

Review

Population Dynamics of Green Crabs (*Carcinus maenas*) – A Review

Alan M. Young¹, James A. Elliott²

¹ Biology Department, Salem State University, Salem, Massachusetts, USA;
ayoung@salemstate.edu

² School of Forest Resources, University of Maine, Orono, Maine, USA;
jameselliott978@gmail.com

* correspondence: ayoung@salemstate.edu

Abstract: *Carcinus maenas* (the “shore crab” or “European green crab”) is a very proficient invader (considered to be one of the world’s 100 worst invaders by the IUCN) due to its phenotypic plasticity, wide temperature and salinity tolerance, and an extensive omnivorous diet. Native to Atlantic Europe, it has established two well-studied nonindigenous populations in the northwestern Atlantic and northeastern Pacific and less-studied populations in Australia, Argentina and South Africa. Green crabs are eurythermal and euryhaline as adults, but they are limited to temperate coastlines due to more restrictive temperature requirements for breeding and larval development. They cannot tolerate wave-swept open shores so are found in wave-protected sheltered bays, estuaries and harbors. *C. maenas* has been the subject of numerous papers, with over 1000 published in the past decade. This literature review provides an up-to-date account of the current published information on the population dynamics of this very important species, including habitat preferences, physical parameter tolerances, reproduction and larval development, sizes of crabs, densities of populations, sex ratios, ecosystem dynamics and ecological impacts in the various established global populations of green crabs.

Keywords: *Carcinus maenas*; shore crab; European green crab; population dynamics

1. Introduction

1.1 Native European Population

The native range of *Carcinus maenas* (commonly known as the “shore crab”) is the

northeast Atlantic coastline, from Mauritania in northern Africa to Norway, the British Isles and Iceland [1-5]. It is the most common intertidal decapod crustacean in Europe. In its native region, *C. maenas* is considered to be an important and profitable species, commercially fished for use as bait or food [6, 7]. A decade ago the biology and population dynamics of *C. maenas* in the UK was reviewed in response to concerns that its abundance was declining due to overfishing and a maintenance program might be needed to insure sustainability [7]. In contrast, in other parts of the globe *C. maenas* is thought of as a very destructive invasive species and is considered to be one of the world's 100 worst invaders by the International Union for the Conservation of Nature (IUCN) [8-12]. It was the first marine organism to be designated as an aquatic nuisance species by the Aquatic Nuisance Species Task Force (ANSTF) [13]. There are invasive populations in various locations throughout the world, where the species is referred to as the "European green crab," just "green crab" or sometimes the "European shore crab" (see reviews of [3, 14-16]). Three distinct lineages have been identified within the native range, a northern Europe lineage found north of the Netherlands, a southern Europe lineage found from the Netherlands south, and a third lineage found off the continental shelf in the Faeroe Islands and Iceland [4].

1.2 Northwestern Atlantic Nonindigenous Population

Carcinus maenas was introduced to the mid-Atlantic United States (location not given but assumed to be New Jersey or New York) in 1817, presumably carried in solid ballast or on the outside of wooden ship hulls [3, 5, 17-21]. The range now extends over approximately 1,000 – 1,200 kilometers of coastline [12, 22, 23]. It spread southward to Chincoteague Bay, Virginia, with occasional sightings of individuals further south, but further southward expansion of the population apparently is limited by both temperature and the predatory blue crab *Callinectes sapidus* [24]. The range has expanded mostly northward, arriving in northeastern Massachusetts, New Hampshire, and southern Maine waters in the 1890s or early 1900s, and eventually to southern Nova Scotia, Canada by the early 1950s and Prince Edward Island by 1997 [3, 15, 16, 25-29]. *Carcinus maenas* was found in Newfoundland in 2007 [10], but it is likely that this population represents subsequent invasions, beginning in 1980, of five new haplotypes from northern Europe, probably Norway, rather than a northward expansion of the single southern European lineage haplotype introduced in 1817 [5, 11, 30-35]. A single haplotype comprising 30% of the Nova Scotia population is found only in the area of Mongstad and Trondheim in

Norway, a center for Norwegian oil trade, and oil tankers from Mongstad dock frequently in the Strait of Canso superport in Nova Scotia, making tanker ballast water carrying *C. maenas* larvae the likely transmission route for the recent northern Europe lineage invasion into northern Nova Scotia [30].

1.3 Northeastern Pacific Nonindigenous Population

In 1989-90 a few individuals were found on the northeastern Pacific coast, in San Francisco Bay in California. They spread only 125 km southward to Elkhorn Slough in the Monterey Bay area but over 1500 km northward in just 12 years, reaching Oregon in 1995-1996, British Columbia, Canada in 1998 and more recently Vancouver Island in 2005 and Gales Passage, mainland British Columbia by 2015 [15, 22, 36-38]. This population contains the single haplotype found in the northwest Atlantic population south of Nova Scotia so is almost certainly a secondary introduction from that population to the northeastern Pacific coastline [11, 30]. The likely transmission route is juvenile or adult crabs transported in seaweed packed around baitworm shipments and live lobsters shipped from New England to west coast restaurants [20, 39].

