and ecological effects of the invasive populations in Europe and in the San Francisco Bay area, there is much concern about the potential impacts of this species along the east coast of the USA.

3. Morphological characteristics

3.1. Larval forms

Early work in the 1930s provided incomplete descriptions of the larval development of *E. sinensis* (Panning, 1939), but the individual larval stages were not examined in greater detail until much more recently. Kim and Hwang (1995) and Montu et al. (1996) produced a detailed description of all larval stages of *E. sinensis*. In addition, recent work has provided keys to the identification of brachyuran zoeae of the San Francisco Bay Estuary (Rice and Tsukimura, 2007) and the Sea of Japan (Kornienko and Korn, 2009). Normal development consists of five zoeal stages and a megalopal stage. Differences in several morphological characters allow discrimination of *E. sinensis* zoeae from the other two species of *Eriocheir* (Shy and Yu, 1992; Kim and Hwang, 1995; Montu et al., 1996) and the respective megalopal stages can be distinguished based on differences in maxillipeds and antennae (Ng et al., 1998). Kim and Hwang (1995) have developed a taxonomic key to the first zoeal stage of several species in the family Varunidae, including the Asian shore crab *Hemigrapsus sanguineus*, which has recently established invasive populations along the east coast of the USA (Epifanio et al., 1998; McDermott, 1998). The ability to distinguish the larval stages of *E. sinensis* from those of *H. sanguineus* may be

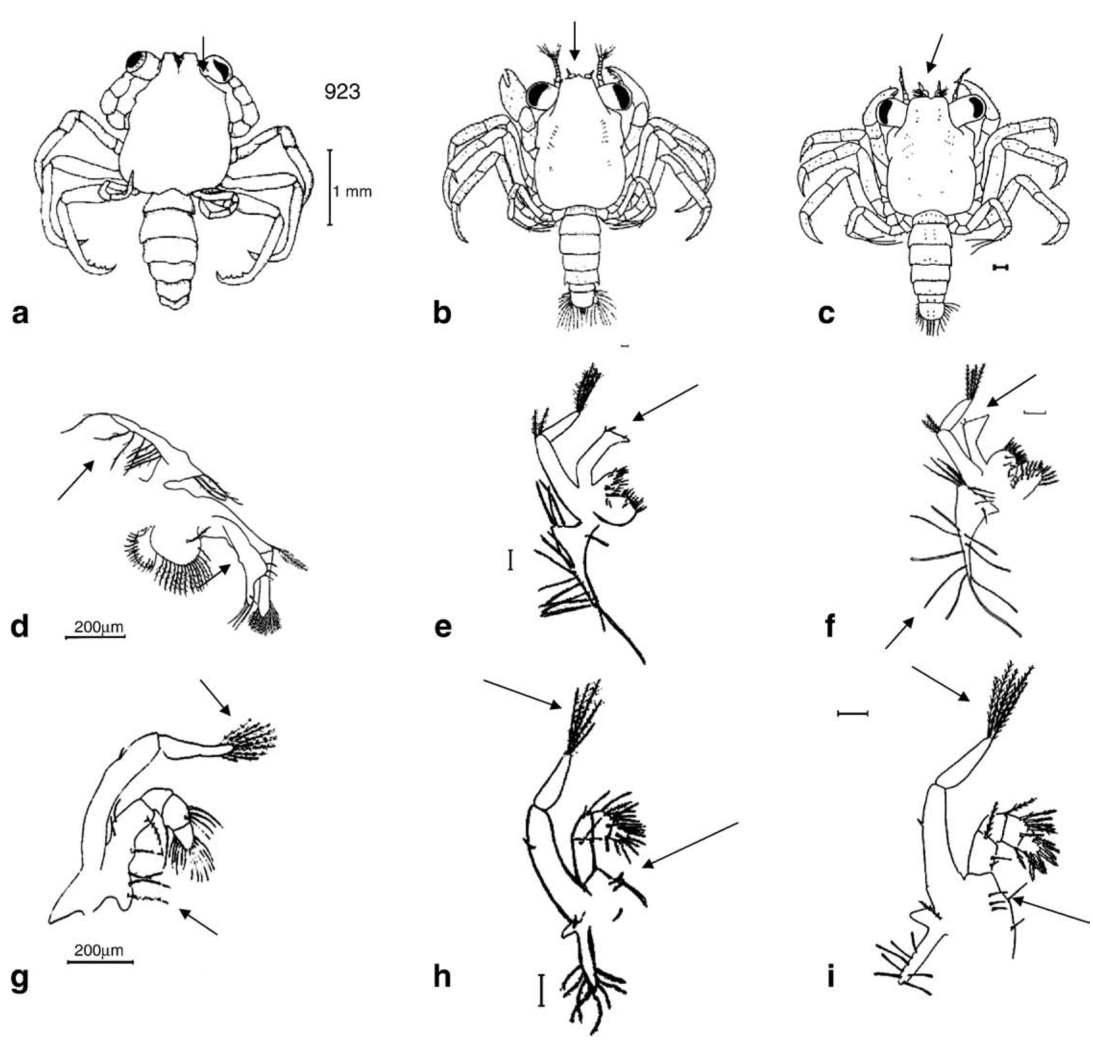

Fig. 3. Comparison of distinguishing morphological features in the megalopa stage of two species of mitten crabs (*Eriocheir sinensis and E. japonica*) and the Asian shore crab *Hemigrapsus sanguineus*. a = dorsal view of *E. sinensis*. b = dorsal view of *E. japonica*. c = dorsal view of *H sanguineus*. d = 1st maxilliped of *E. sinensis*. e = 1st maxilliped of *E. japonica*. f = 1st maxilliped of *H sanguineus*. g = 2nd maxilliped of *E. sinensis*. h = 2nd maxilliped of *E. japonica*. i = 2nd maxilliped of *H. sanguineus*. Scale bars for *E. japonica* and *H sanguineus* = 0.1 mm. Arrows indicate examples of differences in shape of rostrum and setation patterns on maxillipeds. (Taken from Kim and Hwang 1990; Hwang et al., 1993; Montu et al., 1996).

