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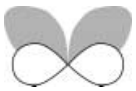

Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*

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Abstract

Aim This paper evaluates global collection records, evidence of anthropogenic transport methods, and experimental and distributional data relative to temperature requirements to understand the historical and potential dispersal of a well-known genus of estuarine crab.

Location The records analysed are from temperate and tropical coastal ocean areas.

Methods The study is based primarily on literature analysis and examination of museum specimens.

Results The human-mediated successful global dispersal of the European shore crabs *Carcinus maenas* (Linnaeus, 1758) and *C. aestuarii* (Nardo, 1847) occurred in three major episodes: around 1800, in the 1850s–70s, and in the 1980s–90s. The nineteenth century introductions occurred through transport by ships (probably in hull fouling or in solid ballast), while the introductions in the 1980s could have occurred through a greater variety of dispersal mechanisms (ships' hull fouling and seawater system fouling; fouling on semisubmersible drilling platforms; ballast water; transport with fisheries products intended for food or bait; scientific research; releases from aquaria maintained for educational or scientific purposes; or intentional non-governmental releases for human food production). These introductions have resulted in *Carcinus*' establishment in five temperate regions outside of its native Europe in Atlantic North America, Australia, South Africa, Japan and Pacific North America, while releases into tropical regions have not established populations. *C. maenas*' range in both its native and introduced regions appears to be regulated by similar temperature parameters, enabling an assessment of its potential distribution.

Main conclusions The second episode of *Carcinus*' global dispersal, the period from the 1850s to 1870s, may be part of a broader surge of world-wide invasions caused by an increase in shipping.

Keywords
Australia, ballast water, biological invasion, California, *Carcinus aestuarii*, *Carcinus maenas*, *Carcinus mediterraneus*, dispersal, Europe, fouling, green crab, introduction, invasion history, Japan, South Africa, United States.

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INTRODUCTION

Despite growing recognition of the extent of invasions in coastal waters (Cohen & Carlton, 1998; Carlton, 1999a, 2001; Ruiz *et al.*, 2000; Grosholz, 2002), little is known of the temporal patterns of these invasions. Detailed histories of marine invasions and the timing of human-mediated transport mechanisms have been developed for only a few species. These include the Atlantic snail *Littorina littorea* Linnaeus, 1758 (Carlton *et al.*, 1982), the Asian seaweeds *Sargassum muticum* Yendo (Fensholt) (Critchley, 1983) and *Codium fragile tomentosoides* (van Goor) Silva (Carlton & Scanlon, 1985), the Indian Ocean isopod *Sphaeroma walkeri* (Stebbing, 1905) (Carlton & Iverson, 1981) and the Asian isopod *Synidotea laevidorsalis* Miers, 1881 (Chapman & Carlton, 1991, 1994).

The recent establishment of the European shore (or green) crab *Carcinus maenas* (Linnaeus, 1758) (Fig. 1) on the Pacific coast of North America (Cohen *et al.*, 1995; Grosholz & Ruiz, 1995) prompted us to review and correct the description of its global spread over the past two centuries, both to clarify patterns in its dispersal and to provide a basis for predicting its further range expansion. We also review the distribution and spread of its congener *C. aestuarii* (Nardo, 1847) (= *C. mediterraneus* Czerniavsky, 1884), briefly consider other invasion episodes contemporaneous with one major period in *Carcinus*' dispersal history, and suggest that further investigation may reveal a period in the nineteenth century when new invasions began to increase dramatically because of a surge in global shipping.

MATERIALS AND METHODS

We examined collections for older reported material of *Carcinus* at the Smithsonian Institution National Museum of Natural History, Washington, DC (NMNH) and at the Yale University Peabody Museum of Natural History, New Haven, CT (PMNH). In addition, we assembled and reanalysed all previous (and some long overlooked) reports and records of *Carcinus* from around the world.

The existence of two species, *C. maenas* and *C. aestuarii*, has been argued on various morphological grounds. In material that we examined we distinguished these species using morphological characters as previously described (Cohen *et al.*, 1995). Recently, molecular genetic techniques have been utilized to distinguish these species (Geller *et al.*, 1997; Bagley & Geller, 2001).

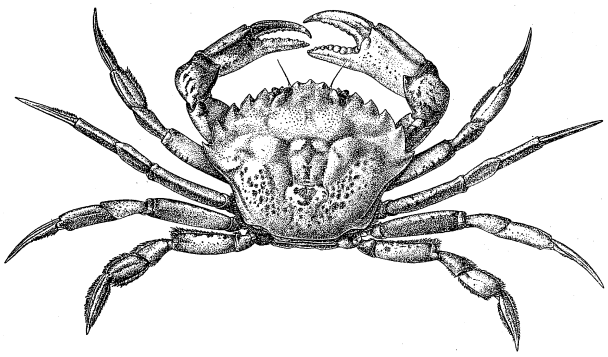

Figure 1 *Carcinus maenas* (Linnaeus, 1758) from Rathbun (1930).

