Pacific Northwest aquatic invasive species profile:

the European green crab, *Carcinus maenas* (Linnaeus, 1758)

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Figure 1. Dorsal and ventral (male at left, female at right) views of the European green crab, *Carcinus maenas*.

Figure 2. Color morphs of the European green crab, *Carcinus maenas*.
Diagnostic Information
Scientific name
Order: Decapoda Latreille, 1802
Family: Portunidae Rafinesque, 1815
Genus/Species: Carcinus maenas (Linnaeus, 1758)

Common names: European green crab, European shore crab, green shore crab, green crab, shore crab, Joe rocker

Basic identification key
The European green crab, Carcinus maenas (Fig. 1), is placed within the crustacean order Decapoda, a well–studied group that includes many commercially important species of crabs, lobsters, and shrimps. Within the decapods, C. maenas is considered a true crab of the Infraorder Brachyura and placed in family the Portunidae, the swimming crabs (Martin and Davis 2001). Only two species of Carcinus are currently recognized, C. maenas and the closely–related Mediterranean shore crab, C. aestuarii (Behrens–Yamada and Hauck 2001).

Although known as the European green crab, color is highly variable in this species and therefore a poor character for identification. Individual dorsal coloration is typically mottled and varies from light green/yellow to bright or dark green, olive–brown, or red, with lighter and more mottled coloration typical in small specimens (Crothers 1968; McDonald 2006; Fig. 2). Green crabs and red crabs can be found in all size classes, but the relative proportion of red crabs increases dramatically at sizes > 50–60 mm carapace width (CW) (Wolf 1998; Styrishave et al. 2004). Ventral coloration may be shades of yellow, light green, orange, or red (Behrens–Yamada 2001; Fig. 2).

Figure 3. Diagnostic information used to identify the European green crab. Note: shell width and coloration information indicate typical conditions, but larger sizes and a range of colors have been reported (image courtesy of New South Wales Government).

Regardless of its highly variable coloration, C. maenas is easily identified from other Pacific Northwest (PNW) species by meristic counts and morphology. It is the only PWN species with five teeth, which are evenly spaced along each side of the anterior–lateral margins of the carapace (Behrens–Yamada, 2001; McDonald 2006; Fig. 3). This species also has three lobed, frontal teeth between the eye stalks and a carapace that is nearly as long as it is wide (Behrens–Yamada and Hauck 2001). Among portunid crabs, C. maenas is somewhat anomalous in morphology and behavior, in that it is adapted for walking rather than swimming.
Although its fifth pair of legs are flattened, they are not nearly as flattened as those of other portunids and lack the typical portunid paddle–shape (Jenson 1995; Behrens–Yamada 2001; Fig. 3). *Carcinus maenas* reaches a maximum size of 100 mm CW, with males larger than females (≤ 79 mm CW; Behrens–Yamada et al. 2005).

**Life History and Basic Ecology**

*Life cycle*

Mating in *C. maenas* occurs immediately after adult females moult, typically with males of larger sizes (Behrens–Yamada 2001). In the Pacific Northwest, this commonly occurs during summer months. Prior to moultting, females release a powerful pheremone that attracts males (Bambler and Naylor 1997). An attracted male will grasp the female beneath it and carry her in a precopulatory embrace for two to sixteen days (Behrens–Yamada 2001). After the female moultts, mating occurs during which the male injects sperm packets into the paired gonopores of the female. Stored sperm can remain viable for up to a year (Behrens–Yamada 2001). Since copulation can take almost three days, the mating pair shelters during this time. After copulation, the male continues to hold the female for a time period ranging from less than a day (no other males present) to more than two days (other males present) (Behrens–Yamada 2001).

After mating, a female can produce one or more broods. Eggs are fertilized as they descend the reproductive tract, encased in a sticky membrane, and attached to the hairs of the pleopods where they engulf the abdomen to form a “sponge” (Fig. 4). The number of eggs per brood increases with size of the female (Behrens–Yamada 2001), and > 185,000 eggs have been reported from a relatively small female (Broekhuysen 1936). Brooding females migrate to deeper waters during winter months in the Pacific Northwest where salinity and temperature are more stable and either hide in rocky structure or bury themselves in soft sediments (Dries and Adelung 1982). The duration of brooding is contingent on water temperature. Captive females kept at 12° in a seawater tank in Oregon brooded eggs for just over two months (Behrens–Yamada 2001). During this time, they remove foreign materials from the sponge and aerate the eggs with their pleopods. Hatching typically occurs at night at the ebb of a high tide so that the eggs are carried out to sea (Queiroga et al. 1994; Zeng and...
Naylor 1996a). In the Pacific Northwest, hatching usually occurs during winter months. There are six larval stages in *C. maenas*; one extremely short protozoea stage, four zoea stages, and one megalopa stage (Fig. 5). Total planktonic development is estimated at 62 days at 12° and 32 days at 18° (Dawirs 1985). Vertical migration to surface waters occurs early in the first zoeae stage, which facilitates transport out to sea on the ebb tide (Queiroga et al. 1994). Conversely, late megalopa migrate to the surface just after a low tide and are carried shoreward on high flood tides (Zeng and Naylor 1996b). Settlement and metamorphosis of megalopae occurs in the upper tidal zone to ensure that new recruits are left in the intertidal after the high tide recedes, as refuge against predation. Recruitment in the Pacific Northwest typically takes place during late winter and spring.