Table 3a
Distinguishing morphological features in the first zoeal stage of two species of mitten crabs (*Eriocheir*) and three species of shore crabs (*Hemigrapsus*).

	Eriocheir sinensis	*Eriocheir japonicus*	*Hemigrapsus sanguineus*	*Hemigrapsus nudus*	*Hemigrapsus oregonensis*
Carapace	Lateral spines spinulous Dorsal and rostral spines covered with small spines;dorsal spine longer than rostral and lateral spine; posterolateral region with 6–9 spines on each side; lacking setae	Lateral spines naked; posterolateral region lacking spines; 10–13 setae	Dorsal and rostral spines smooth and naked; posteroventral region with 8 teeth and smaller ones on each side		
Abdomen	Pleomeres II,III,IV with small lateral spines. Pleomere V with posterior lateral extensions overlapping telson		Somites 2-3 with distinct lateral knobs	Pleomere II and III with lateral spines; smaller on III	Pleomere II with lateral spines
Carapace spines	Ratio of rostral carapace spine/second antenna <1.25	Ratio of rostral carapace spine/second antenna >1.30			
	Total length from tip of rostral spine to tip of dorsal spine = 1.25–1.27 mm		Total length from tip of rostral spine to tip of dorsal spine = 0.93 mm	Total length from tip of rostral spine to tip of dorsal spine = 1.2 mm	Total length from tip of rostral spine to tip of dorsal spine = 1.1 mm
Maxillule	Basal and coxal endite each with 5 setose spines; 1,5 spines on endopod	1,4 spines on endopod		Basal and coxal endite with 6 and 5 setose spines, respectively	
Maxilla	Basal endite bilobed with 8 spines; scaphognathite with 3 plumose, 2 smooth setae plus 1 plumose projection; coxal endite bilobed with 2, 3 spines	Basal endite bilobed with 9 spines; coxal endite bilobed with 2, 4 spines	Basal endite bilobed with 9 setae; scaphognathite with 4 plumose setae and terminal process with dense microtrichia; coxal endite bilobed with 2, 4 setae	Basal endite bilobed with 7 setae; scaphognathite with 4 plumose setae	
Maxilliped I	Basis with 6 ventral setae; endopod 5-segmented with 1, 1, 2, 2, 5 setae.	Basis with 10 setae; endopod 5-segmented with 2,2,1,2,5 setae	Basis with 10 setae; endopod 5-segmented with 2,2,1,2,5 setae.		
Maxilliped II	Basis with 3 sparsely plumose setae; exopod with 4 natatory setae; endopod with 0, 1, 5 sparsely plumose setae	Basis with 4 plumose setae ; endopod with 0, 1, 6 setae	Basis with 4 plumose setae; exopod with 4 plumose natatory setae; endopod with 0, 1, 6 setae		

Eriocheir sinensis co-occurs with *H. sanguineus* in its native Asian range and along the east coast of North America. *Eriocheir sinensis* co-occurs with *H. nudus* and *H. oregonensis* along the west coast of North America. *Eriocheir japonica* co-occurs with *H. sanguineus* in Asia. Sources: Kim and Hwang, 1990; Hwang et al., 1993; Montu et al., 1996;Rice and Tsukimura, 2007.

valuable for ecological studies in areas of the east coast of the USA where invasive populations of these two species might co-occur in the future. On the west coast there is already potential for co-occurrence of *E. sinensis* larvae and the larvae of two native species of *Hemigrapsus* (*H. nudus* and *H. oregonensis*). Morphological characteristics commonly used in distinguishing zoeal stages include setation on antennules, maxillas and maxillipeds, among others (Figs. 2 and 3). Various distinct morphological features in two species of *Eriocheir* and 3 species of *Hemigrapsus* are found on Tables 3a and 3b.

3.2. Juveniles and adults

Adults and juveniles in the genus *Eriocheir* are characterized by the presence of patches of brown setae on the inner and outer surface of their white-tipped chelae (Veldhuizen, 2001). Males have a denser mat of setae, but there is no gender-based dimorphism in claw size. Sakai (1976) described *E. sinensis* as having a markedly convex and very uneven carapace, with four sharply edged epigastric lobes. The anterior surface is characterized by four acuminate teeth that are deeply separated; the fourth anterolateral tooth is distinct. The propodus of the last ambulatory leg is narrow and slender, and the dactylus is sharply claw-shaped. Legs of the adult crab are generally twice the length of the carapace. The crab is light brownish-orange to greenish-brown in color.

Juvenile crabs resemble adults except for the lack of setae on the claws of crabs smaller than 20 mm in carapace width. As with other species of brachyuran crabs, males and females are distinguished by the shape of their abdomen; males have a narrow abdominal flap while that of females is generally wider. Once the females have undergone their final molt, which is known as the puberty molt, the abdomen extends to the edge of the carapace and the crabs are sexually mature. Carapace width of mature crabs ranges from 34 to about 100 mm (Veldhuizen, 2001).

Table 3b
Distinguishing morphological features in the megalopa stages of two species of mitten crabs (*Eriocheir*) and one species of shore crab (*Hemigrapsus*).

	Eriocheir sinensis	*Eriocheir japonicus*	*Hemigrapsus sanguineus*
Carapace	Length/width = 1.71/1.35 mm; carapace subquadrate with 2 indistinctly round lobes on anterolateral region; front margin with triangular depression	Length/width = 1.86/1.34 mm subquadrate with 2 indistinctly round lobes on anterolateral region; rostrum slightly forward and deflected downwards	Length/width = 1.74/1.54; carapace subquadrate in dorsal view; rostrum ending in pointed tip, curved ventrally
Antennule	12 aesthetascs, 4 setae; 3 setae on endopod	14 aesthetascs, 3 setae; 4 Setae on endopod	
Maxilliped I	Endopod with 4 subterminal and 3 terminal setae; epipod with 11 aesthetascs	Endopod with 3 terminal setae; epipod with 13–15 aesthetascs	Endopod with 2 setae; epipod with 8 setae and 9-10 aesthetascs
Maxilliped II	7 setae on basal segment; 1,9 setae on exopod	3–5 setae on basal segment; 1,5 setae on exopod	5 setae on basal segment; 1, 5 setae on exopod
Abdomen	Long posterolateral projection on somite 5; 6 setae on posterolateral margin of somite 6; well defined posterolateral spines on segments 2–4	Short posterolateral projection on somite 5; setae on posterolateral margin of somite 6 lacking	All somites with simple setae; telson semicircular in shape
Telson	10–12 setae on posterior margin; 4 dorsal setae and 4 lateral setae on each side and	3 setae on posterior margin; setae on lateral margin lacking	3 plumose setae on posterior margin; 4 simple dorsal setae