1.4 Other Nonindigenous Populations

The northwestern Atlantic and northeastern Pacific populations are the most established and most-studied invasive populations. Additional secondary and tertiary introduced populations are now located in South Africa, Australia and Argentina [11, 15, 40-55]. Green crab populations are established in South Africa between Saldana Bay to the north and Camps Bay to the south after being introduced in 1983 to the Table Bay Docks area in Cape Town, likely from northern Europe via ballast water. In Australia the population extends from near Sydney in New South Wales south to Port Phillip Bay, Victoria; Bruny Island, Tasmania and the Coorong, South Australia, likely introduced into Port Phillip Bay, Victoria, from Atlantic Europe prior to 1900 via solid ballast and hull fouling. There is a population in Atlantic Patagonia, Argentina, from Camarones Bay north to San Jorge Gulf, introduced from Australia or Tasmania in 1999 via ballast water.

1.5 Additional Introductions and Potential Invasion Sites

There are populations of green crabs on every continent except Antarctica but introductions into tropical regions, including Brazil, Panama, Hawaii, the Red Sea, Sri Lanka, Madagascar, Union of Myanmar, Pakistan and India have not resulted in established

populations (see reviews [3, 10]). Although there have been reports of an established population in Japan, the species is likely not *C. maenas* but its congener in the Mediterranean, *C. aestuarii* or a mixture and possible hybridization of the two species [5, 29, 48, 56, 57]. Based on suitable temperature regimes and depending on the European lineage, additional potential invasion sites have been identified where populations could be established, including coastal areas of Chile, China, Russia, Northern Japan, The Yellow Sea, Alaska, Namibia Uruguay, southern Brazil, and New Zealand [58].

1.6 Literature Overview

There are numerous studies of *C. maenas*, but most have concentrated on laboratory-based experiments and observations of physiological and biological processes. There remains considerable lack of consensus about many of the species' ecological attributes, especially among populations from different geographical regions. This is due at least in part, if not mostly, to the phenotypic plasticity of the species. *Carcinus maenas* is able to alter many aspects of its biology to fit particular environments, a characteristic that makes it an ideal invader. In addition, the three different genetic lineages in the native range (northern Europe, western Europe, and off-shelf of the Faroe Islands and Iceland) [4, 5] differ in physiology. A more complex population structure is suggested through the use of microsatellite markers to detect subtle genetic differentiation [59].

Of the numerous studies on *C. maenas* (a literature search conducted by Darling [11] revealed 1393 papers published in the first decade of the new millennium) the vast majority have involved the three main populations -- the native population in Europe and the two prominent nonindigenous populations in the northwestern Atlantic and northeastern Pacific. Interestingly, very few, if any, studies have been conducted on the most southern portions of the ranges any of these three major populations. The majority of papers from Europe involve *C. maenas* populations in the United Kingdom and Portugal; while other European populations have been studied, we are not aware of any published reports from the northwestern Africa region of the native range other than a sample of 40 crabs from Morocco analyzed for DNA [59]. Most of the northwestern Atlantic studies have been conducted on Atlantic Canada and New England populations, with data from south of those regions included in only a few publications. Almost all of the research from the northeastern Pacific has involved British Columbia, Washington and Oregon populations, with a few papers dealing with the more southern portion of the range in California. There are relatively few studies on the established nonindigenous populations in South Africa, Argentina or

Australia. This review examines published papers by various researchers studying *C. maenas* in the native European and northwestern Atlantic and northeastern Pacific nonindigenous populations, with occasional mention of relevant data from other populations when available and appropriate.

2. Habitat Preferences

Carcinus maenas is able to occupy a variety of sheltered habitats such as estuaries, harbors, and other wave-protected areas but are not able to survive on open shore wave swept coastlines because they lack sufficient vertical tenacity and ability to grip onto rocky substrates [29, 53, 60]. Megalopae settle out of the plankton in protected areas of the intertidal zone. Juvenile crabs prefer gravel or cobble areas or mussel beds where they can shelter under rocks and seaweed to avoid predation and cannibalism [29, 61- 71]. As crabs age they move into lower intertidal and subtidal zones, where they are able to shelter under rocks and boulders and macroalgae in rocky areas and amidst eelgrass and fouling communities or in burrows along *Spartina* banks in estuaries. Both juveniles and adults prefer areas with high structural complexity [72-74] and avoid open sandy areas that do not offer any refuge, although adults are common in muddy sands where they can burrow for concealment [65, 75, 76]. Mussel beds on mudflats offer optimal refuge from predators such as large crabs, fishes and birds [72]. In an experiment conducted on the Swedish west coast predation mortality of tethered crabs was 80-90% in open sand habitats and much lower in mussel beds and vegetated areas that provided shelter [66]. Adult *C. maenas* are very tolerant of low oxygen levels as well as temperature and salinity variations (see Tolerances below) so are able to remain in moist burrows above the neap high tide line for up to 10 days until water returns with the next spring high tide [29]. Adult crabs forage over extensive areas of their habitat, travelling as much as 2 km in 6 hours [77], but do not return to a home shelter after excursions [78].

Adult *C. maenas* can be found to depths of 10 m or greater [79-81] but they are most commonly found at depths not exceeding 6-7 m and their numbers diminish greatly below this depth [1, 10, 76, 82-86]. In some locations they migrate into deeper water during the cold winter months but in other areas many appear to remain in the shallow subtidal throughout the year, although numbers are reduced [76, 87]. Following a colder than normal winter the density of the population is reduced [76, 88] and many crabs can be found dead inside their *Spartina* bank burrows [89], evidence that they did not migrate. During the summer months females tend to be found in higher salinity subtidal areas except when they

congregate in shallow water to mate.