Growth rates are highly variable in *C. maenas*, but conditions in the Pacific Northwest favor rapid growth compared to other regions (Table 1). Key thresholds are reported at 7° C, when crabs stop feeding and seek shelter, and 10° C, when crabs stop molting (Ropes 1968; Eriksson and Edlund 1977). Water temperatures in the Pacific Northwest are typically > 10° C for most of the year, facilitating relatively rapid growth and development in this region (Table 1).

Based on data collected in Oregon and Washington during 1998, crabs grew to sizes of 32–60 mm DW at the onset of their first winter, during which growth stopped until May. By the onset of winter 1999, sizes ranged from 52–80 mm CW (Behrens–Yamada et al. 2005), with sizes 60–92 reported during winter 2000 (Behrens–Yamada 2001). This facilitates very short generation times in the Pacific Northwest, typically less than one year as compared to two to three years in Maine (Berrill 1982). Gravid females may be observed in this region from 8–12 months/year (Behrens–Yamada et al. 2005).

**Feeding habits**

Organisms from at least 104 families in 14 animal and 5 plant and protist phyla have been recorded in the diet of *C. maenas* (Cohen et al. 1995). This species is also cannibalistic, and small individuals can be an important food source for larger *C. maenas* (Moksnes et al. 1998). Although such a diverse diet would suggest an opportunistic feeding strategy, *C. maenas* has been shown to select prey by size and species in a substantial number of laboratory experiments (Cohen et al. 1995). Additionally, the diet of *C. maenas* has been shown to vary by size, location, time of year, and occasionally sex.
Therefore, this crab be characterized as having immense dietary plasticity, but exhibits specific prey preferences under different life history and environmental conditions. A sampling of prey items include: bacteria and foraminiferans, carrion, snail eggs, marsh vegetation, algae, polychaetes, crustaceans, insects, bivalves, gastropods, urchins, fishes, tunicates and jellyfishes. *Carcinus maenas* becomes more carnivorous with age and older, larger individuals show a strong preference for bivalves (Behrens–Yamada 2001). This species is a voracious predator and has been shown to consume up to 62.3 bivalves (19–23 mm) per day in laboratory experiments (Palacois and Ferraro 2003).

*Carcinus maenas* is thought to be mainly a tactile and chemo sensory rather than visual predator (Cohen et al. 1995). Visual cues are mainly limited to assessing prey size and detecting moving prey (Hughes and Seed 1995). *Carcinus maenas* commonly excavates buried bivalves and other infauna to depths of 15 cm deep (Smith and Chin 1951). These digging efforts can cause considerable environmental disturbance, and can substantially modify community structure (Congleton et al. 2005; Garbary and Miller 2006).

### Reproductive strategies

Male *C. maenas* exhibit two different reproductive strategies, with trade-offs in reproductive fitness and *C. maenas*, and aggressive encounters are common among males (Styrishave et al. 2004). Long thought to be simply a consequence of different intermoult periods, the red and green coloration in male *C. maenas* are now understood to infer considerable physiological and ecological differences (Reid et al. 1997; Wolf 1998). Red males remain in intermoult for longer durations.

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**Table 1. Comparison of life history characteristics of *Carcinus maenas* from different regions of the world (from Behrens–Yamada et al. 2005)**

<table>
<thead>
<tr>
<th>Location</th>
<th>Ref.</th>
<th>Length of Growing Season, number of months water temperature is above 10 °C</th>
<th>Peak* and range of settlement</th>
<th>CW by first winter (mm)</th>
<th>CW by second winter (mm)</th>
<th>CW of mature female (mm)</th>
<th>Age at first moulting (years)</th>
<th>Maximum carapace width (mm) males</th>
<th>Maximum carapace width (mm) females</th>
<th>Maximum life span (years)</th>
<th>Generation time (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Maine</td>
<td>1</td>
<td>5</td>
<td>September*</td>
<td>3–10</td>
<td>13–28</td>
<td>34</td>
<td>2–3</td>
<td>82</td>
<td>70</td>
<td>5–6</td>
<td>3</td>
</tr>
<tr>
<td>Baltic/Germany</td>
<td>2</td>
<td>6</td>
<td>Sept<em>em</em>ber</td>
<td>7.5</td>
<td>25–45</td>
<td>30</td>
<td>2</td>
<td>75</td>
<td>60</td>
<td>4+</td>
<td>3</td>
</tr>
<tr>
<td>Kattegat/Flemishmark</td>
<td>3</td>
<td>6</td>
<td>Septem*ber</td>
<td>7–11</td>
<td>30–45</td>
<td>30</td>
<td>7</td>
<td>97</td>
<td>4+</td>
<td>4+</td>
<td>1</td>
</tr>
<tr>
<td>Western Sweden</td>
<td>4</td>
<td>6</td>
<td>July–Aug<em>ust</em></td>
<td>5–20</td>
<td>25–55</td>
<td>30</td>
<td>2</td>
<td>100</td>
<td>estimate</td>
<td>4+</td>
<td>2+2</td>
</tr>
<tr>
<td>Southern North Sea</td>
<td>5</td>
<td>7</td>
<td>July*–June*–November*</td>
<td>5–30</td>
<td>35–50</td>
<td>30</td>
<td>1–2</td>
<td>86</td>
<td>70</td>
<td>3–4</td>
<td>1–2</td>
</tr>
<tr>
<td>Oregon/Washington 1998 El Nitto year class</td>
<td>6</td>
<td>8–12</td>
<td>Winter to Spring, estimate</td>
<td>32–60</td>
<td>52–80</td>
<td>32</td>
<td>&lt;1</td>
<td>99.6</td>
<td>79</td>
<td>4–6</td>
<td>1</td>
</tr>
<tr>
<td>Portugal</td>
<td>7</td>
<td>12</td>
<td>Late April–June*</td>
<td>5–30</td>
<td>30–50</td>
<td>21</td>
<td>&lt;1</td>
<td>7.5</td>
<td>estimate</td>
<td>4+</td>
<td>1</td>
</tr>
</tbody>
</table>