Eriocheir sinensis co-occurs with *H. sanguineus* in its native Asian range and along the east coast of North America. *Eriocheir japonica* co-occurs with *H. sanguineus* in Asia. Sources: Kim and Hwang, 1990; Hwang et al., 1993; Montu et al., 1996.

4. Reproductive biology

4.1. Ovarian development

Reproductive studies of *E. japonicus* and *E. sinensis* have shown that, as in other brachyuran species, ovaries change color as the eggs undergo development. Histological work with *E. japonicus* determined that as ovaries mature, the external appearance undergoes a sequence of color changes starting with light-yellow—passing through yellow, beige, bright-violet, light-brown, brown, dark violet—and ending as dark-brown (Kalinina and Semenkova, 2005). For example, Kalinina et al. (2008) reported that ovaries of *E. japonicus*, which include both oogonia and oocytes during the early developmental stages, change from light purple and light brown as vitellogenisis progresses. At completion of vitellogenisis, the ovaries become dark brown, due to accumulation of yolk and pigments in the developing eggs (Kobayashi and Matsuura, 1995a). Based on increases in the gonadosomatic index and oocyte diameter, the authors concluded that it takes about 4 months for the gonads to mature.

4.2. Migration, mating, and larval release

Fertilization in brachyuran crabs typically includes copulation that in some taxa occurs immediately after the female has molted and in other taxa occurs after the carapace of the female has hardened (Epifanio, 2007). In both cases, the male deposits sperm packets in the seminal receptacles of the female, providing her with the potential to fertilize more than one batch of eggs. Clusters of fertilized eggs are eventually deposited on abdominal appendages known as pleopods and are brooded externally until hatching. In shallow-water crabs, the duration of brooding varies widely among species and ranges from a few days to several months.

Mating in both *E. sinensis* and *E. japonica* occurs after females have completed the puberty molt and have hardened (Kobayashi and Matsuura, 1999). Females do not release pheromones to attract males, but a contact pheromone is most likely involved once actual mating begins (Herborg et al., 2006). Laboratory experiments indicate that mating may be synchronized to the spring-tide/neap-tide cycle, but this has not been confirmed in the field (Herborg et al., 2006).

Female mitten crabs are highly fecund, producing between 100,000 and 1 million eggs that are brooded on the ventral surface of the abdomen in typical crab fashion (Panning, 1939; Cohen and Carlton, 1995). Eggs are extruded within 24 h after mating and may be brooded for as long as two months before hatching (Panning, 1939; Lee and Yamazaki, 1990; Rudnick et al., 2005a). Egg diameter ranges from 350 to 380 µm (Du et al., 1995; Jin et al., 2002).

Female *E. sinensis* produce multiple broods during the reproductive season (Panning, 1939), and similar patterns have been observed in *E. japonica*. Kobayashi (2001) found that *E. japonica* kept in the laboratory had up to 3 broods in a single reproductive season and that 93% of the crabs extruded a second brood within 21 days of the initial hatching (Kobayashi and Matsuura, 1995a; Kobayashi, 2001). Fecundity in *E. japonica* increased with female size, and the greatest number of eggs was typically produced in the first brood.

In their native habitat, mitten crabs migrate downstream from fresh water regions to higher salinity areas to mate in late fall and winter (Jin et al., 2001, 2002; Zhang et al., 2001). Downstream migration begins once females have gone through the puberty molt. Zoea larvae hatch in early spring, and megalopae are first seen in May and June (Zhao, 1980; Jin et al., 2002). Studies of invasive mitten crabs in northern Europe have shown that adults living in freshwater habitat begin a seaward migration in late summer and that crabs reach puberty in brackish waters of tidal estuaries (Ingle, 1986). Nonetheless, there is considerable variability in life history aspects of the various life stages of mitten crab populations from native and invasive ranges (Table 4). Herborg et al. (2003) estimated that mature animals

Table 4
Synopsis of the natural history of the Chinese mitten crab *Eriocheir sinensis* in native and invasive habitats.

Area	Spawning period	Settlement	Juvenile upstream migration	Downstream migration	Mating/reproduction period	Time to maturity (years)	Size range of mature crabs (mm)
San Francisco Bay	Mid-late spring	Spring-early summer	Year-round; peak May–June	Mid-late fall; peak Sept.–Oct.	Oct.–June; peak late fall, early winter; 50% gravid females between Nov–April	2–4; avg. 3	30–95
Elbe River, Germany	Spring–early summer	July–Aug. during warm springs; Oct. when weather is unfavorable	March–July	Late summer early winter; peak Sept.	Oct.–Jan.	3–5	38–84
Thames River, Great Britain	Spring–summer	April–May	Spring–summer	Sept.–Dec.	?	?	38–50
France	**?**	April–July	?	Aug–Oct	?	?	50–90
Odra Estuary, Poland	?	?	Spring	?	March–Nov.	?	45–90
Lake Bao/Biandantang, China	Fall–winter	megs enter river- May–June	?	Fall–winter	Fall–winter- mate and spawn	1–2	26–50 (CL)
Yantze River, China	Jan.–April	April–June	Year-round; peak May–June	Aug.; peak Sept–Oct	Oct.–April; peak Dec.	1–2	38–90
Fukuoka Kagoshima, Japan[a]		**October-November May–June**		**Sept.–Dec.**	**Early fall–early summer (10 months) in Fukuoka; 5 months in Kagoshima**		**38–68**
Data sources	Panning, 1939; Hymanson et al., 1999; Jin et al., 2001; Zhang et al., 2001; Rudnick et al., 2003, 2005a; Robbins et al., 1999	Panning, 1939; Robbins et al., 1999; Jin et al., 2001; Zhang et al., 2001; Rudnick et al., 2003	Panning, 1939; Hymanson et al., 1999; Veldhuizen and Stanish, 1999; Robbins et al., 1999; Veldhuizen, 2001; Kobayashi, 2003	Panning, 1939; Anger, 1991; Kobayashi and Matsuura, 1995a; Hymanson et al., 1999; Robbins et al., 1999; Jin et al., 2001; Rudnick et al., 2005a; Czerniejewski and Wawrzyniak, 2006b	Panning, 1939; Kobayashi and Matsuura, 1995a; Hymanson et al., 1999; Jin et al., 2001; Zhang et al., 2001; Rudnick et al., 2003; Czerniejewski and Wawrzyniak, 2006b	Cabral and Costa, 1999; Hymanson et al., 1999; Jin et al., 2001; Zhang et al., 2001; Rudnick et al., 2005a	Cabral and Costa, 1999; Robbins et al., 1999; Normant et al., 2000; Jin et al., 2001; Zhang et al., 2001; Kobayashi, 2003