RESULTS

Global pattern of episodic dispersal

Carcinus maenas is native to Atlantic Europe and perhaps northwest Africa (Appendix 1, Fig. 2) while *C. aestuarii* is native to the Mediterranean Sea and perhaps the Canary Islands (Appendix 1). In common with many coastal marine invertebrates, the extreme high and low latitude range records may represent occasional larval sets to the north or south, or temporary range expansions related to favourable but transient climatic and environmental conditions.

Outside of Europe, *C. maenas* or *C. maenas*-hybrids have become established in five major regions of the globe (the northwest and southeast Atlantic Ocean, and the northwest, northeast and southwest Pacific Ocean) and *C. aestuarii* or *C. aestuarii*-hybrids in two of these (the southeast Atlantic Ocean and the northwest Pacific Ocean). We suggest that *Carcinus* has successfully spread around the world in three major episodes: (1) in a period around 1800, (2) in the 1850s–70s, and (3) in the 1980s–90s.

Carcinus maenas was first reported in two regions outside of Europe in 1817. Material recently relocated in the 'Historical Collections' of the Muséum Nationale d'histoire Naturelle (MNHN) and labeled 'Red Sea' was collected by Savigny either during the expedition to Egypt in 1799–1801 or a little later, and illustrated and identified as *C. maenas* (Savigny, 1817; Audouin, 1826; D. Guinot, pers. comm., 1999). Based upon pleopod morphology, the specimens are *C. maenas* (D. Guinot, pers. comm., 1999). The collection of *C. maenas* in the Red Sea prior to the 1869 opening of the Suez Canal suggests transport on a ship travelling around Africa.

The only other early nineteenth-century record of *Carcinus* outside of Europe was in North America, where it became established. Major transatlantic trade routes were in place by this time, with ships carrying manufactured goods from Europe to North America in trade for tobacco, furs, indigo, naval stores, and other products (Natkiel & Preston, 1986). Say (1817) reported *C. maenas* [mistakenly describing it as a new species (Appendix 1)] from the east coast of the USA without providing a specific locality. Rathbun (1930) believed that Rafinesque's (1817) report of '*Portunus menoides*' from New York and New Jersey referred to *C. maenas*, but since Rafinesque noted two wrist spines as opposed to the single spine of *Carcinus*, his material may have been *Ovalipes ocellatus* (Herbst, 1799). De Kay (1844) reported *C. maenas* abundant in Long Island Sound and at Newport, Rhode Island.

Writing in 1871, Verrill *et al.* (1873) reported *C. maenas*' distribution to be from New Jersey to Cape Cod and suggested that the crab's failure to range as far north as it did in

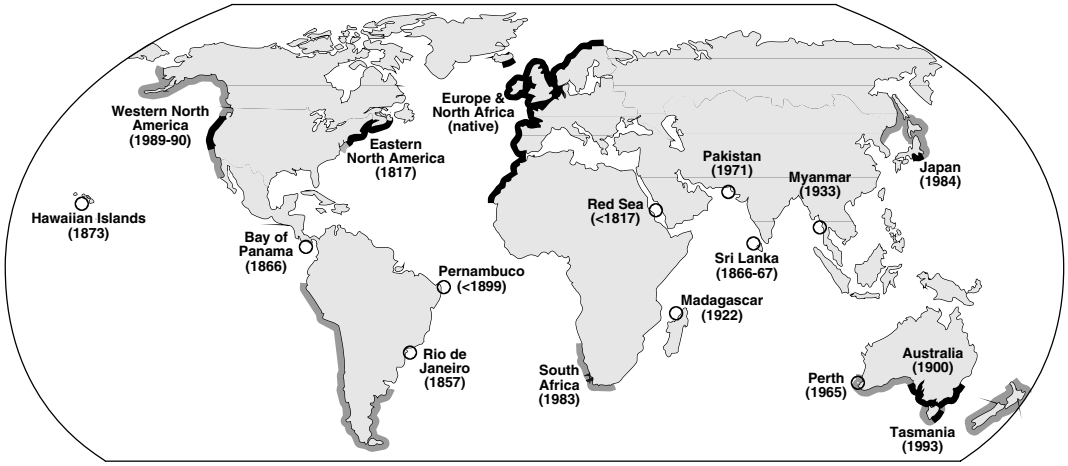

Figure 2 Occupied and Potential Range of *Carcinus maenas* (Linnaeus, 1758). *Black bands*: occupied range of *C. maenas* or populations with *C. maenas* genes. *Gray bands*: potential range of *C. maenas*. *Black circles*: one-time collections of *Carcinus* species in regions without established populations. First or one-time collection dates are given. See text and appendix for details of records, ranges, genetic information and species identification.

Europe indicated that it was a distinct species. However, *C. maenas* continued to move north. It was collected at Provincetown on the northeast tip of Cape Cod in 1872, at Boston and in southern Maine in the 1890s, and at the Canadian border in 1951. By 1964, it had spread around the Bay of Fundy and south-eastern Nova Scotia as far as Halifax, by 1982 had advanced another 130 km to Marie-Joseph, and in the late 1990s reached Cape Breton Island, passed through Canso Strait and arrived on the eastern shore of Prince Edward Island (Smith, 1879; Glude, 1955; Welch, 1968; Nova Scotia Museum collections; Gillis *et al.*, 2000). Several workers, including Rachel Carson in *The Edge of the Sea* (Carson, 1955), have suggested that *C. maenas*' northward expansion along the Gulf of Maine and into Canada was related to warming trends (Glude, 1955; Taylor *et al.*, 1957; Welch, 1968; Vermeij, 1978), but it is possible that these movements were a gradual post-introduction filling of *C. maenas*' potential range.