developing stronger, thicker carapaces and chelae and routinely winning mating conflicts over similarly-sized green males (Fig. 6). By exerting greater forces with their chelae, red males are also able to eat larger and higher quality prey organisms (Kaiser et al. 1990; Reid et al. 1997). This advantage comes at the cost of reduced physiological tolerance, however. Green crabs are better adapted to living in intertidal regions, to changes in their surrounding environment, and to the effects of pollution (Reid et al. 1997; Styrisolve et al. 2004).

Environmental optima and tolerance

Carcinus maenas exhibits an extremely wide physiological tolerance of temperature but will only persist in a much more limited range. Adult C. maenas can tolerate temperatures between 0° C and 33° C (Eriksson et al. 1975). However, the minimum temperature needed for growth and molting is 10° C (Berrill 1982). Upper temperature limits are 18° C for brooding and 26° C for long-term survival. Therefore, for long term sustainability and population growth, optimal temperatures for C. maenas range from 10° C to 18° C (Behrens–Yamada 2001).

Similarly, although adult C. maenas can tolerate a considerable ranges of salinities, optimum salinity conditions are much narrower. Carcinus maenas can survive at salinities ranging from 4‰ to 54‰ (Eriksson et al. 1975), but are much more affected by low salinities. The minimum salinity for long-term survival is 11‰ (Behrens–Yamada 2001). Additionally, there is a trade-off between salinity and temperature tolerances. Carcinus maenas is also well adapted to low oxygen conditions and can survive at low tide in near anoxic tide pools (Klein–Breteler 1981).

Recruitment is an important part of the life history of C. maenas and megalopae prefer to recruit to protected upper-intertidal habitats.

Figure 6. Color–based mating trials (Reid et al. 1997).
New recruits are typically found in sea grass bed, on filamentous green algae, in muddy regions, along cord grass banks, in mussel beds, and in gravel beds. *Carcinus maenas* does not typically recruit to sandy habitats (Klein–Breteler, 1976). Mussel beds have been reported as optimum habitat for recruits as they provide a natural refuge from predators as well as abundant food resources (Thiel and Dernedde 1994; Gunther, 1996). However, it seems that survival of new recruits is actually greater in filamentous algae, whereas predatory juvenile crabs move preferentially to mussel beds (Hedvall et al. 1998).

Adult *C. maenas* are common in protected marine and estuarine habitats to depths of 60 m (typically < 6 m), but are scarce in high-energy, outer–coast regions (Cohen et al. 1995). This is especially true in the Pacific Northwest, where the occurrence of *C. maenas* is limited to bays and estuaries (Behrens–Yamada 2001). Adults typically occur on rocky shores, under rocks, in macroalgae or eelgrass beds, in marshes, or burrowed into cordgrass beds (Behrens–Yamada 2001). *Carcinus maenas* is itinerant, and does not maintain a permanent home shelter (Singh 1991). Juveniles and young adults can live above the high water mark in marsh burrows or under algae for up to 10 days. As crabs grow, they occupy lower portions of their depth ranges, moving from intertidal regions to the subtidal zone (Behrens–Yamada 2001). Additionally, intertidal regions are more typically occupied during summer and of lowest abundance in winter (Aagaard et al. 1995).

**Biotic associations**

*Carcinus maenas* has a variety of parasites and pathogens in its home range and in other invaded regions, but largely exhibits an enemy release in the Pacific Northwest (Torchin et al. 2001). This is likely one of the reasons why *C. maenas* individuals in the Pacific Northwest are largest recorded (McDonald 2006). In its native habitat, parasites include: the protozoan *Thelohaninia maenadis*, the flatworms *Fecampia erythrocephala*, *Microphallus similis* and *M. primas*, the acanthocephalan *Profilicollis botulus*, the nemerteans *Carcinonemertes carcinophila*, the parasitic barnacle *Sacculina carcini*, the isopod *Portunion maenadis*, the dinoflagellate *Hematodinium perezi*, and nicothoid copepods (Behrens–Yamada 2001; Stentiford and Feist 2005). Additionally, filamentous bacteria and ciliates have been detected on the gill lamellae of *C. maenas* (Stentiford and Feist 2005). One parasite that has affected California populations of *C. maenas* is *Carcinonemertes epialti*, which is native to the West Coast of the United States. This nemerteans worm is an egg predator that typically preys on native crabs, but has infected the *C. maenas* population in Bodega Harbor with 11–93% prevalence depending on sex and season (Torchin et al. 1996). To date, this parasite has not been reported in *C. maenas* populations for the Pacific Northwest.
Pathogens in *C. maenas* include baculoviruses, a parovirus, reoviruses, and a bunyalike virus (Brock and Lightner 1990).