[a]For comparison purposes, data for the Japanese mitten crab *E. japonica* are included in bold. Note: Size ranges correspond to carapace width except where noted. CL = carapace length. Modified from Rudnick et al. (2005a).

from the Wesser and Elbe Rivers in Germany could move distances of 400 km during a three-month migration period. After mating, females release their larvae in higher salinity estuarine waters during spring (Anger, 1991; Herborg et al., 2003). Panning (1939) determined that mating and extrusion of eggs occurred from October through January in German waters and reported that larval release was dependent on weather conditions and occurred during the five-month period extending from March through July. More recent laboratory studies have confirmed the temperature-dependent variability in brooding time of European mitten crabs (Anger, 1991). Investigations in San Francisco Bay have described similar patterns of migration, mating, and larval release (Veldhuizen, 1998; Rudnick et al., 2000, 2003). Adults in both native and invasive populations of *E. sinensis* make a single reproductive migration and die once the spawning season is over (Kobayashi and Matsuura, 1995b).

Additional information about migration patterns in the genus *Eriochier* is available for the Japanese mitten crab *E. japonicus* (Kobayashi and Matsuura, 1991, 1995a; Kobayashi, 1998, 2003). Downstream migration of adult crabs in Japanese waters takes place from September through February, and zoeae are released in high salinity regions of estuaries. Megalopae settle and metamorphose to the juvenile stage in autumn (October–November) and again in late spring to early summer (May–June). These two settlement periods most likely reflect two separate periods of larval release (Kobayashi and Matsuura, 1995b). Shortly after settlement, the juvenile crabs begin their upstream movement and dispersion in riverine areas (Kobayashi, 2003).

5. Larval biology and dispersal

Despite the abundance and impact of *E. sinensis* in invaded ecosystems, relatively few studies have addressed the larval biology of the species. Panning (1939) noted that zoeae are released in estuarine water and eventually move to fresh water during the megalopal stage. But the transport mechanisms proposed by Panning were purely conjectural and had little relation to our present understanding of estuarine circulation. More recently, Anger (1991) showed that salinity tolerance varied greatly among different larval stages of *E. sinensis*. Stage I zoeae were euryhaline, tolerating salinities between 10 and 30‰. However, the late zoeal stages required high salinity water, and euryhaline capabilities were not developed again until the megalopa stage. Anger suggested that larvae are hatched in low-salinity estuarine water and are transported to high-salinity coastal water where zoeal development occurs. He surmised that megalopae are then transported back to the estuary where they settle in juvenile habitat and eventually undergo upstream migration as juveniles. Under such circumstances, larvae would depend on favorable oceanographic conditions to recruit back into the estuary (Epifanio and Garvine, 2001).

An alternative dispersal scenario was proposed by Hanson and Sytsma (2008), who suggested that mitten crab larvae are retained within the estuary in their native habitat because rivers along the east coast of Asia experience low flow in the summer months when larval release occurs. However, there have been no direct investigations of larval transport in either native or invasive populations of *E. sinensis* (Veldhuizen and Stanish, 1999; Veldhuizen, 2001; Rudnick et al., 2000, 2003, 2005a), and there have been no investigations of vertical swimming behavior, which would determine the possibility of larval retention within the estuary (Park et al., 2004). Moreover, there has been no attempt to identify the physical processes responsible for the transport of mitten crab larvae in Asian, European, or North American populations.

There has also been a limited amount of work on the larval biology of the Japanese mitten crab *E. japonica* (Kobayashi, 2002). It is not clear if zoeal development occurs within the estuary or on the adjacent continental shelf. But megalopae are first seen in the upper regions of estuaries where they settle and undergo metamorphosis. Newly metamorphosed juveniles remain in settlement areas and do not migrate upstream to freshwater areas until they reach a carapace width >5 mm. Juveniles reach sizes of about 20 mm in carapace width by the time they reach freshwater areas. The crabs remain in fresh water until they grow to about 40 mm after which they migrate downstream to the estuary to mate and reproduce. According to Kobayashi, the crabs take advantage of freshwater flow for transport to the estuary and after reaching tidal areas, benefit from ebb tides to reach coastal areas. But actual studies of this putative transport mechanism have not been done.

6. Growth of juveniles

In their native habitat, the lifespan of Chinese mitten crabs is about 24 months (Cohen and Carlton, 1995; Xu and Li, 1996; Jin et al., 2002). Nonetheless, crabs under aquaculture conditions are capable of completing their life cycle in as little as one year (Jin et al., 2002). Some authors have attributed this rapid aquacultural growth to genetic factors (Jin et al., 2001, 2002), but the consensus of opinion points to more favorable environmental conditions and optimal diet in aquaculture systems (de Leersnyder et al., 1980; Jin et al., 2001; Zhang et al., 2001). However, the lifespan and duration of the individual life stages may vary greatly (Table 5).