Carcinus resumed its transoceanic voyages in the late 1850s. Crabs reported as *C. maenas* were collected in 1857 at Rio de Janeiro, Brazil (Heller, 1865), in 1866 in the Bay of Panama (Smith, 1879), in 1866 or 1867 in Sri Lanka (Wood-Mason, 1873), and in 1873 in the Hawaiian Islands (Streets, 1877). Alcock (1899), followed by later workers, reported *C. maenas* 'off the coast of Pernambuco, Brazil', but provided neither a reference nor a collection date. Records from 'India' cited by various authors also originate with Alcock (1899) who, however, was apparently referring to the Sri Lanka record (Chopra & Das, 1937). Later workers (Edmondson, 1954; Almaça, 1962, 1963) questioned Streets' report of *Carcinus* from Hawaii. For all these records the last reported examination of any specimens occurred prior to *C. aestuarii*'s being recognized as a separate species in the 1950s (Forest, 1957; Holthuis & Gottlieb, 1958). However, we examined Streets' Hawaiian specimen (NMNH 2299) and the 1866 specimen from the Bay of Panama (PMNH 9535), and confirm that both are *C. maenas*. Although some modern workers continued to include these many locations within the distribution of *C. maenas*, there have been no additional records reported from these sites and we conclude that *Carcinus* is established only at the locations described in Appendix 1A.

Of all the *C. maenas* transported to the corners of the world from Europe or North America in the latter half of the nineteenth century, one distant population survived. In the spring of 1900, Fulton & Grant (1900) reported *C. maenas* as 'plentifully distributed' in the region of Port Phillip, Victoria, Australia, where local anglers frequently caught it in their nets. While Fulton & Grant (1900) noted that *C. maenas* was neither found in a careful search of Port Phillip in 1855 nor mentioned in Haswell's (1882) monograph on Australian decapods, they later (1902) suggested that *C. maenas* may have been transported to Australia as early as the 1850s on lumber ships from Europe. In concert with the pattern noted above, we suggest that *C. maenas* may have arrived in Port Phillip by the 1870s or 1880s, and was well established by 1900. At the least, the date of establishment of *C. maenas* in Australia can be assumed to be no later than the mid 1890s, given its abundance in the spring of 1900. Indeed, in 1877, Streets had already noted the existence of a specimen of *C. maenas* (which we have been unable to locate) questionably labelled from Australia.

In a pattern reminiscent of its invasion of the northwestern Atlantic, *C. maenas* dispersed along the Australian coast after a long quiescent period. In 1971, it was first found to the north of Victoria, in 1976 to the west, and in 1993 on the northeast coast of Tasmania. These movements may represent a combination of natural spread and introductions by shipping (Zeidler, 1978; Rosenzweig, 1984; Gardner *et al.*, 1994). Genetic analyses indicate that the

southern Australia population was founded from Europe, and the Tasmania population was founded from southern Australia (Bagley & Geller, 2001).

There were surprisingly few reports of *Carcinus* in new locations from 1900 to 1970s and, curiously, all verified records are from the greater Indian Ocean. *Carcinus* specimens collected in the Suez Canal in 1924 at 5 km from the northern end (Calman, 1927) and in 1934 (Monod, 1938) were apparently *C. aestuarii* (Holthuis & Gottlieb, 1958). Three specimens of *C. maenas* were collected in Nossi (Nosy) Be, Madagascar in 1922 (Guinot, 1967; D. Guinot, pers. comm., 1995, 1997). Four large, parasitized (castrated) male *C. maenas* were collected from Maungmagan, Myanmar (Burma) in 1933 (Chopra & Das, 1937; Boschma, 1972). A single male *C. maenas* was collected at Perth, Australia in 1965 (Zeidler, 1978), and a single ovigerous female was collected at Karachi, Pakistan, in the Arabian Sea in 1971 (Tirmizi & Ghani, 1983; Tirmizi & Kazmi, 1996). There are no additional records of *Carcinus* from any of these sites, and thus no indication of the establishment of reproducing populations. The periodic appearance of *Carcinus* in the greater Indian Ocean during the twentieth century could be related to the opening of the Suez Canal in 1869, or to the establishment of a substantial population in southern Australia by the 1920s, or to both. If genetic material can be recovered from these museum specimens (as has been carried out with dried mollusc specimens from the nineteenth century; Geller, 1999), then it may be possible to determine the source population (Bagley & Geller, 2001) and thus the likely transport route of these crabs.