**Current Geographic Distribution**

*Carcinus maenas* is currently found along the Northeast and West coasts of North America. In the northeast, it is distributed continuously from Virginia (Perry 2009) to Nova Scotia (Cameron 2003; Fig. 7). The West Coast distribution of *C. maenas* is much more patchy. In this region, it is confined to estuaries, bays, and other protected coastal and inland waters from Morro Bay, California to the west coast of Vancouver Island, British Columbia (Fig. 7; Behrens–Yamada 2001; Behrens–Yamada and Gillespie 2008).

In the Pacific Northwest, *C. maenas* is established in several coastal estuaries and wave–protected embayments in Oregon, Washington, and along the west coast of Vancouver Island (McDonald 2006). Its range in this region extends from the Coquille River, Oregon to Kyoquot Sound, British Columbia (Behrens–Yamada and Gillespie 2008; Fig. 8). Contrary to McDonald, 2006, it has not been reported from the inland sea between Vancouver Island and the mainland (Behrens–Yamada and Gillespie, 2008). Population levels are still believed to be relatively low in the Pacific Northwest compared to the Northeast, though it has established breeding populations throughout the region (Behrens–Yamada and Gillespie 2008).
History of Invasiveness

Carcinus maenas is native to the Atlantic shores of Europe, the North Sea, and the western Baltic Sea (Carlton and Cohen 2003). Its natural range also includes Northwest Africa from Morocco to Mauritania, the Faroe Islands, the British Isles, southern Iceland, and northern Norway (Fig. 9). In total, the native range spans 49° of latitude (Behrens–Yamada 2001).

Carcinus maenas was first reported outside of its native range from the Red Sea 1817, but did not establish a viable population (Carlton and Cohen 2003). During the same year, it was reported from the east coast of the United States but a specific location was not provided. By 1871, C. maenas was distributed from New Jersey to Cape Cod, Massachusetts. It reached Maine in the 1890s and the Canadian border in 1951. By the late 1990s it had reached the eastern shore of Prince Edward Island and is now found throughout Nova Scotia (Cameron 2003; Carlton and Cohen 2003).

Several additional reports of introductions are available during the 1800s. In the mid century, C. maenas was collected from Rio de Janeiro, Brazil (1857), the Bay of Panama (1866), Sri Lanka (1866 or 1867), and the Hawaiian Islands (1873). By the turn of the century, it had also been reported in Pernambuco, Brazil, but no collection date was given. All these introductions failed to establish viable populations (Carlton and Cohen 2003).

In Australia, C. maenas was reported as abundant around Port Phillip, Victoria in 1900, but information regarding its initial occurrence is vague (Carlton and Cohen 2003). It may have arrived by the 1870s or 1880s but remained a small founder population at that time. After a
long quiescent period, much like the situation in the Northwest Atlantic, *C. maenas* dispersed along the Australian coast. In 1971 and 1976, it was reported to the north and west of Victoria, respectively. It reached Tasmania in 1993 (Carlton and Cohen 2003). During the early to mid 20th century, there were few reports of *C. maenas* from new locations. All verified records are from the greater Indian Ocean, including: Nossi, Madagascar (1922); Maungmagan, Myanmar (1933); Perth Australia (1965); Karachi, Pakistan (1971). None of these introductions resulted in established populations (Carlton and Cohen 2003).

South Africa was invaded by *C. maenas* in 1983, when this species was collected at Table Bay, Cape Town (Cohen and Carlton 2003). By 1988, it had spread north to Melkboosstrand (20 km) and south to Camps Bay (15 km). This remains the established range, and an observation 117 km north of Cape Town is the only record outside the area of original spread (Carlton and Cohen 2003).

Green crabs identified as *C. aestuarii* were collected in Tokyo Bay, Japan during 1984 and in Sagami, Osaka, and Dokai bay in the 1990s (Cohen and Carlton 2003). However, recent genetic evidence has shown this invasion to actually consist of a hybrid of *C. maenas* and *C. aestuarii*. It has not spread outside these extremely polluted bays, possibly because of biotic resistance from a high diversity of native crabs (Behrens–Yamada 2001).