Early field studies in northern Europe concluded that mitten crabs require 3–5 years to reach sexual maturity (Panning, 1939), while crabs in California waters typically reach maturity in 2–3 years (Rudnick et al., 2003). Rudnick et al. (2005a) developed a growth model based on their own studies in San Francisco Bay and on laboratory data from Anger (1991). Model simulations indicated that San Francisco Bay crabs could reach sizes between 39 and 78 mm carapace width by age 2 years.

6.1. Spatial and temporal variation in size and abundance of crabs

Several studies have examined the population structure of Chinese mitten crabs outside their native range. Results of these investigations have uncovered small seasonal differences in the sex ratio of the sampled populations. For example, sampling in the Odra estuary in Poland revealed that adult males were slightly more abundant than females during late summer and fall, while females were more abundant in spring (Normant et al., 2000; Czerniejewski and Wawrzyniak, 2006a). Similar patterns have been observed in mitten crab populations from the San Francisco Bay system where male crabs were more abundant in fall and early winter, but where females were more abundant in spring (Rudnick et al., 2003). Presumably, these differences are caused by sex-based variation in patterns of migration.

Likewise, studies of population structure of *E. japonica* in the Kaminokawa River in Japan have revealed temporal and spatial differences in male and female proportions (Kobayashi and Matsuura, 1995a). Results indicated that females dominated the assemblage of large crabs (>55 mm) at freshwater stations in the upper region of the estuary and that greater numbers of large females migrated from the

Table 5
Duration and habitat of the life history stages of the mitten crab *Eriocheir sinensis*.

Stage	Duration	Habitat
Adult (non-reproductive stage)	2–4 years	Lakes, levees, rivers, streams
Adult (reproductive stage)	4–10 months	Brackish open waters
Zoea Larva (5 stages)	2–8 weeks	Estuarine/marine
Megalopa Larva (one stage)	3–6 weeks	Estuarine/marine
Early Juvenile	6–12 months	Brackish waters
Late Juvenile	12–24 months	Lakes, levees, rivers, streams

upper regions during the breeding period (September–December). In contrast, there was a male bias among smaller crabs at locations in the lower estuary. The authors concluded that adult females are generally distributed farther up-river than males.

A number of studies have examined the size distribution of Chinese mitten crabs in their extended range. However, these investigations have come to varying conclusions, probably because of sampling limitations. For example, a survey of fishing operations in the Odra Estuary in Poland reported the absence of juveniles in the main stem of the estuary (Normant et al., 2000; Czerniejewski and Wawrzyniak, 2006b). However, Normant et al. (2000) attributed this to a sampling bias because fishing gear was not deployed in shallow near-shore water where juveniles normally occur.

In contrast, more extensive studies of crab populations in San Francisco Bay (USA), the Elbe River (Germany) and the Thames Estuary (England) have revealed the presence of juvenile crabs in a variety of habitats (Herborg et al., 2003; Rudnick et al., 2003; Gilbey et al., 2008). Herborg et al. (2003) analyzed data from the 1932–1936 crab invasions in the lower Elbe River and found the presence of at least two cohorts in the estuary. Changes in the spatial distribution of these cohorts reflected the migratory patterns of the age classes constituting the respective cohorts.

Recent studies in the upper portion of the Thames estuary have shown that juvenile crabs are common in structured intertidal habitat, which apparently provides refuge from predation (Gilbey et al., 2008). In this habitat, groups of up to 18 crabs have been found under a single rock. As reported in other studies, the typical size of crabs varied along the river, with larger crabs found near the head of the estuary and smaller crabs collected in lower estuarine areas (Panning, 1939; Veldhuizen, 2000; Herborg et al., 2003; Rudnick et al., 2003). Gilbey et al. (2008) also observed that juvenile crabs were more abundant in summer compared to winter months and concluded that crabs might move to deeper waters during the winter. Size-related differences in spatial distribution have also been reported for *E. japonicus* where large crabs are more common in freshwater and small crabs more abundant in brackish water (Kobayashi and Matsuura, 1995b). Again, this reflects the migratory patterns of the different size groups.

6.2. Interannual variation in population size

Fluctuations in the abundance of mitten crabs have been documented in both native and introduced populations. Abundance of native populations has been declining for the past two decades, probably due to a combination of factors such as pollution, habitat loss and over-fishing (see above). But the size of invasive populations has been more variable over time. A typical case is the invasion of German waters where the population grew very rapidly in the first 20 years after the introduction and then declined over the following decade (Panning, 1939; Attrill et al., 1996). Similar patterns have been observed in the Netherlands and Belgium (Veldhuizen and Stanish, 1999).

However, circumstances were different in the United Kingdom where the first record of *E. sinensis* dates to 1935, but where the population remained at a very low level until the early 1990s when it began to grow rapidly, especially in the Thames River Estuary (Ingle, 1986; Attrill et al., 1996; Gilbey et al., 2008). This rapid increase has been attributed in part to reduced water flow during severe drought during 1989-1992, which purportedly allowed settlement and development of juvenile crabs. But the physical mechanisms underlying this hypothesis have not been investigated in the field.

7. Adaptation to freshwater

There is a large body of information regarding adaptations of crustaceans to freshwater environments. While some freshwater crustaceans are unable to tolerate even brackish salinities, others like the Chinese mitten crab function equally well in freshwater or marine situations (Rathmayer and Siebers, 2001). Consequently, *E. sinensis* has been used as a model species in a number of physiological investigations (see review by Pequeux, 1995). Much of this work has emphasized the function of the gill and gill epithelium. In particular, many studies have focused on ion transport using techniques such as short-circuit current, radioactive tracer fluxes, microelectrode impalements, and current-noise analyses (see review by Onken and Riestenpatt, 1998). Other investigations have dealt with enzyme activity in relation to the effects of neuro-endocrine factors such as dopamine and carbonic anhydrase on ion transport through the gills (Mo et al., 1998; Olsowski et al., 1995). Yet other studies have examined the role of the sodium pump in active transport of ions across crab gills (see reviews by Lucu and Towle, 2003; Torres et al., 2007). In recent years, there has been increased interest in examining the effects of trace metal uptake on various aspects of osmoregulation (Silvestre et al., 2002, 2005; Roast et al., 2002).