3. Tolerances

3.1 Temperature

Carcinus maenas can tolerate a wide range of environmental conditions, due at least in part to its phenotypic plasticity, whereby it can alter its physiology and other responses to match local conditions [90]. For example, *C. maenas* is eurythermal, able to survive short-term exposure to temperatures between 0 and 33-35°C [10, 29, 63, 88, 91, 92]. Adult *C. maenas* exposed to air on mud flats at low tide are able to evaporatively cool their bodies by as much as 2°C, making them more resistant to high temperature than a subtidal relative, *Portunus marmoreus* [93]. A critical thermal maximum (CTMax) of 35.1°C was estimated for crabs collected in Portugal [94] and of 35.8°C for North Sea crabs caught in the fall and acclimated to 22°C [95]. Crabs from California near the southern part of the northeast Pacific range had higher thermal tolerance (36.2°C) than those near the northern limit in British Columbia (34.7°C) [23]. Green crabs, like many species that inhabit variable hot environments such as estuaries and intertidal zones, have high levels of heat shock proteins (eg., HSP70) that are important components in the cellular defense against proteotoxic stress [94]. The abundance of green crabs has declined after harsh winters in their native range [64, 96, 97] as well as in nonindigenous populations [76, 88, 98, 99]. Adult *C. maenas* from British Columbia survived an 18-week duration period in the lab at temperatures at or below 5°C [100]. The maximum temperature tolerated for breeding is 26°C [101] and for brooding eggs, 18°C [29], restricting sustainable populations to sub-polar and temperate coasts in both the northern and southern hemispheres where temperatures range from – 1°C to 22°C [3, 20, 23]. There are no populations of *C. maenas* in tropical or sub-tropical environments, despite introductions in many such locations [3]. This explains why nonindigenous populations have expanded only slightly southward but much more extensively northward from introduction sites.

The minimum temperature for growth is 10°C [29, 102]. The lower temperature limit for feeding is generally considered to be 7°C [29], although Ropes [65] concludes that at temperatures as low as 7°C crabs from Massachusetts do not suppress feeding but activity and presumably feeding probably cease at some temperature below 7°C. In most populations, adult crabs migrate offshore when the water temperature drops below 8°C in winter and then return as the water warms in the spring [1, 82, 87, 103-110]. Audet et al. [111] report that *C. maenas* in Prince Edward Island waters may feed at temperatures below

6°C but only in the fall, not in the spring, and Eriksson et al. [63] indicates that feeding may occur below 7°C but almost ceases below 3-4°C for crabs in Sweden. The lower temperature limits reported for the Sweden population may represent the more cold-tolerant Scandinavian lineage identified by Roman [30] and introduced to northern Nova Scotia. It is quite possible that it is this lineage that is represented in the PEI population studied by Audet et al. [111] and is presumed to be more cold-tolerant than the southern European lineage found in the nonindigenous populations in the northwestern Atlantic south of Nova Scotia and in the northeastern Pacific region. To date no tolerance studies have been conducted with *C. maenas* from northern Nova Scotia and Newfoundland to determine if they are indeed more cold-tolerant than their southern relatives.

Larvae exhibit higher physiological tolerance to temperature fluctuations than adults [112, 113] and juveniles are more tolerant of temperature variations than older individuals [12, 120, 124]. deRivera et al. [113] found that mortality of cultured larvae at temperatures below 12.5°C was very high due to extended exposure to cold. Development time is temperature dependent in that it takes 62 days at 12°C and 32 days at 18°C for a crab to complete its early development to where it is considered an adult [112].

3.2. Salinity

Carcinus maenas is also euryhaline, with the long-term adult survival minimum salinity variously reported as 11‰ [29], 9‰ [114], 5‰ [63, 106] or 4‰ [91]. It is important to consider the synergistic effect of temperature and salinity in combination because stress due to sub-optimal values of one variable can result in diminished survival at sub-optimal values of other variables. Broekhuysen [91] found that in water of about 15‰ *C. maenas* died at a temperature of 0.6°C in about thirty days but at a temperature of 9.7°C no deaths occurred. Perkins et al. [115] reported that *C. maenas* were commonly found in salinities of 1.4-3.2‰ at 8.0-11.0°C for periods of at least 8 hours and, while crabs maintained at a temperature of 6.6-10.0°C died rapidly in salinities of 1-2‰, they survived for at least 34 days at salinities at or above 3‰. *Carcinus* does not acclimate rapidly to reduced salinity and still exhibits an increase in oxygen consumption after 3-4 days of immersion [116]. Newly molted crabs are green in color but as an intermolt period progresses the color transitions through yellow and orange to red. Green phase crabs are known to be more tolerant of low salinity than red phase crabs and males are generally considered to be more tolerant than females [106, 110, 117, 118] although Himes et al. [87] found that females

were more tolerant than males. These differences in tolerance to low salinity as well as to oscillating salinities result from greater expression of the osmoregulatory genes behind ion transport (Na⁺/K⁺-ATPase, cytoplasmic carbonic anhydrase) in green phase and female *C. maenas*, making green more tolerant than red, and females more tolerant than males [87]. In the native range, green crabs are more common in estuarine and intertidal habitats while red crabs are more common in the more saline waters of open shore and subtidal environments [1, 119, 120]. Bessa et al [74] found that the green color morph comprised 93% of all crabs caught in an estuarine study site in Portugal. Furthermore, red females are more abundant than red males at estuarine sites [1, 106, 110, 120]. These different distributions were not seen, however, in the nonindigenous population in southern Maine, where there was an even distribution of green phase crabs across sex in the intertidal and red phase crabs of both sexes were present in the intertidal throughout the year and at nearly the same abundances as green phase crabs during the summer months [87]. Adult *C. maenas* can tolerate short-term exposure to high salinities of up to 54‰ [29, 63, 91, 121] but the preferred salinity range based on laboratory choice experiments performed with Isle of Man crabs is reported to be 27-40‰ [77, 122], and Broekhyusen [91] indicated that crabs are rarely found in salinities >31‰.