The west coast of the United States was invaded in the late 20th century. An established population was discovered in San Francisco Bay in 1989, indicating a much earlier, unnoticed arrival (Cohen et al. 1995). Molecular evidence indicated that the founding population was from the east coast of the United States (Bagley and Geller 2000). Also in 1989, a single individual of *C. maenas* was collected from Estero Americano, a small estuary 45 km to the north (Carlton and Cohen 2003). During 1993, newly recruited *C. maenas* spread north to Bolinas Lagoon, Drakes Estero, Tomales Bay, and Bodega Harbor (80 km north of San Francisco Bay) (Grosholz and Ruiz 1995). By 1994, it was
observed 150 km south of San Francisco at Elkhorn Slough and by 1998, it had reached Morro Bay, 220 km further (Carlton and Cohen 2003). This embayment remains the southern extent of its West Coast distribution. Northward expansion was more rapid and extensive. Specimens were found in Humboldt Bay, 320 km north of Bodega Bay, in 1995. Based on observations of early adult crabs in Coos Bay (300 km north of Humboldt Bay), Oregon during 1997 and sightings of the same cohort in five more Oregon estuaries, Willapa Bay and Grays Harbor, WA during 1998 (400 km from Coos Bay), it was deduced that a colonization event occurred in the Pacific Northwest during 1995 or 1996 (Behrens–Yamada 2001; Carlton and Cohen 2003). *Carcinus maenas* was subsequently reported in British Columbia in 1999 and 2000 and now ranges throughout the west coast of Vancouver Island (Behrens–Yamada and Gillespie 2008). In 2003, *C. maenas* was found in Camarones Bay, Argentina, on the Atlantic coast of Patagonia (Hidalgo et al. 2005). Size frequency distributions and reproductive condition of females indicated that the introduction had occurred at least 3–4 years prior to discovery and that the population was established (Hidalgo et al. 2005). Niche modeling indicates a potential distribution on the east coast of South America from southern Brazil (29° S) to the Magellan Strait (52° S) (Hidalgo et al. 2005).

**Invasion Process**

*Pathways, vectors, and routes of introduction*

Anthropogenic activities have been solely implicated in the transoceanic introductions of *C. maenas* (Carlton and Cohen 2003). Rafting via floating algae, wood, or other flotsam has not been observed for this species and planktonic larval duration is not long enough to facilitate the type of extreme long distance dispersal necessary to transport ocean basins (Cohen et al. 1995; Carlton and Cohen 2003). International trade is a primary invasion pathway for *C. maenas*, and shipping has been implicated as the likely vector for several introductions. Ship boring and fouling or solid ballast transport are the probable mechanisms for all invasions noted during the 1800s (Carlton and Cohen 2003). During the early and mid 1900s, the opening of the Suez Canal (1969) is the likely source of several failed introductions to the Indian Ocean, and ballast water began to be a major transport vector during this time (Carlton and Cohen 2003). Introduction of *C. maenas* to South Africa was also believed to have occurred several times via shipping vectors from the Northeast Atlantic, whereas the introduction of hybrid *Carcinus* to Japan is believed to be from a single shipping event from Europe (Bagley and Geller 2001; Roman 2006). Expansion of *C. maenas* to Canada, often believed to be directly from expansion of the Northwest Atlantic invasion, was actually augmented by multiple invasions via shipping events from the Northeast Atlantic (Roman...
The introduction of *C. maenas* to Argentina was also from a shipping vector, either through ballast water or hull fouling (Hidalgo et al. 2005). The Argentina introduction, like those of South Africa and Canada, was from a secondary invasion, in this case from Australia (Darling et al. 2008). By contrast, the source the *C. maenas* introduction to San Francisco Bay is considered to be either the live seafood or bait trade. The donor region for the San Francisco introduction was determined to be the Northwest Atlantic, precluding ocean shipping as a possible vector (Bagley and Geller 2001). Lobsters (*Homarus americanus*) and baitworms (glycerid and nereid polychaetes) are routinely packed in seaweed and shipped cross-country and *C. maenas* has been observed hitchhiking on such shipments to California. The seaweed is routinely discarded into coastal and estuarine waters by anglers and restaurant owners (Carlton and Cohen 2003). Additional transport mechanisms of *C. maenas* that have not been specifically implicated in introductions include: 1) fouled seawater pipes or sea chests, and 2) the movement of fouled frames of exploratory drilling platforms, and 3) scientific research activities. *Carcinus maenas* is routinely used in experimental studies and escape, accidental release, or intentional release are all possible introduction vectors (Carlton and Cohen, 2003). The relatively small size of *C. maenas* has so far precluded stocking to create fisheries or for aquaculture purposes, though a substantial bait fishery is active in the southern UK and has led to the transport of crabs within its native range (Sheehan et al. 2008).

**Factors influencing establishment and spread**

Factors influencing establishment of *C. maenas* are largely based on a combination of physiological suitability, environmental suitability, and propagule pressure. Like many invasive marine species, *C. maenas* has typically become established in large, international shipping ports where propagule number is likely to be maximized (Behrens–Yamada 2001). Furthermore, because crabs are short-lived broadcast spawners, the persistence of introduced populations is dependent upon local recruitment (Behrens–Yamada 2001; Behrens–Yamada and Gillespie 2008). *Carcinus maenas* populations therefore typically establish in sites where larvae are more likely to be retained and not flushed out to sea (Cohen et al. 1995; Banas et al. 2009). Although larval supply from regional populations is a key factor in increasing genetic diversity and facilitating local population establishment, local reproduction and recruitment in these “closed” embayments may be enough to maintain a population (Behrens–Yamada et al. 2005). Because of their trophic plasticity, food resources are unlikely to be a limiting factor to establishment of *C. maenas* (Cohen et al. 1995). However, habitat selection is a key factor in determining recruitment success, as mortality of newly settled crabs is lowest in algal habitats or mussel beds of inshore or protected coastal regions (Gunther
In other habitats, predation pressure or wave surge may severely impact recruitment success. Although there have been many tropical introductions, all have failed largely because they are above the 18°C threshold needed for sustainability (Behrens-Yamada 2001, Carlton and Cohen 2003). Spread of *C. maenas* can occur naturally or may be mediated by human vectors, and often occurs after a considerable lag time. Once a founding population is of sufficient size, it can produce enough larvae to seed additional sites via current transport (Behrens-Yamada 2001). Larval dispersal is thus the dominant mechanism for range expansion. However, the previously identified human vectors that result in introductions (e.g., live seafood trade, hull fouling, ballast water) have also been shown to supplement the regional spread of *C. maenas* (Carlton and Cohen 2003). The spread of *C. maenas* is typically episodic. Once established, it may take decades before a *C. maenas* population to build up sufficient propagule size to expand its range (Behrens–Yamada 2001). For example, in both the Northwest Atlantic and Australia, *C. maenas* spread after a long quiescent period (Carlton and Cohen 2003). Additionally, even well established populations of *C. maenas* can exhibit cycles of range contractions and expansion. In the Northwest Atlantic, for example, *C. maenas* range contracts after unusually cold winters but expand again when temperature regimes are more favorable (Behrens–Yamada 2001).