Carcinus' third episode of successful dispersal began in the 1980s. In 1983, crabs identified as *C. maenas* were collected at Table Bay Docks in Cape Town, South Africa. By 1988 these crabs had spread 20 km to the north to Melkboostrand and 15 km south to Camps Bay (Le Roux *et al.*, 1990; Griffiths *et al.*, 1992). *Carcinus* remains established only in the greater Cape Town region; a mating pair found 117 km to the north on a bed of cultured mussels in Saldanha Bay in 1990 remains the only record outside of the Cape Town area, and none have been found at Saldanha since (C. Griffiths, pers. comm., February 2000). Genetic analyses revealed genotypes of both *C. maenas* and *C. aestuarii* at Table Bay Docks, with genetic variability indicative of multiple invasions from the Atlantic and Mediterranean region of Europe (Geller *et al.*, 1997; Bagley & Geller, 2001).

Crabs identified as *C. aestuarii* were collected in Japan in Tokyo Bay in 1984, and in Sagami, Osaka and Dokai bays in the 1990s (Sakai, 1986; Takeda & Horikoshi, 1993; Watanabe, 1997; Furota *et al.*, 1999). The 1959 date given by Sakai for the initial collection of these crabs is incorrect (S. Watanabe, pers. comm., 1997). Genetic analyses revealed genotypes of both *C. maenas* and *C. aestuarii* in Tokyo Bay (Geller *et al.*, 1997). Microsatellite DNA indicates a single invasion by a hybrid population from Europe (Bagley & Geller, 2001), possibly from the transition zone in the western Iberian Peninsula where crabs resembling both *C. maenas* and *C. aestuarii* are found (Almaça, 1961; Geller *et al.*, 1997), or from bays or harbours where the two species have been mixed through human transport.

In 1989–90 crabs identified as *C. maenas* were collected in San Francisco Bay, CA, along with a single large male from the Estero Americano, a small estuary 45 km to the north. By 1993–94 *Carcinus* had spread to five small, nearby estuaries from Elkhorn Slough (Monterey Bay) in the south to Bodega Harbor, CA, in the north, a total distance along the coast of 230 km. *Carcinus* was found in Morro Bay, 200 km south of Elkhorn Slough, in 1998 (E. Grosholz, pers. comm., 1998). From central California *Carcinus* spread rapidly northward (Appendix 1A). Specimens were found in Humboldt Bay, CA, 320 km north of Bodega Bay, in 1995; in Coos Bay, OR, 300 km further, in 1997; in several additional bays in Oregon and in Willapa Bay, WA, and Grays Harbor, WA, reaching 400 km further north, in 1998. Specimens were then found in British Columbia in 1999 and 2000 (Appendix 1A). Multiple generations and considerable numbers of crabs, including some ovigerous females, have been found in some of these embayments. Some of these populations may result from local reproduction, or from recruitment of larvae from central California populations in years with strong northward currents (El Niño events). As of June 2003 it is unclear which locations north of California support established populations.

Genetic analysis of Bodega Harbor crabs indicate that the population was founded from Atlantic North America (Bagley & Geller, 2001).

DISCUSSION

Dispersal mechanisms

Carcinus has been transported around the world by a variety of dispersal mechanisms associated with human activity, with new mechanisms added over time. Natural transport does not appear to have been responsible for founding any of the transoceanic populations. Timing and genetics indicate that the populations in Atlantic North America, Australia, South Africa and Japan were founded from Europe, and the Pacific North American population from Atlantic North America (Bagley & Geller, 2001). *Carcinus* has not been reported from floating algae or wood in the open ocean (Cohen *et al.*, 1995), and in several laboratory studies its planktonic larval period has been found to range from 17–27 days at 25 °C to 44–80 days at 12 °C (Williams, 1968; Dawirs, 1982; Dawirs and Dietrich, 1986; Harms and Seeger, 1989; Mohamedeen and Hartnoll, 1989), with its planktonic period potentially extended a few weeks more by drift of postlarval crabs. Drifting from Europe or North Africa via the Canary Current, North Atlantic Equatorial Current, Antilles Current and Gulf Stream to reach nearshore waters in the vicinity of New York would entail a much longer voyage, including a passage through warm equatorial waters estimated at 120–150 days (Scheltema, 1971) to 200–280 days (Thorson, 1961). The route from Europe to South Africa runs counter to the prevailing current

systems (Sverdrup *et al.*, 1942). The other passages are even less likely. As with most other neritic, and particularly inner shelf, invertebrates, transoceanic and interoceanic dispersal in historical time is largely linked to human transport mechanisms.

Carcinus may have been moved about the world by at least eight different transport mechanisms. These are:

(1) *Ship boring and fouling assemblages*. A number of workers have linked *Carcinus*' dispersal in the nineteenth century to the movement of wooden-hulled vessels which often were extensively bored by shipworms and coated with dense fouling communities (Carlton, 1992; Cohen *et al.*, 1995; Carlton, 1999a). Fulton & Grant (1902) noted that many older vessels 'had been patched up with false bottoms which had become riddled with [the shipworm] *Teredo navalis* and were fouled with marine growths, affording ample shelter for the fry and young crabs on their long voyage'. The change from wooden to iron and steel ships that commenced in the 1880s, effectively began to eliminate these 'internal' boring habitats in the hull. External ship fouling, while vastly reduced in the twentieth century because of the use of effective antifouling paints, faster vessel speeds, and shorter time spent in ports, remains a potential dispersal mechanism.