In contrast to the pattern for temperature, larvae are less tolerant of salinity fluctuations than juveniles but juveniles are still more tolerant than adults [12, 117, 118, 120, 123, 124]. Anger et al. [125] found that *C. maenas* early larvae from the North Sea showed reduced respiration at low salinities, suggesting a very low or lacking osmoregulatory capacity, but salinity tolerance increases with successive larval stages to megalopae and euryhalinity is finally achieved in juveniles [114, 126].

Based on observation records of temperature and salinity from both native and invasive ranges of *C. maenas*, Compton et al. [58] identified several new sites at risk of invasion: coastal areas of Chile, China, Russia, Northern Japan, The Yellow Sea, Alaska, Namibia Uruguay, southern Brazil, and New Zealand. Perhaps all that is needed is a means of introduction into these new environments, especially of the northern Europe lineage into the colder at-risk regions.

3.3 Oxygen

As long as they remain moist and at a moderate temperature, *C. maenas* adults are able to survive out of water for at least 10 days [1, 127]. In response to lower oxygen

tension they are able to breath air by reversing the direction of the scaphognathite beat to cause air to enter the branchial chamber via the normally exhalent openings and exit through the normally inhalant Milne-Edwards openings, a process referred to as “bubbling” [1, 10, 117, 128, 129]. Perhaps this ability allows green crabs to be introduced from New England into California and Oregon by transport in shipments of live bait worms and seafood packed in wet seaweed [3, 11]. Red phase crabs leave the water and begin bubbling at much higher oxygen tension, are less able to compensate for hypoxia and die more rapidly in anoxic conditions than green phase crabs [117, 130] and therefore avoid the intertidal zone. Adult *C. maenas* are less able to compensate for low levels of oxygen when their oxygen consumption rate is high, especially during ebb tide [130]. Under conditions of declining oxygen tension, the degree of respiratory independence shown by *C. maenas* is dependent on the animal’s level of activity and inactive animals can maintain respiratory independence down to a P_{O_2} of 60-80 mmHg [131]. Both male and female adult crabs from Helgoland, Germany, increased their respiration with increases in temperature as expected for an ectothermic animal, but had relatively low Q10 values, suggesting that *C. maenas* has a capacity to stabilize its metabolic rate under physically diverse habitats [132]. Large numbers of crabs move into the intertidal to forage during high tide [1, 81, 117] and some remain in the intertidal during low tide [81] so can experience hypoxia. As is the case with other animals living in tidepool environments, *C. maenas* can continue to function even in extreme hypoxia by a variety of mechanisms, described in [133].

4. Population Characteristics

4.1 Population Density

There is a significant knowledge gap in green crab population dynamics concerning estimates of population densities. Estimates of numbers of individuals in populations are rare for both juveniles and adults and rare, owing to several factors. There are a variety of possible methods to estimate numbers within a population, each of which presents difficulties. Four of the most commonly used methods are discussed here; a review of additional methods can be found in [64]. Individuals can be counted directly along a transect or within quadrats (see for example [37, 87, 90, 109, 134]) but this method is practical only for the intertidal zone at low tide where mostly juveniles will be found or in very shallow water. Extremely high densities of small juvenile crabs ranging from 200 – 2000 m⁻² have been estimated using this method [72, 135-137]. Divers can count crabs in subtidal areas but

the type of vegetated or rocky bottom that offers suitable refuge also makes crabs very difficult to see. The most common method of collecting *C. maenas* is through the use of baited traps of various designs. Surveys by trapping do not determine the abundance of crabs in a population but rather the number of crabs captured based on foraging activity [76]. With this method, only feeding crabs will be caught and crabs below a certain size can escape through the trap mesh. Additional issues that affect catch (and therefore an accurate estimate of population size) include suitable bait, time of day and tide (crabs tend to be more active at night and during high tide, presumably because they are less visible to predators [1, 86, 107, 138], crab state (newly molted and ovigerous females tend to burrow and do not feed [1, 65], and mobility (the population as a whole is very active, migrating many meters, even kilometers, in a matter of a few hours) [6, 77]. Furthermore, there are concerns that the presence of large crabs or large numbers of crabs in a trap dissuades additional crabs from entering [139]. It is estimated that only 80% of a green crab population can be caught at any one time using traps ([1]). Underwater video used to evaluate the effectiveness of Fukui traps to catch green crabs revealed only a 16% success rate out of 1,226 entry attempts [140]. Passive nets are sometimes used but this method trusts to the currents and wandering crabs to enter the net so may be equally unreliable as a population density estimate. Lastly, a common method for estimating population numbers of a mobile species is tag and recapture. This method requires that a tag not be lost during the study period so care must be taken to ensure that a tag or mark stays intact if a tagged crab molts. Although snapped spines will be replaced when a crab molts, this method of tagging was used successfully to estimate the density of *C. maenas* population in areas of the Kattegat in Denmark [141]. There also must be a sufficient number of tagged crabs recaptured to make calculations meaningful. In an attempt to determine growth rate of green crabs in the Ria de Aveiro Lagoon in Portugal, Gomes [6] used a suture-tag method described by Edwards [142] whereby suture filaments with numbered plastic buttons were inserted into the suture line between the gills and the digestive tube, just over the last leg, where there is some flesh. The tags remained in place through a molt, but, despite offering a bounty to crab fisherman for tagged crabs, the recapture of tagged individuals was extremely small (490 out of 6,800 or 0.7%), making any accurate determination of growth rate or population size impossible. Nearly 3,000 crabs tagged with Floy tags inserted into the right gill chamber along the suture line yielded approximately a 15% recovery [143]. Crabs marked by branding a code on the dorsal carapace with a battery charged soldering bolt retaining the marks after molting, although the marks changed color from red to white [144]. Due to the difficulty obtaining accurate