Juvenile and adult mitten crabs are osmoregulators in fresh and brackish water and maintain hyper-osmotic hemolymph under those conditions (Mantel and Farmer, 1983). In coastal sea water, adults are osmoconformers, but are hyporegulators at higher salinities (Schoffeniels and Gilles, 1970; Gilles, 1975). Therefore, osmotic gains of water and diffusive losses of ions occur when crabs migrate from coastal seawater to freshwater (Onken and Riestenpatt, 1998). These gains and losses are minimized by reducing the permeability of gill membranes (Mantel and Farmer, 1983; Onken and Riestenpatt, 1998), but active uptake of sodium and chloride ions is necessary to maintain a steady state (Mantel and Farmer, 1983).

It became evident from early studies that active transport of sodium chloride took place in the gills (reviewed in Pequeux, 1995). However, those studies were performed on whole animals; thus, the mechanisms of ion transport at the gill level remained poorly understood. Later investigations based on perfused preparations of isolated gills and on single split-gill lamellae have provided a better understanding of ion transport. Those studies revealed functional differences between the three anterior pairs of gills and the three posterior gills (Pequeux and Gilles, 1981). In freshwater-acclimated crabs, sodium flux is passive in the three anterior pairs of gills, whereas active sodium uptake occurs in the three posterior gills. It is this active uptake that compensates for salt lost by diffusion and urinary excretion. The fact that posterior gills are impermeable to sodium means that sodium loss in fresh water is reduced (Pequeux and Gilles, 1988). In contrast, the anterior gills are impermeable to chloride ion, while the posterior gills show passive diffusion.

Recent studies have focused on mechanisms that control the balance of sodium and chloride ions in freshwater-acclimated mitten crabs. Investigations by Rathmayer and Siebers (2001) have revealed that uptake of sodium and chloride ions from surrounding water is always coupled and always occurs at 1:1 ratio. This work was corroborated by Onken and Riestenpatt (1998) who showed that inhibitors of sodium uptake always affected uptake of both ions.

Compared to the numerous studies on adult mitten crabs, there has been relatively little study of the physiology of the early life-history stages. One recent investigation examined changes in osmoregulation patterns of larval and early juvenile stages by quantifying survival and osmoregulatory capacity at different salinities ranging from fresh water to 45‰ (Cieluch et al., 2006). The authors concluded that newly hatched zoeae showed strong hyper-regulation, but this capacity declined in subsequent zoeal stages before finally reappearing in the megalopa stage. Thus, the specific adult pattern of hyper-regulation at low salinity and hypo-regulation at high salinity appear in the megalopa stage and continue through the subsequent juvenile stages. These patterns of osmoregulation of the various life stages are coherent with the salinity tolerance studies discussed above (Anger, 1991) and with the reproductive and migratory patterns of this species (Cieluch et al., 2006).

8. Economic and ecological impacts

Impacts of invasive populations of *E. sinensis* derive mainly from the burrowing, migratory, and feeding behaviors of the crabs (Table 6). These behaviors bring the species into conflict with a number of human enterprises. Effects of burrowing are restricted to freshwater and brackish habitats where mitten crabs spend most of their adult lives. Early reports for European populations came from investigations in the Elbe tributaries where burrows were observed in firm marsh bottoms as well as areas along the banks of canals (Panning, 1939). More recent work in San Francisco Bay has reported that burrows are tightly packed and often interconnected in areas where crabs are abundant (Dutton and Conroy, 1998; Rudnick et al., 2000). Burrows are usually excavated on a downward-sloping angle such that water remains in the chamber during low tide (Ingle, 1986; Rudnick et al., 2000, 2005b). Burrows vary in complexity and range from single chambers to a matrix of interconnected tunnels as long as 0.5 m.

Burrowing activity can affect the integrity of stream banks and can exacerbate loss of sediment to adjacent open water. Studies in German rivers have noted that burrowing by *E. sinensis* may result in collapsed levees and dikes due to sediment erosion, and similar impacts have been observed more recently in the Thames River in the United Kingdom (Dutton and Conroy, 1998; Rudnick et al., 2005b).

Other impacts result from the synchronized migration of adults during the spawning season. The entanglement of mitten crabs in fish and shrimp nets increases handling time and damages the target species within the net (Crosier and Molloy, undated; Veldhuizen and Stanish, 1999; Rudnick et al., 2000). During migration periods in German rivers, large numbers of mitten crabs have been reported to enter traps intended for eels, consume the bait, and substantially reduce the catch of eels (Panning, 1939).

Mitten crabs also have an indirect effect on both fisheries and agriculture in the San Francisco Bay region. Agriculture in the Central Valley of California is dependent on diversion of water from the Sacramento–San Joaquin Delta. The systems that provide this diversion incorporate fish collection facilities that are intended to prevent fish from entering the diversion canals. Mitten crabs are a major problem in these facilities because crabs are entrained in the salvage tanks along with the intended fish and clog the collection facilities. In 1998, over 1 million crabs were entrained at the Tracy Fish Collection Facility near Stockton, California, most of them during their autumn seaward migration (Siegfried, 1999; Veldhuizen and Stanish, 1999).

In contrast to the well documented effects of mitten crabs on human activities, there is surprisingly little known about their interactions with native species (Gilbey et al., 2008). However, a few studies have examined interactions of mitten crabs with indigenous species of crabs and crayfish. In estuarine habitats, mitten crabs co-occur with a number of native crab species. For example, Gilbey et al. (2008) reported on competitive interactions between *E. sinensis* and juvenile *Carcinus maenas*, a native crab species in the Thames Estuary, and found that mitten crabs were better space competitors.