(2) *Solid Ballast*. *Carcinus* could have been transported among rocks and stones used as solid ballast (Carlton, 1985, 1992) as suggested by G.M. Thomson (in Fulton & Grant, 1900). The damp ballast holds of sailing ships are known to have transported a diverse array of maritime and terrestrial plants and animals (Lindroth, 1957). *Carcinus maenas* can live for at least 94 days without food and resume normal feeding (Perkins *et al.*, 1965, cited in Clay, 1965), can live out of water at least 60 days when sheltered under seaweed, and more than 100 days when kept in bottles with gravel whose interstices are filled with seawater (Perkins, 1967). Thus nineteenth century transport with solid ballast would appear possible. This transport mechanism has become virtually extinct, replaced by the use of water ballast.

(3) *Fouled seawater pipes and sea chests*. In addition to transport on fouled ship hulls, *Carcinus* could be transported among the organisms attached to the interior surfaces of the seawater pipes or sea chests of ocean-going vessels (Carlton, 1985, 1999b).

(4) *Semisubmersible exploratory drilling platforms*. A modern analogue of fouled hulls are the fouled frames of exploratory drilling platforms, which are known to have transported crabs across oceans (Carlton, 1987; Bercaw, 1993). These structures may be deployed at shallow coastal sites for a long period of time, allowing the development of an extensive fouling community, then towed at relatively slow speeds to a new site in a distant part of the world (where, in turn, there is ample time for species to leave the platform). Le Roux *et al.* (1990) suggested that *Carcinus* may have been transported to South Africa by this means.

(5) *Ballast water*. As Cohen *et al.* (1995) noted, *Carcinus* larvae and juveniles are both transportable by ballast water. As noted above, the duration of *C. maenas*' planktonic larval stage is temperature-dependent, ranging from 17 to 80 days. Ship voyages between relevant regions of the globe could range from several weeks to less than 2 weeks, depending upon the route, the type of vessel and the number of port stops (Carlton *et al.*, 1995).

(6) *Seaweed transported with commercial fisheries products*. Baitworms (glycerid and nereid polychaetes) and American lobsters (*Homarus americanus* Milne-Edwards, 1837) are packed in the seaweed *Ascophyllum nodosum* Linnaeus (Le Jolis) and air-shipped to markets in North America, Europe, and elsewhere (Creaser *et al.*, 1983; Carlton, 1992; Lau, 1995; S. Fairservice, pers. comm., 1996). These seaweeds, which harbour an extensive living invertebrate fauna including *C. maenas*, are routinely discarded into coastal and estuarine waters by anglers, lobster importers and possibly restaurateurs (Miller, 1969; Lau, 1995). Cohen *et al.* (1995) described one *C. maenas* shipped with American Atlantic lobsters to the north-eastern Pacific, and we have observed *C. maenas* in baitworm/algae shipments arriving in California from Maine.

(7) *Education/research*. *Carcinus maenas* can be purchased from biological supply houses, which will ship living crabs to many destinations by overnight air express. The popularity of *C. maenas* for experimental biology means that at any given time it is probably present in many college and university aquaria, poised for the escape or release of adults or the discharge of small crabs or larvae in flowing seawater systems, as has been documented for other decapods in academic settings (Cohen *et al.*, 1995).

(8) *Private releases for fisheries purposes*. Finally, members of the public could intentionally transport and release *Carcinus* in order to create new crab fisheries, as has occurred with other crabs (Cohen *et al.*, 1995).

Predictions of future spread and range limits

Given the multitude of potential dispersal mechanisms now operating to transport larval, juvenile, and adult *Carcinus* around the world, and given the potential for shorter-distance dispersal by natural or human-assisted mechanisms once *Carcinus* has become established in a new region, it is likely that these crabs will continue to both spread within the regions they now inhabit outside of Europe and invade new regions.

Cohen *et al.* (1995) reviewed the observational and experimental evidence showing that *C. maenas* has an upper temperature limit in the range of 18 °–26 °C based on temperatures needed for successful reproduction and a lower limit of around 0 °C based on mortality of adult crabs. Gillis *et al.* (2000) also report the death of crabs held in ambient water after an extended exposure to water temperatures of 0–1 °C. Although other physical factors, or

biological factors such as the presence of competitors, predators or disease, can also influence distribution, Cohen *et al.* (1995) concluded that temperature explained the general latitude limits of *C. maenas* in the Atlantic, with equatorial limits characterized by average summer surface temperatures of *c.* 22 °C, and polar limits by average winter ocean surface temperatures of −1 ° to 0 °C (Sverdrup *et al.*, 1942).