numbers, in most cases, the number of green crabs in a population is merely described subjectively, based on various collections and observations, using such terms as “uncommon,” “common,” “abundant,” “extremely abundant” or “very large concentration.” In well-established populations, green crabs are almost always abundant or extremely abundant except perhaps at the range limits where they might be uncommon.

4.2 Sex Ratios

Another aspect of *C. maenas* population dynamics is the male to female sex ratios determined by trapping or other survey methods. Ratios can vary depending on the sub-range characteristics (water depth, temperature, salinity) as well as when sampling is conducted because migration patterns and habitat preferences of male and female green crabs differ. Some migration behaviors can be attributed to sex-specific differences in physiological tolerances [76, 120]. It is generally stated that female *C. maenas* are less tolerant of low salinity than males, which keeps the majority of females in the subtidal zone while males migrate in and out of the intertidal zone [107, 108, 110, 145]. Multiple studies in Europe [91, 109, 146, 147] and the western Atlantic [76, 124, 148-150] have shown that in waters with a higher salinity sex ratios favor females. However, a recent study in Maine, US, found that females were more tolerant of low salinity than males and there were many females in the intertidal zone [87]. Skewed sex ratios have also been attributed to migration behavior during the mating periods of mature female *C. maenas* because the females likely migrate to downstream areas where the salinity is higher when they are ready to mate, leaving a greater proportion of males in upstream areas. In addition, more males than females may be caught in traps because males are more likely to enter traps because they are more active than females [107-109, 151] and ovigerous females tend to be inactive and burrow into soft sediment to avoid predation so they do not feed and also will not be caught [65, 76, 149, 152].

Most of the sex ratios reported for the native European population show male bias (see Table 1) but it is interesting that there is only one published report of sex ratios from the southern portion of the range (where female biased results are seen in the nonindigenous ranges). In the Mondego estuary in Portugal (latitude 41 ° N) females outnumbered males caught whereas the sex ratio of juvenile *C. maenas* in upstream areas favored males in the winter months [120], suggesting that females migrate to downstream areas when they are approaching maturity and will be ready to mate.

Table 1. Sex ratios (M:F) for various populations of *C. maenas*. Values >1 indicate a higher proportion of males; values <1 indicate a higher proportion of females. Latitude has been rounded to nearest degree.

Location	Latitude	Sex Ratio (M : F)	Reference
native European population			
Herdla, Norway	60° N	1.55; 1.48	[144]
Kattegat, Denmark	57° N	51.63* (shallow) 21.99* (deeper)	[141]
Forth Estuary, Scotland	56° N	0.68	[146]
Kerteminde Fjord, Denmark	55° N	2.99	[109]
Kerteminde Fjord, Denmark	55° N	1.01	[153]
Menai Strait, Anglesey, UK	53° N	1.86	[154]
Ynys Faelog, Menai Strait, North Wales	53° N	2.33	[107]
Den Helder, Netherlands	53° N	0.62	[91]
Bullens Bay, Ireland	51° N	1.89	[155]
Mondego estuary, Portugal	41° N	0.89	[120]
northwestern Atlantic nonindigenous population			
Placentia Bay, Newfoundland, Canada	48° N	1.00 (September) > 1.00 (June)	[156]
Placentia Bay, Newfoundland, Canada	48° N	1.76 (fall) 1.33 (spring) 1.29 (summer)	[157]
Basin Head, PEI, Canada	46° N	1.63	[111]
Bras d'Or Lakes, Nova Scotia, Canada	46° N	2.70	[158]
Port L'Hebert, Nova Scotia, Canada	44° N	1.18 (May) 0.79 (August)	[85]
Boothbay Harbor, Maine	44° N	1.29	[102]
Biddeford Pool, Maine	43° C	< 1.00 in 74.4% of samples	[87]
Great Bay Estuary, New Hampshire, USA	43° N	1.00	[159]
Great Bay Estuary, New Hampshire, USA	43° N	0.37	[149]
Houlton-Seabrook Estuary, New Hampshire, US	43° N	0.98	[149]
Plum Island Sound, Massachusetts, US	43° N	0.34 (upstream) 0.90 (downstream)	[65]
Great Marsh, Rowley, Massachusetts, US	43° N	0.73	[150]
Great Marsh, Rowley, Massachusetts, US	43° N	1.11	[160]
Salem Sound, Massachusetts, US	42° N	0.37	[76]
Nauset Marsh, Eastham, Massachusetts, US	42° N	0.26	[150]
northeastern Pacific nonindigenous population			
Nootka Sound, British Columbia, Canada	49° N	4.18	[148]
Clayoquot Sound, British Columbia, Canada	49° N	3.88	[148]
Barkley Sound, British Columbia, Canada	49° N	1.58	[148]
Barkley Sound, British Columbia, Canada	49° N	2.45	[154]
Pipestem Inlet, British Columbia, Canada	49° N	1.71	[38]
Tillamook Bay, Oregon, US	45° N	8.25	[38]
Netarts Bay, Oregon, US	45° N	4.04	[38]
Yaquina Bay, Oregon, US	44° N	6.00	[38]
Coos Bay, Oregon, US	43° N	3.45	[38]
Bodega Harbor, California, US	38° N	3.07	[38]
Tomales Bay, California, US	38° N	2.36	[38]
Seadrift lagoon, California, US	38° N	0.73	[38]
San Francisco Bay, California, US	37° N	0.63	[38]
Elkhorn Slough, California, US	36° N	0.72	[38]
Argentina nonindigenous population			