In freshwater habitats, mitten crabs co-occur with various native crayfish. In oligohaline regions of San Francisco Bay, mitten crabs have the potential to reduce populations of two species of crayfish through aggressive behavior and competition for shelter (Veldhuizen and Stanish, 1999). However, laboratory investigations indicate that aggressive behavior of crabs toward crayfish is significantly reduced in situations where shelter is not limited (Rudnick et al., 2000). Nevertheless, the authors concluded that mitten crabs are generally better space competitors than either species of crayfish.

Early studies on the feeding habits of *E. sinensis* described the crabs as opportunistic omnivores capable of eating a wide variety of invertebrates as well as algae and detritus (Thiel, 1938; Panning, 1939). More recent findings in San Francisco Bay indicate that *E. sinensis* prey on freshwater shrimp, and there are concerns that mitten crabs can feed on an endangered species of shrimp (*Syncaris pacifica*) in areas of the bay where these two species overlap (Rogers, 2000).

Additional studies in Coyote Creek at the south end of San Francisco Bay utilized stable isotope analysis to determine that mitten crabs relied mainly on invertebrate prey, although benthic algae and terrestrially derived detritus were also incorporated in the diet. Other work in San Francisco Bay indicates that mitten crabs prey on eggs of nest-building fish such as centrarchids and salmonids, which could have substantial effects on the salmon fishery (Veldhuizen and Stanish, 1999).

Potential human and wildlife health risks associated with mitten crabs include the bioaccumulation of contaminants and the possibility that the crab serves as an intermediate host for a parasitic trematode known as the oriental lung fluke (Veldhuizen, 2001). Mitten crabs are known to inhabit agricultural ditches and other areas that contain high levels of contaminants (Veldhuizen and Stanish, 1999; Veldhuizen, 2001). However, analysis for organochloride pesticides and heavy metals revealed that the levels of these contaminants in crab tissue were usually below detection limits and always below FDA guidelines (Veldhuizen, 2001). In addition, there is no evidence that supports the argument that Chinese mitten crabs are intermediate hosts for the oriental lung fluke in either their native or invasive habitats (Hymanson et al., 1999).

9. Risk assessment

Shipping and aquacultural activities are the dominant agents for introduction of non-indigenous crabs in estuaries around the world (Gollash, 2006), but other vectors include the biofouling of ship hulls

Table 6
Summary of economic and ecological impacts of invasive populations of the Chinese mitten crab *Eriocheir sinensis*.

Population	Burrowing	Migration	Feeding/Competition
European			
United Kingdom	Bank/levee slumping, collapse; sediment erosion	Nuisance at intake tanks of power stations	Habitat alteration; decreased biodiversity; change in community structure
Germany	Bank slumping or collapse, undermining of support structures like boulders; erosion	Increased fish mortality at fish salvage operations; gear damage of fishing operations; clogging of nets and traps; bait stealing; reduction in catch	
The Netherlands		gear damage of fishing operations	
North American			
South San Francisco Bay	Erosion of marsh sediments	Nuisance to commercial bay shrimp operations; damage to nets and catch	Decrease in vegetation in natural habitats
Sacramento–San Joaquin Delta	Bank/levee slumping, collapse; sediment erosion	Loss of bait in recreational fisheries	Potential catch reduction of crayfish (*Pacifastacus leniusculus*), which supports a commercial fishery; decrease in abundance and growth rates of crayfish
South Delta		Increased fish mortality at fish salvage operations	

and activities associated with the aquarium and bait industry (Carlton and Geller, 1993; Cohen et al., 1995; Ruiz et al., 1997). The first presumed invasion by a non-indigenous crab via ballast water was the introduction of the Chinese mitten crab in the rivers of Germany in the second decade of the 20th century (Carlton, 1996 and see above). However, it was not until much later in the century that crab zoeae and megalopae were actually identified in ballast water taken from ships in a number of ports in the USA (Carlton, 1989; Carlton and Geller, 1993; Hamer et al., 1998; Smith et al., 1999). While these larvae were not identified to species, the results confirmed the suspicion that crab larvae are capable of surviving long voyages in ballast water. Thus, it is surprising that *E. sinensis* did not become established on the west coast of North America for almost eighty years after its initial appearance in Europe, particularly in light of the extensive shipping between Asia and the West Coast and the relative proximity of the two regions (Cohen and Carlton, 1997).

Different approaches have been used to analyze the risk of invasion by mitten crabs in regions where the crab does not presently occur. For example, Hanson and Sytsma (2008) conducted risk analysis studies to evaluate the vulnerability of estuarine systems in the Pacific Norwest. The authors used a habitat comparison approach in which ecological characteristics of areas with established populations of crabs were compared to those of a number of estuaries in Oregon, Washington, and Alaska. Parameters included: (1) the area of the watershed and estuary, which is a measure of potential habitat and (2) horizontal salinity profiles and residence time of estuarine water, which are indicators of areas where larval development and dispersal may occur. The authors also used a temperature-driven regression model of larval development (Anger, 1991) to estimate larval duration in the various estuaries. Results indicated that large estuaries in Oregon and Washington could support crab populations, but that the majority of Pacific Northwest and Alaskan estuaries are not at risk for invasion.

Another approach for assessing the risk of bioinvasions uses a technique called *genetic algorithm for rule-set prediction* (GARP). This technique creates an ecological niche model for the species of interest. The model is based on a set of mathematical rules that represent the limiting environmental conditions. The model describes environmental conditions under which a species should be able to maintain populations (Stockwell, 1999; Stockwell and Peters, 1999). This approach was used to generate a predictive model of mitten crab distribution in Europe (Herborg et al., 2007b). Results showed strong correlation between predicted and observed sites of infestation by mitten crabs. In another study, Herborg et al. (2007a) used a similar approach to predict the potential distribution of *E. sinensis* on the east coast of North America. In this case, the authors used GARP in combination with patterns of ballast-water discharge. Results showed that ports like Norfolk and Baltimore in the Middle Atlantic region would be likely conduits for importation of the species. Thus, the large estuaries of the region (e.g., Chesapeake, Delaware, and Hudson) would appear to be at high risk.