If *C. maenas*' potential range limits are in fact set by factors correlated with average summer and winter surface temperatures, then expansions of its populations within the five regions outside of Europe where it now exists will be limited as follows:

(1) In the northwest Atlantic, *C. maenas* will not extend north of the lower Gulf of Saint Lawrence in Canada or south of Chesapeake Bay.
(2) In Australia, *C. maenas* will reach a northern limit in Western Australia around Jurien Bay, and in eastern Australia south of Queensland. All of Tasmania lies within its potential range.
(3) In southern Africa, *C. maenas* could spread north along the west coast to the northern border of Namibia. It will not become established in the Indian Ocean, where summer water temperatures are too high.
(4) In the northwest Pacific, the waters along the north-eastern shore of Honshu, the western shore of Hokkaido, and a part of the North Korean shore in the Sea of Japan, fall within its temperature range. The distribution of the two *Carcinus* species in Japan may ultimately mimic their distribution in the north-eastern Atlantic: *maenas* to the north, *aestuarii* to the south (including the Seto-naikai or Inland Sea, the 'Japanese Mediterranean') with a transitional zone in which crabs of either genotype or hybrids may be found (around Tokyo, corresponding to northern Morocco and the western part of the Iberian Peninsula; Almaça, 1961).
(5) In the northeast Pacific, the potential range limits for *C. maenas* are, to the south, around Magdalena Island, Baja California, Mexico, and to the north, north of the Aleutian Peninsula around 60° N latitude.

These limits correspond generally with the borders of the temperate shelf fauna as described by Ekman (1953). It follows from this analysis that the many sites where one-time collections of *C. maenas* have been reported – the Hawaiian Islands, the Bay of Panama, Rio de Janeiro and Pernambuco in Brazil, the Red Sea, Sri Lanka, Madagascar, Myanmar, Pakistan and possibly Perth in Western Australia – are in retrospect all too warm to support reproducing populations. However, *C. maenas* remains absent from climatically suitable regions including New Zealand and the Pacific and Atlantic coasts of South America from Tierra del Fuego, Chile, to the northern border of Peru and the southern border of Brazil. In all areas, *C. maenas*' potential range may be modified locally by bodies of water with naturally or artificially warmer winter or cooler summer temperatures, or altered on a larger scale by global climate change.

With *C. aestuarii*'s native range bounded within the extent of a largely enclosed sea (the Mediterranean) rather than by latitude along ocean coasts, with a less extensive history of invasion than *C. maenas*, and with considerably less published work on its ecological and physiological tolerances, there is less basis for estimating its potential range. However, *C. aestuarii* could likely become established in regions equatorward of *C. maenas*' potential range, with a transitional zone of overlap.

Episodic dispersal of introduced marine organisms

One hypothesis among several regarding an apparent post-1970s surge in global marine invertebrate, fish, and algal invasions is that the increased invasion rate results from new or intensified transport vectors (Carlton, 1996; Cohen & Carlton, 1998). However, there is little information on earlier periods marked by new or altered patterns of shipping when there may have been similar episodes of global invasions.

Patterns of episodic dispersal have been noted for a few species. Carlton & Scanlon (1985) noted that the Asian green alga *Codium fragile tomentosoides* spread to Europe *c.* 1900, to Atlantic North America in the 1950s, and then to Pacific rim ports in the 1970s. Carlton & Iverson (1981) similarly described episodic synanthropic dispersal for the ship-fouling isopod *S. walkeri*, comprising a pre-1870 period of spread around the Indian Ocean, southern Africa and Australia, a post-1870 period related to the opening of the Suez Canal in 1869, and a post-1940 period coincident with increased ship traffic during and after World War II.

In the present paper, we suggest that *Carcinus* travelled out from Europe in four episodes, first appearing in the Red Sea and North America after 1800, then at several distant global sites in the 1850s–70s, then a period of regional dispersal in the greater Indian Ocean after 1920 (which did not lead to any established populations because the receiving environment was inappropriate), and finally a series of successful leaps to Japan, South Africa and the Pacific Coast of North America (along with a shorter jump from southern Australia to Tasmania) in the 1980s–90s.

The discovery of specimens or populations of *C. maenas* at several widespread locations (Brazil, Panama, Sri Lanka, Hawaii and possibly Australia) around the world between 1857 and 1877 may be related to a post-1850 expansion of world shipping. Global shipping patterns, in terms of increased traffic, increased speed and new and expanded routes, changed rapidly during this period (Natkiel & Preston, 1986). With the advent of the clipper ships as a mainstay, the California and Australian Gold Rushes altered global shipping patterns for over a decade (1849–61, Natkiel & Preston, 1986). The opening of the Suez Canal in 1869 changed shipping patterns again, forcing the Atlantic clipper ships out of the China tea trade (the Red Sea being more suited to steam than sail) and into the Australian wool trade (outward via Cape of Good Hope, homeward via Cape

Horn). During this period many long-distance sailing records were set. For example, in 1853 the *Sovereign of the Seas* sailed from New York to Liverpool in 13 days, and in the 1866 'Great Tea Race' between China and London, three ships sailed 25,000 km in 99 days.