San Jorge Gulf, Patagonia	45° S	2.36	[54]
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* ratios calculated from percentages of males and females published

A similar trend of male biased ratios being more common in the higher latitude portion and female biased ratios being more common in the lower latitude portion of a range is seen in the northeastern Pacific nonindigenous population. At ten trapping sites between Barkley Sound, British Columbia, Canada and Elkhorn Slough, California, US, the sex ratios were biased toward males at the colder sites and became more female biased at the warmer sites [38] (See Table 1 for details).

In reality, there are just as many published studies that report female biased M:F sex ratios (< 1) as there are that report male dominated populations (see Table 1). Male biased ratios appear to be more common in the higher latitude portion of a range (colder in the Northern Hemisphere populations) whereas female biased ratios appear to be more common in the lower latitude (warmer) region. For example, within the nonindigenous northwestern Atlantic range, the M:F sex ratio is reported to be male-biased in the Prince Edward Island, Canada, region [111], but female-biased in the more southerly area of southern Maine [87], New Hampshire [149] and Massachusetts [76, 150]. It is entirely possible, even likely, that the actual ratio of males to females in the population is very close to 1 (the same number of males and females) and the bias comes from sex differences in activity as well as the survey process itself. In Plum Island Sound, Massachusetts, Ropes [65] found that the sex ratios of downstream and upstream sites were 0.34 and 0.90, respectively. A recent study assessing the distribution and relative abundance of *C. maenas* in Chignecto Bay, upper Bay of Fundy, Canada, found that the ratio of male to female crabs decreased as the season progressed (but no actual SR values were reported) indicating that season greatly influences sex ratios [88]. Similarly, in Placentia Bay, Newfoundland, the overall proportion of sexes was 60% male and 40% female (SR= 1.72) but the sex ratio varied from a high of 1.76 in the fall to a low of 1.29 in the summer [157].

5. Reproduction and Development

5.1 Molting

The molting cycle for *C. maenas* consists of an intermolt period (diecdysis if short, anacdysis if longer) during which *C. maenas* feeds actively, followed by a relatively shorter molting period (ecdysis) when the old exoskeleton is shed to increase the body size. The

molting process itself takes approximately 2-3 hours [91], followed by a hardening of the carapace that varies with temperature from 3-4 days at 16°C to 16 days at 10-11°C [91]. As stated previously, newly molted crabs are green in color but as an intermolt period continues the color transitions through yellow and orange to red. It is accepted that green phase crabs are devoting energy to growth (so molt more frequently) whereas red phase crabs are devoting energy to reproduction (so are not molting and growing) [1, 76, 87, 117, 145, 147, 161].

It is believed that molting occurs throughout the year for *C. maenas* in all populations, although Queiroga [162] suggests that the actual molting period in the native European range is only between February and October, rather than all year. In any case molting is age and temperature dependent, and the process peaks at certain intervals [120]. Several studies describe peak molting times for populations in the Netherlands, South Wales and France as between May and June [82, 91, 163], but in Mondego estuary, Portugal, the peak is April to June for males, and July to October for females [120]. For the western Atlantic population molting in male *C. maenas* in Prince Edward Island, Canada, occurs in a synchronized 'molting window' during July [164]. In New Hampshire and Massachusetts *C. maenas* populations, molting in males is most common during the summer whereas molting in females is most common during the fall months [76, 165]. In comparison, male *C. maenas* in the Southern Hemisphere (e.g., Argentina) molt in November (early summer) and females molt in January–March (summer and fall) [54]. It is assumed that green crabs molt significantly less in the coldest temperatures of the year (below about 10°C) due to observed low activity [10].

Whatever the true peak time of molting is for each regional population, age is always inversely proportional with molting frequency [10]. Green crabs molt much more frequently when young, with short intermolt periods (diecdysis) and intermolt intervals become much longer (anecdysis) as crabs age, until the crab enters a terminal anecdysis.

5.2 Mating

Mating in *C. maenas* can take place only after the female has molted, so a peak in mating behavior is synchronized with sexually mature female ecdysis [91]. Males can mate without molting, and therefore typically molt earlier in the year in comparison to females [1, 166, 167]. They wait in shallow water closer to the shore for females to arrive [7]. Males locate receptive females by sensing pheromones that females release just prior to molting

[10]. A male green crab then embraces a pre-molt female before, during, and after copulation to both claim the female and ensure her safety after copulation. Large red phase males have a competitive advantage in acquiring and mating with females over smaller male rivals [144]. The seasonality of mating varies among populations. In the native European population, *C. maenas* mating behavior is reported to occur between June and October [168], with a peak in August [91]. Studies in both Prince Edward Island [111] and Maine [102] suggest that the northwestern Atlantic population shares July-October mating behavior seasonality with the native European population. No studies of mating period specifically in the northeastern Pacific population have been published, but Klassen and Locke [10] indicate that *C. maenas* in British Columbia, Canada are seen in mating pairs around July. In Argentina, female *C. maenas* mate beginning in January (mid-summer) prior to moving to lower littoral levels where they remain through the fall and winter [54].