10. Summary and conclusions

In this paper, we have reviewed an extensive scientific literature concerning both native and invasive populations of the Chinese mitten crab *E. sinensis*. The mitten crab belongs to the family Varunidae, which includes two other species of *Eriocheir* (*E. japonica* and *E. recta*) and the closely related *Neoeriocheir leptognathus* (Chan et al., 1995). *E. sinensis* is native to freshwater and estuarine habitats along the east coast of Asia, and the Asian range of the species is well described (Hymanson et al., 1999). Mitten crabs were first discovered in northern Europe in 1912, which represents one of the earliest reports of invasive species in aquatic habitats (Panning, 1939). Ballast water is the most probable vector for the initial introduction, although the larval stages of *E. sinensis* have never been identified in ballast inspections (Carlton, 2003).

Our review has shown that *E. sinensis* has wide environmental tolerance and that invasive populations have persisted in Western Europe for nearly 100 years. During that time, the species has spread to Eastern Europe and adjacent areas of Asia. However, mitten crabs did not appear on the west coast of North America until the very end of the 20th century, despite the relative proximity to Asian populations and the extensive shipping connections to Asian ports (Rudnick et al., 2000). Mitten crabs have also been found in Chesapeake and Delaware Bays along the east coast of the USA (Ruiz et al., 2006), but it is not clear if a breeding population has been established. However, *E. sinensis* has not been reported from Australia, Africa, or South America—again, despite available habitat and extensive shipping connections. Reasons for the failure to colonize appropriate habitat in those areas are not apparent.

Invasive populations of *E. sinensis* have caused millions of dollars in damage in Europe and North America (Gollasch, 2006; White et al., 2000). Impacts of invasive populations center largely on the burrowing activity of the crabs, which damages stream banks and levees (Rudnick et al., 2005b), and on the annual spawning migration, which interferes with fishing activities and irrigation projects (Siegfried, 1999; Veldhuizen and Stanish, 1999).

The species is unique because its various life-history stages occur all the way from freshwater streams to the coastal ocean. Adults and juveniles have well developed osmoregulatory capacities, and the physiological basis for salinity tolerance is well described at the level of individual organs and specific biochemical processes (Pequeux, 1995; Rathmayer and Siebers, 2001). Reports on the life span of the crabs vary from two to five years (Panning, 1939; Jin et al., 2002; Rudnick et al., 2003). Most of the adult phase is spent in freshwater with females extending farther upstream than males. Reproduction is characterized by the synchronized migration of large numbers of mature crabs (Rudnick et al., 2005a). Mating and egg-brooding occur in the meso- and euhaline regions of estuaries. Adults die within a few months of spawning and do not migrate back to freshwater (Kobayashi and Matsuura, 1995b). Larval development includes five zoeal stages and a single megalopal stage (Kim and Hwang, 1995). The literature contains conflicting scenarios for larval dispersal, but there has been virtually no study of larval distributions in nature (Anger, 1991).

Wild Asian populations of *E. sinensis* have undergone steep decline in recent years due to over-fishing and habitat loss (Hymanson et al., 1999). In contrast, an Asian aquaculture industry based on *E. sinensis* has been developed recently and is purportedly valued at more than 1 billion dollars per year (Wang et al., 2006). There are no reports of aquaculture activities associated with invasive populations of *E. sinensis*. The dynamics of wild invasive populations are typified by a rapid increase in population size in the first two decades after introduction, followed by a slow decline to a smaller, more stable population size (Attrill et al., 1996; Veldhuizen and Stanish, 1999). The factors controlling these dynamics have not been determined.

Our literature review has shown two disparate approaches for prediction of new invasions of *E. sinensis*. The first is a comparison of ecological characteristics of areas with and without established populations of mitten crabs (Hanson and Sytsma, 2008). Comparisons include assessment of spatial and temporal variation in factors such as salinity and temperature. The second approach uses a modeling technique called GARP, which describes environmental conditions under which an invasive species should be able to maintain populations and assigns risk factors to areas of potential invasion (Stockwell, 1999; Stockwell and Peters, 1999). Both techniques require accurate information on the biology of *E. sinensis* and the ecology of the area at risk.

Major gaps in our understanding of the biology of *E. sinensis* concern: (1) competitive interactions between invasive mitten crabs and native species and (2) patterns of dispersal and settlement of the larval stages. Competition studies are limited to a few investigations of interactions with co-occurring freshwater crustaceans (Veldhuizen and Stanish, 1999; Rogers, 2000; Rudnick et al., 2000) and a single study involving an estuarine crab (Gilbey et al., 2008). There is no information whatsoever concerning potential interactions with commercially valuable crustaceans such as the Dungeness crab (*Cancer magister*) on the west coast of North America or the blue crab (*Callinectes sapidus*) on the east coast. Moreover, there is nothing known about the competitive abilities of *E. sinensis* at different stages in its life cycle.

Likewise, the larval ecology of *E. sinensis* is largely unknown. Hatching occurs in the estuary, and the ontogeny of salinity tolerance suggests that zoeal development occurs in high-salinity water (Anger, 1991). However, there have been no studies of vertical migration by the larvae, which would allow inference concerning retention of larvae in the estuary, and there are virtually no data concerning spatial distribution of larvae in natural systems. This missing information is critical to the invasion biology of *E. sinensis* because the spread of a crab species after its initial introduction is partly a function of larval dispersal (Epifanio et al., 1998). Laboratory protocols for determination of vertical migration in crab larvae are well developed and have been applied to another invasive crab in the family Varunidae (Park et al., 2004). Techniques are also available to locate patches of larvae in nature and to tag them with satellite-tracking devices that allow determination of larval trajectories in the estuary and coastal ocean (Natunewicz and Epifanio, 2001; Natunewicz et al., 2001). Recent years have seen the development of mathematical modeling procedures that provide simulations of zoeal dispersal under a variety of physical conditions, and relevant physical data are routinely collected at metrological and coastal observing stations worldwide (Tilburg et al., 2006, 2007a,b). Application of these techniques in future work would allow simulation of the patterns of spreading in nascent populations of *E. sinensis* such as those recently discovered along the east coast of the USA.

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