It was during this period that the Atlantic barnacle *Balanus improvisus* Darwin, 1854, was first collected in the northeast Pacific Ocean (in 1853 in San Francisco Bay; Carlton & Zullo, 1969); the Eurasian hydroid *Cordylophora caspia* (Pallas, 1771) was first collected in the northwest Atlantic (in 1860 in Massachusetts; Verrill *et al.*, 1873); the Indian Ocean isopod *S. terebrans* Bates, 1866 and the Eastern Atlantic barnacle *Balanus trigonus* Darwin, 1854 were first collected in the southwest Atlantic (in Brazil in 1866 and 1867, respectively; Zullo, 1992; Carlton & Ruckelshaus, 1997); and the Western Atlantic crab *Rhithropanopeus harrisii* (Gould, 1841) was first collected in Europe (in 1874 in the Netherlands; Buitendijk & Holthuis, 1949).

For many of these species these dates mark the beginning of the next century of their global voyages. Whether proportionally more taxa commenced global spread in the period of the 1850s–70s, as opposed to the first half of the nineteenth century, remains to be investigated. Still to be sorted out are additional factors in the discoveries noted, including the effect of an increasing number of exploratory naturalists deployed in the latter half of the nineteenth century across the rapidly opening – and rapidly changing – seas.

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APPENDIX 1. GLOBAL DISPERSAL AND DISTRIBUTION OF *CARCINUS MAENAS* AND *C. AESTUARII*

(A) Regions with established populations

Europe and North Africa

Carcinus maenas. Native to the Atlantic coast of Europe and Great Britain north to Iceland, the North Sea and Norway to just north of 70° N latitude (Christiansen, 1969); south to Portugal and Spain, and thence to Morocco and the northern border of Mauritania (Monod, 1956, 1967; Forest & Gantes, 1960). Almaça (1961) also identified material from Ceuta, Morocco, just inside the Strait of Gibraltar, as *C. maenas*.

Carcinus aestuarii. Native to the Mediterranean, Marmara and Black seas (Alcock, 1899; Holthuis & Gottlieb, 1958). Holthuis & Gottlieb (1958) also assign Suez Canal records to *C. aestuarii*. Almaça (1961) identified material from the Canary Islands (Heller, 1863) as 'forma *mediterranica*' (*aestuarii*), where it remains 'rare to occasional' in abundance (Perez, 1995).

Atlantic North America

Carcinus maenas. Introduced by 1817 and reported as a new species, *Cancer granulatus* (Say, 1817). Ranges from New Jersey to Prince Edward Island. Prior to the 1870s ranged north only to Cape Cod; starting in the late nineteenth century moved east and north along the Atlantic coast: Provincetown, Massachusetts (MA) by 1872 (Smith, 1879), Boston, MA region and Kittery, Maine (ME) by 1893 (Bryant, 1906), Casco Bay, ME by 1904 (Rathbun, 1905), south of Rockland, ME by 1907 (Glude, 1955), Winter Harbor, ME by 1939 (Scattergood, 1952), Passamaquoddy Bay, New Brunswick by 1951 (Scattergood, 1952), Minas Basin to Wedgeport, Nova Scotia (NS) by 1953–54 (Glude, 1955) and Lockeport, NS by 1961 (Welch, 1968). By the 1960s it was well established in central western Nova Scotia in the Halifax region (Peggy's Cove, 1964, and other locations) (Nova Scotia Museum collections), and *Carcinus* carapaces and claws were found 130 km to the northeast at Marie-Joseph, Guysborough County, in 1982 (D. Davis, pers. comm., 1982, and Nova Scotia Museum collections).

After 16 years with no further reports along the western or north-western Nova Scotia shore, *Carcinus* was detected in 1998 on Cape Breton Island in the Bras d'Or Lakes and along the Gulf of St Lawrence coast. In August 1998, it was reported on the eastern end of Prince Edward Island in St Mary's Bay, and by 1999 was collected at sites from North Lake in the northeast to Gascoigne Cove in the southeast (M. Campbell, pers. comm., 1999; Gillis *et al.*, 2000).

Several workers had earlier reported *C. maenas* from Cape Breton Island and Northumberland Strait, NS (Vermeij, 1982; Williams, 1984, repeated by Squires, 1990; Gillis *et al.*, 2000) and from eastern Nova Scotia (Vermeij, 1982), all based on Bousfield & Laubitz (1972). However, the stations reported by Bousfield and Laubitz are actually from south-western Nova Scotia, within the previously known range.

Records south of New Jersey that may represent transient larval sets derived from northern populations include Delaware Bay (Deevey, 1960: larvae; Leathem & Maurer, 1980; not observed every year), Lewes, Delaware (A. Hines, pers. comm., 1993), and the Atlantic shore of Northampton County, Virginia (Kingsley, 1879). *Carcinus* is not known from Chesapeake Bay.

Genetic analysis of specimens collected at Mystic, CT detected only *C. maenas* haplotypes (Geller *et al.*, 1997).

Australia

Carcinus maenas. Introduced possibly prior to 1877 (Streets, 1877), and abundant in Port Phillip Bay near Melbourne, Victoria by 1900 (Fulton & Grant, 1900, 1902). First found northeast of Victoria in New South Wales in 1971, and west of Victoria near Adelaide, South Australia in 1976. Ranges from near Adelaide to Narooma in southern New South Wales (Fulton & Grant, 1900; Zeidler, 1978, 1988; Rosenzweig, 1984). One specimen collected at Perth in 1965 (Zeidler, 1978), with no further records from Western Australia. Introduced to northeast Tasmania by 1993; ranges from Little Musselroe Bay to Georges Bay (Gardner *et al.*, 1994). Genetic analysis of specimens collected at Falmouth, Tasmania detected only *C. maenas* haplotypes (Geller *et al.*, 1997).