5.3 Ovigerous Females and Egg Release

There is no predictable link between time of mating and time of egg bearing because female *C. maenas* have the capacity to store male spermatophores for 4 1/2 months or longer [91]. The seasonality of ovigerous females differs considerably with study and region due to latitude (temperature) and other factors (see Table 2). Studies from the

Table 2. Seasonality of *C. maenas* reproductive events in different populations. Empty cells indicate no data are available for that location. [reference]

Location	Copulation	Females Ovigerous	Larvae Released
native European population			
Norway		January [169]	
Scotland		All year (Peaks October to Spring Months) [170]	April to end of July [170]
Denmark	May and June [171]		
Baltic Germany	August [105]		
United Kingdom	November to December [172]		
Wales	August to September [82]	February to June (Peak in March and April) [82]	February to July [82]
The Netherlands	July to September (Peaks in August) [91]	November and December, and during the spring and early summer [91]	After winter season and in June [91]
Belgium	June to October [168]	December to August [168]	March to mid-October [168]
France	May to November (Peak in August and September) [163]	November to July (Peak in April) [163]	
Portugal	April-May and September-December [173]	All year [120];	All year [120];

		October to June (Peaks in January-February) [173]	October through May [120]; February to June [174]
northwestern Atlantic nonindigenous population			
Newfoundland, Canada		July and August [157]	Late May or Early June to August (Peak in June and July) [157]
Prince Edward Island, Canada	Peak from mid-August to September [111]	July to mid-September; (Peak in early July) [111, 175]	August to December [111, 175]
Maine, US	July to October (Peaks in August) [102]	April to August (Peaks from May to June) [102]; December to August, peak in summer months [87]	Peaks in September [102]
Massachusetts, US		November to January, and May to August [76]	
northeastern Pacific nonindigenous population			
British Columbia, Canada	July [10, 148]	April and May [10, 148]	May [10, 148]
Argentina nonindigenous population			
San Jorge Gulf, Patagonia, Argentina		May to September [54]	

Netherlands and Wales independently observed the appearance of ovigerous females between March and April [82, 91], and observations from the Netherlands found that there are two windows in which ovigerous females are prevalent -- during November and December, and during the spring and early summer [91]. At a site on the southwest coast of Ireland, there were two reproductive events annually, a primary winter cycle in which the larger crabs reproduced and a secondary summer cycle when smaller crabs reproduced [155]. It is possible for the same female to be ovigerous in more than one season, both because one fertilization event can yield two clutches for a female *C. maenas* [91] and because females carry their eggs for several months, depending on the water temperature [29]. In Massachusetts, Young et al. [76] found that 79% of ovigerous females were caught between May and August, and all others were caught between November and January, similar to the seasonality of the native European population. In British Columbia, female *C. maenas* are ovigerous during April and May [10, 111]. In comparison, ovigerous females are most abundant from May to September (winter months) along the Argentina coast [54]. Using baited traps to determine peak ovigerous periods could be misleading because ovigerous females tend to burrow into sediment or other shelter and remain inactive to avoid predation so do not feed and will not be caught in traps [10, 65, 110, 111, 120, 149]. Perhaps the use of Fyke nets or other passive collection methods in addition to traps might catch a broader range of *C. maenas* to mitigate the error inherent in using only baited traps [111].

Depending on the persistence of colder temperatures ($<10^{\circ}$), ovigerous females produce one to two clutches per year in all populations [10, 102]. The number of clutches and eggs per gravid female varies with the size of the female, resources availability, and temperature [71]. Larger females, in warmer water with high food availability, are the optimal variables for greatest number of eggs per clutch [111, 176, 177]. In the native European population, the earliest estimation of *C. maenas* clutch size is 200,000 eggs [178] and Broekhuysen [91] calculated the number of eggs on a *C. maenas* of moderate size (46 mm CW) to be 185,000. Estimates of clutch size in the northwestern Atlantic population vary considerably, from 4,781 to 165,940 eggs, with a mean of $75,577 \pm 37,808$ eggs [179]. However, the clutch size when the female is first ovigerous is not the same as when the eggs are released, because eggs are lost during the brooding period. Early and late developmental stages of *C. maenas* in Prince Edward Island had average estimated clutch sizes of $195,833 \pm 83,673$ and $140,374 \pm 60,717$ eggs, respectively [111]. Therefore, fecundity likely varies for the same ovigerous female during different stages of embryonic development.

Carcinus maenas employs diverse strategies for egg release [157], and the timing of egg extrusion can vary by region because females have the capacity to release eggs when conditions are optimal [91]. After reaching sexual maturity, *C. maenas* females migrate to downstream areas where eggs can be shed near the open ocean [120]. In the native European population, eggs are generally released between February and July [174]. In the Wadden Sea off the coast of the Netherlands, the megalopal stage of *C. maenas* settles in large numbers from the end of June or early July onwards [135], most likely from the clutch carried in the winter [91]. In the Canal de Mira, Portugal, eggs generally were released between February and June, usually soon after a nighttime high tide [174].