The invasion of the Pacific Northwest by *C. maenas* was greatly augmented by anomalously strong northern currents associated with the 1997/1998 ENSO event (Jamieson et al. 2002; Behrens–Yamada and Gillespie 2008). During this time, currents of up to 50 km/day resulted in a considerable northward population expansion of *C. maenas* to Oregon, Washington, and British Columbia from California populations (Yamada et al. 2005; Tepolt et al. 2009). Although populations persist, temperature regimes and current patterns have not facilitated northern larval transport in subsequent years (Behrens–Yamada and Gillespie 2008). Another northern colonization event could occur with the next ENSO, however, as warm years with favorable currents have been linked to increased larval production, survival, and dispersal in *C. maenas* regardless of location (Behrens–Yamada 2001). Under these circumstances, introductions of *C. maenas* are likely throughout expanded regions of British Columbia and into Alaska, as temperatures in these regions are adequate for their long-term persistence (Carlton and Cohen 2003). Ocean warming will serve a similar function in promoting northern population expansion of *C. maenas*. Although currents are the dominant mechanism of spread in the Pacific Northwest, anthropogenic vectors could play a critical role in spreading *C. maenas* to the inland waters of Puget Sound and Dixon Strait (Behrens–Yamada 2001).
Potential ecological and/or economic impacts

Ecological impacts of *C. maenas* are considerable in some regions, and include effects of predation, competition, and behavior. *Carcinus maenas* can decimate bivalve populations when it is present in high numbers as a result of its high consumption rate compared to most other comparably sized crab species (Behrens–Yamada 2001). One such example is the invasion meltdown scenario created by *C. maenas*’ preference for native clams (*Nutricola* spp.) over an introduced species (*Gemma gemma*). A minor component of bay and estuarine communities since its introduction over 50 years ago, populations of *G. gemma* have rapidly spread and greatly increased as a result of competitive release in accordance with the arrival and spread of *C. maenas* (Grosholz 2005). The long–term occurrence of *C. maenas* has also resulted in shell thickening in Northwest Atlantic bivalve prey species such as *Mytilus edulis* and *Littorina obtusa* at energetic and developmental costs (Freeman and Byers 2006; Brookes and Rochette 2007). In addition to single–species impacts, *C. maenas* predation can modify community structure in intertidal sandflats through predation and prey excavation (Grosholz and Ruiz 1995), and can substantially reduce population size of newly recruited flatfish (Taylor 2005). Foraging and burrowing (sheltering) behavior of *C. maenas* can also have considerable negative effects on eelgrass beds and are especially disruptive to transplants, thereby directly impacting restoration efforts (Davis et al. 1998; Garbary and Miller 2006). This species is a superior competitor for food over the native blue crab, *Callinectes sapidus*, in the Northeast United States, and the yellow shore crab (*Hemigrapsus oregonesis*) on the West Coast which may result in energetic losses to the natives (MacDonald et al. 2007).

The ecological impact of *C. maenas* on the West Coast appears to be mitigated in relation to other regions through biotic resistance from a comparatively rich native crab fauna. This is especially true of comparisons to the Northwest Atlantic. For instance, whereas nine species of crabs or crab–like anomurans have been recorded form intertidal zones of Maine, twenty–six are found in Washington at similar latitudes (Jensen et al. 2002). As a result of competition and especially predation with a richer native fauna, *C. maenas* has been excluded from hard substrates on the West Coast and is further restricted within soft bottom regions of inshore waters to shallow sloughs and mudflats far from the main channels (Jensen et al. 2007). *Cancer productus* and to a lesser extent *C. antennarius* are the species largely controlling the distribution of *C. maenas* on the West Coast through predation (Jensen et al. 2007). *Hemigrapsus oregonesis* is competitively dominant over *C. maenas* in contests for shelter and further excludes it from complex habitat in intertidal regions (Jensen et al. 2002). In addition, the Asian shore crab (*H. sanguineus*) has been shown to outcompete *C.
*maenas* for both food and shelter in the Northwest Atlantic, where it has recently been introduced (Jensen et al. 2002; Griffen et al. 2008). The introduction of *H. sanguineus* to the West Coast would therefore probably further impact *C. maenas* populations. In West Coast regions where *C. maenas* has established, however, it reaches larger sizes than it does at distant locations where it has a much broader habitat distribution, such as South Africa and the Northwest Atlantic (Grosholz and Ruiz 1996). *Carcinus maenas* may therefore limit biotic resistance in the West Coast by occupying intertidal habitats with high intertidal area-to-boundary ratios where it is especially robust because of predatory release from parasites. In these warmer, shallow regions *C. maenas* can occur at high densities and under such conditions will have intense, localized effects on benthic community structure and stability (Jensen et al. 2007). Such are the scenarios on sandy intertidal regions of Bodega Bay and muddy intertidal regions of San Francisco Bay (Grosholz and Ruiz 1995; Grosholz 2005).