South Africa

Carcinus maenas and C. aestuarii. One or both species, or hybrids, were introduced by 1983 when crabs identified as *C. maenas* were collected at Table Bay Docks, Cape Town. They remain established in the greater Cape Town area. One pair found north in Saldanha Bay in 1990, and none since (Le Roux *et al.*, 1990; C. Griffiths, pers. comm., February 2000). Barnard (1950) had noted that *C. maenas* 'may eventually find its way to South Africa'. Genetic analysis of Cape Town specimens detected haplotypes of both species (Geller *et al.*, 1997).

Japan

Carcinus maenas and C. aestuarii. Hybrids introduced by 1984 when crabs identified as *C. aestuarii* were collected in Tokyo Bay. Spread to Sagami, Osaka and Dokai bays by 1990s [Sakai, 1986 (date of collection incorrectly given as 1959); Takeda & Horikoshi, 1993; Watanabe, 1997; Furota *et al.*, 1999; W. Walton, pers. comm., 1996). Genetic analysis of specimens collected in Tokyo Bay in 1995 detected haplotypes of both species (Geller *et al.*, 1997), with microsatellite DNA indicating a single invasion by hybrids (Bagley & Geller, 2001).

Pacific North America

Carcinus maenas. A 1961 report of *C. maenas* in Willapa Bay, Washington (Ricketts *et al.*, 1968) cannot be confirmed (J. Hedgpeth, pers. comm., 1991) and may represent either a reporting error or an introduction that failed to establish (Cohen *et al.*, 1995), as there were no further records from

the region for 36 years. Similarly, a report of *C. maenas* in Willapa Bay in the 1930s (Niesen, 1997) appears to be in error (T. Niesen, pers. comm., 2001).

The first clear Pacific Coast records are from 1989-90 when *C. maenas* was collected in San Francisco Bay, California (CA), where it is well established (Cohen *et al.*, 1995) and a single 85 mm-wide crab was collected in Estero Americano, CA, 45 km north of San Francisco Bay, in 1989 (J. Roth, pers. comm., 1989; Commins *et al.*, 1990). The latter specimen may not have been part of an established population, as no other *Carcinus* were collected north of San Francisco Bay until 1993, despite collecting and other field activities in the area by students and staff of the Bodega Marine Laboratory, and one trapping effort in Estero Americano in 1992 (Cohen *et al.*, 1995). To the south, *C. maenas* was collected in Elkhorn Slough in Monterey Bay, CA in 1994, where it is established; and a single crab was collected in Morro Bay, CA in 1998 (Grosholz & Ruiz, 1995; E. Grosholz, pers. comm., 1998). To the north of San Francisco Bay, crabs, claws or exuvia were collected in Bolinas Lagoon, Drakes Estero, Tomales Bay, and Bodega Harbor, CA in 1993; Humboldt Bay, CA in 1995; Coquille Bay and Coos Bay, Oregon in 1997; Alsea Bay, Yaquina Bay, Siletz Bay, Salmon River estuary, Netarts Bay and Tillamook Bay in Oregon, and Willapa Bay and Gray's Harbor in Washington, in 1998; Esquimalt Harbor and Barkley Sound on Vancouver Island, British Columbia (BC) in 1999; and Clayoquot Sound, BC in 2000 (Miller, 1996; N. Richmond, pers. comm., 1997; B. Dumbauld, pers. comm., 1998; J. Morrison, pers. comm., 1999 and 2000; Jamieson *et al.*, 1998; Yamada *et al.*, 2001). The crab appears established in Elkhorn Slough, San Francisco Bay, Tomales Bay and Bodega Harbor. Records at some of the other sites may indicate self-sustaining populations, or may result from transient larval sets from populations established elsewhere. Genetic analysis of Bodega Harbor specimens detected only *C. maenas* haplotypes (Geller *et al.*, 1997).

(B) Records in regions without established populations

Indian Ocean

Carcinus maenas collected in the Red Sea by 1817 (Savigny, 1817); one specimen of *Carcinus* sp. in Sri Lanka in 1866 or 1867 (Wood-Mason, 1873); three specimens of *C. maenas* in Madagascar in 1922 (Guinot, 1967, and pers. comm., 1995, 1997); four specimens of *C. maenas* in Myanmar in 1933 (Chopra & Das, 1937; Boschma, 1972); and one specimen of *C. maenas* in the Arabian Sea in Pakistan in 1971 (Tirmizi & Ghani, 1983; Tirmizi & Kazmi, 1996).

Atlantic South America

Carcinus sp. collected at Rio de Janeiro, Brazil in 1857 (Heller, 1865), and off Pernambuco, Brazil before 1899 (Alcock, 1899).

Tropical Pacific

Single specimens of *C. maenas* collected in the Bay of Panama in 1866 (Smith, 1879), and in Hawaii in 1873 (Streets, 1877).