Economic impacts of *C. maenas* are primarily associated with reductions in population sizes of commercially important bivalve species. The most cited example concerns the decimation of the soft-shelled clam (*Mya arenaria*) fishery in New England during the mid 1900s (Glude 1955). Although specific estimates of economic losses are not available, clam landings dropped from 6,664 metric tons in 1938 to 1,043 metric tons in 1959 in association with expanding *C. maenas* populations. Other factors such as increasing temperatures, disease, or the effects of other predators may have contributed, but losses in clam harvests occurred eight years earlier in Massachusetts than Maine and correspond well with the northward spread of *C. maenas* (Smith 1950; Glude 1955). Additionally, in the North Sea, *C. maenas* predation on commercially important cockles (*Cerastoderma edule*) and clams (*Macoma balthica, M. arenaria*) severely impacts recruitment, especially during mild winters (Jensen and Jensen 1985). Recently, it has been demonstrated that *C. maenas* may negatively impact populations of newly recruited American lobsters (*Homerus americanus*) through predation (Rossong et al. 2006). However, *C. maenas* is also prey for larger size classes of lobster and this association is of greater magnitude (League–Pike and Shulman 2009; Lynch and Rochette 2009).

On the West Coast of North America, there is currently no evidence that *C. maenas* is causing significant economic impacts (Jensen et al. 2007). Although Lafferty and Kuris (1996) claimed that damage to commercial and recreational fisheries and aquaculture by *C. maenas* could exceed $40 million/year in this region, economic losses thus far are limited to damage in 1993 sustained by one mariculture operation in Tomales Bay (Behrens–Yamada 2001). This resulted in harvest reductions of 23% (1.6 kg/bag) of cultured Manila clams (*Venerupis philippinarum*). The primary reason
for these limited effects on the West Coast is low abundance of *C. maenas* compared to other regions. Reported densities range from up to 500/m² on the east coast of North America (MacPhail 1955) to lows of 0.04–0.4/m² in Bodega Bay, California (Grosholz et al. 2000). Furthermore, densities in the Pacific Northwest are even lower than they are in Bodega Bay (Behrens–Yamada 2001). If West Coast populations increase, however, several commercially important species could be affected (Table 2). In addition to bivalves, there is some concern that *C. maenas* could impact Dungeness crab (*Cancer magister*) and flatfish fisheries in the Pacific Northwest through predation on new recruits (Lafferty and Kuris 1996; Jamieson et al. 1998).

### Table 2. Commercial and recreational species on the west coast of North America that could be impacted by *Carcinus maenas* (after Behrens-Yamada, 2001)

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Landings (mt)</th>
<th>$US</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pacific oyster</td>
<td>Crassostrea gigas</td>
<td>8,400</td>
<td>25,000,000</td>
</tr>
<tr>
<td>Manila clam</td>
<td>Venerupis philippinarum</td>
<td>3,448</td>
<td>14,800,000</td>
</tr>
<tr>
<td>Geoduck</td>
<td>Panopea abrupta</td>
<td>4,027</td>
<td>34,500,000</td>
</tr>
<tr>
<td>Native littleneck</td>
<td>Prothaca staminea</td>
<td>164</td>
<td>320,000</td>
</tr>
<tr>
<td>Butter clam</td>
<td>Saxidomis gigantes</td>
<td>1,280</td>
<td>113,000</td>
</tr>
<tr>
<td>Cockle</td>
<td>Clinocardium nuttalli</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bent-nose clam</td>
<td>macoma nasuta</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baltic Macoma</td>
<td>macoma bathica</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eastern soft-shell</td>
<td>Mya arenaria</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gaper clam</td>
<td>Tresus sp.</td>
<td>8</td>
<td>10,000</td>
</tr>
<tr>
<td>Dungeness crab</td>
<td>Cancer magister</td>
<td>25,000</td>
<td>133,000,000</td>
</tr>
<tr>
<td>English sole</td>
<td>Pleuronectes vetulus</td>
<td>2,100</td>
<td>1,500,000</td>
</tr>
</tbody>
</table>

### Management Strategies and Control Methods

Management and control of widespread marine species, such as *C. maenas*, is extremely difficult. Eradication is not a viable option for *C. maenas* because adults are highly mobile (up to 15 km; Gomes, 1991) and larvae are planktonic. Since *C. maenas* has spread to establish satellite locations, removal of adults at one site will have no lasting effect as colonists from adjacent sites will keep arriving. For the same reason, containment efforts are also unlikely to be successful. Control is therefore the only viable option (Behrens–Yamada 2001). Many control methods have been investigated for *C. maenas*, but none have proven effective. Poisoned bait was tested in Maine but had little impact and may cause unintentional detrimental environmental and biological effects (Hanks 1961). Fishing is a potential method for controlling *C. maenas* populations, but this too has proven ineffective in practice. Long–term fisheries have existed in Venice Lagoon, Italy and Ria de Aveiro, Portugal with no pronounced long–term effects on abundance (Varagnolo 1968; Gomes 1991). In addition, a bait fishery for *C. maenas* in the southwest United Kingdom has significantly increased abundance, apparently because the tiles used to catch crabs also serve as artificial habitat (Sheehan et al. 2008). In Massachusetts and Maine, where *C. maenas* is extremely common, communities have offered bounties for crabs or have required
clam diggers to collect crabs before being issued a harvesting permit (Behrens–Yamada 2001). Trapping programs have also been conducted in municipalities on Martha’s Vineyard, but have proven ineffective (Walton 2000). Biological control has been proposed for *C. maenas*, but has not been implemented. *Carcinus maenas* has apparently undergone a predatory release in the Pacific Northwest and is largely free from parasites (Torchin et al. 2001). Parasitic castrators (e.g., *Sacculina carcini*, *Portunion meanadis*) and egg predators (*Carcinonemertes* spp., nicothoid copepods) therefore hold promise as control agents, but are not host specific and therefore could have considerable unintended negative consequence to native crab fauna (Behrens–Yamada 2001). Much more research is needed before biological control agents can be considered a viable possibility. Biological control may be better accomplished by enhancing habitat of native crabs who are predators and competitors of *C. maenas* (Behrens–Yamada 2001).

Although management and control of *C. maenas* have not been historically effective, some strategies have been developed both federally and in the Pacific Northwest. In 1998, *C. maenas* was formally recognized as an Aquatic Nuisance Species (ANS) by the Federal ANS Task Force (a national coordinating body). In 2002, a United States management plan for *C. maenas* was completed by the “Green Crab Control Committee,” edited by E. Grosholz and G. Ruiz, and submitted to the ANS Task Force. The document is extensive and evaluates management options for prevention, eradication, and control. It has not been implemented, however. In reaction to the designation of *C. maenas* as an ANS in 1998 and just prior to invasion, Washington made it illegal to possess or transport live *C. maenas*. Washington Department of Fish and Wildlife (WDFW) monitoring and control programs were also initiated in Willapa Bay and Grays Harbor in 1998, after *C. maenas* was locally discovered (Figlar–Barnes et al. 2001). Trapping efforts led to the capture of 94–303 crabs during 1998–2002. However, budget cuts in 2002 curtailed the program and the *C. maenas* population in this region has persisted and become self–sustaining (Behrens–Yamada et al. 2005). During 1998, WDFW established a task force to develop prevention and control strategies for zebra mussels and and *C. maenas* and this effort is ongoing.

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Other Key Sources of Information

10. Pacific States Marine Fisheries Commission – Aquatic Nuisance Species Prevention Program: [http://www.psmfc.org/Aquatic_Nuisance_Species_Prevention_Program](http://www.psmfc.org/Aquatic_Nuisance_Species_Prevention_Program)
12. Smithsonian Environmental Research Center:
   http://www.serc.si.edu/labs/marine_invasions/population_ecology/carcinus.aspx
13. USDA National Invasive Species Information Center – Aquatic Species:
   http://www.invasivespeciesinfo.gov/aquatics/greencrab.shtml
14. USGS – Non–Indigenous Aquatic Species:
15. Washington Sea Grant:
   http://www.wsg.washington.edu/mas/ecohealth/invasive_crabs/green_crab.html
16. WDFW – Aquatic Nuisance Species:

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Current Research and Management Efforts

Current research efforts focused on *C. maenas* are extensive throughout its global range. Topics of interest are widespread and include life history, genetics, parasitology, ecology, and aspects of invasion ecology (e.g., invasion history, ecological and economic impacts, biotic resistance), among others. There is no paucity of literature on this species, as literally hundred of peer reviewed publications are available. Most of the ongoing research on this species in the Pacific Northwest is being conducted by the scientists identified in the previous section of this document.

Although *C. maenas* has been afforded a substantial amount of scientific attention, federal and regional management efforts are lacking. The 2002 federal management plan has not been implemented. Possession of *C. maenas* in California and Oregon is prohibited, but no other management strategies are in place in these states. There are currently no laws in Alaska barring importation of *C. maenas* nor a management plan for this species. No government laws regarding *C. maenas* were found for British Columbia, although a risk assessment was prepared by the Oceans and Fisheries Department in Nanaimo, and monitoring is being conducted (Behrens–Yamada and Gillespie 2008). It is still illegal to possess or transport live *C. maenas* in Washington; however, funding for the previously discussed monitoring and control plan was curtailed in 2002 because of budget cuts. The WDFW now relies on volunteers and shellfish growers to monitor established *C. maenas* populations in Willapa Bay, Grays Harbor, and a potential introduction to Puget Sound. Biological and chemical methods to control *C. maenas* have been proposed through a WDFW task force and recent published literature. However, basic research necessary for the implementation of these methods is lacking. The most effective control or eradication measure available will be implemented in the event of a *C. maenas* introduction to Puget Sound.