In the northwestern Atlantic, the larval release window in Newfoundland is from late May or early June until August, peaking in June and July [157]. In Prince Edward Island the release occurs between the middle of July and the end of September [111], and the peak is in September in Maine [111]. Within the northeastern Pacific population, larval release peaks in British Columbia earlier, in May [10, 148]. Coastal water temperatures in the northeastern Pacific are comparable to those in the northwestern Atlantic in summer months, but the northeastern Pacific waters are warmer in the winter, which offers ovigerous females a longer spawning window [10, 22, 91]. Therefore, it is possible that longer periods of warmer waters could positively influence the success of invasions in the northeastern Pacific. However, Best et al. [157] suggests that temperature is not likely to be the sole cause of difference in larval release patterns, but rather a combination of temperature,

salinity [114], photoperiod [180], and food abundance [121] may all influence the seasonality of various reproductive events in temperate latitudes [181].

5.4 Larval Development

The planktonic component of the green crab life cycle consists of four zoeal stages and one megalopal larval stage [112, 113, 182, 183]. Survival of *C. maenas* larvae is highly dependent on water chemistry parameters and laboratory experiments have shown that they respond negatively to exposure to reduced salinities. Larvae can tolerate salinities between 20 and 40‰ but apparently cannot develop below 20‰ [125], although the lower limit is reported as 19‰ by Rasmussen [184], 17‰ by Behrens Yamada [29] and 10‰ by Broekhuysen [91]. Broekhuysen [91] found that larvae at 10°C require salinity >26‰ whereas those at 16-17°C can develop at salinity as low as 20‰. Nagaraj [114] found that larvae developed to megalopae in all tested combinations of temperature (10, 15, 20, 25°C) and salinity (20, 25, 30, 35‰) but highest survival was in the combinations of lowest temperature (10°C) and highest salinities (30 and 35‰). Oviparous females tend to congregate near the mouth of an estuary [74], allowing the larvae to exit the estuarine habitat via tidal cycles and complete their development in high salinity coastal waters before returning to the estuary as megalopae or juveniles. It is not surprising, then, that zoeae migrate out of the estuary into higher salinity coastal waters to complete development during the developmental period. Early zoeal *C. maenas* vertically migrate nocturnally, utilizing the ebb tide [185] to migrate offshore where they develop [174, 183]. Benthic recruitment of early life stages primarily occurs in the upstream area of estuaries so the megalopal stage reinvades the estuary on a flood tide to restart the cycle [174, 180, 186].

Interestingly, larvae exhibit higher physiological tolerance to temperature fluctuations than adults [112, 113] but larvae are more susceptible to cold temperatures (below 12.5°C), thereby limiting range expansion into higher latitudes [113]. Temperature is inversely proportional to the time needed to complete development of the five larval stages (Zoea 1 through Megalopa) of *C. maenas* [112]. In controlled conditions, all five stages can be completed in as little as 18 days at a constant temperature of 25°C, or in as long as 66 days at a constant temperature of 12°C [112]. In nature, this early development can last for upward of 50 days or up to 82 days in laboratory experiments [113]. This long larval development means that the planktonic larvae remain in the water column for a long time

and may be carried by currents and tides considerable distances to replenish or extend the range of existing populations.

Larval behavior has a significant influence on invasion success [59] but establishment of *C. maenas* populations outside of the native range is contingent on a number of factors in addition to a successful and timely larval development, including environmental variables such as water temperature [112] and day length [180, 183] and biological factors such as food availability [121], competition and predation [24].

5.5 Life Span

The life span of *C. maenas* in the native European and nonindigenous western Atlantic populations is 5-7 years [10, 102, 187] but is much shorter (3-4 years) in the northeastern Pacific nonindigenous population, apparently due to a much faster growth rate [29]. No data are available for life spans in the other nonindigenous populations.

6. Size

6.1 Adult Maximum Size

Green crabs in nonindigenous populations tend to be larger than those in the native population [38, 148, 188] and males are generally larger than females. Moreover, the species appears to follow the temperature-size rule for ectotherms, whereby the largest individuals are found in the coldest parts of the range (see Table 3). A linear regression analyzing male maximum carapace width and the

Table 3. Maximum size (CW, mm) reported and minimum size (CW, mm) at sexual maturity in various populations of *C. maenas*. Latitude is rounded to nearest whole degree. Empty cells indicate that no data are available.

Location	Latitude	Maximum Size		Sexual Maturity		Reference
		Male	Female	Male	Female	
native European population						
Herdla, Norway	60° N			44	28-30	[169]
Western Sweden	58-59° N	100				[189]
Isefjord, Denmark	55-56° N	92				[184]
Schlei fjord, Baltic Sea, Germany	55° N	100				[105]
Isle of Man, UK	54° N				27	[182]
Menai Strait, UK	53° N	83.1	74.1			[37]
Den Helder, Netherlands	53° N	86	70		36-42	[91]
Swansea, S. Wales	52° N	86	70	44		[82]
Bullens Bay, Ireland	52° N	86.5			38.6	[155]
Dale Peninsula, SW Wales	51° N	86		25	15	[121]

Ostend, Belgium	51° N			44	23-45	[168]
Baltic Germany	50° N	75	60			[29]
Luc-sur-Mer, France	49° N				12	[163]
Mondego estuary, Portugal	41° N	71	65		29	[120]
Canal de Mira, Portugal	41° N			27		[174]
Ericeira and Parede, Portugal	39° N			27	21.5	[173]
northwestern Atlantic nonindigenous population						
Bras d'Or Lakes, Nova Scotia, Canada	46° N	91			40	[158]
Placentia Bay, Newfoundland, Canada	48° N	79	72	32	37	[157]
Newfoundland west coast, Canada	48° N				30	[157]
Basin Head, Prince Edward Island, Canada	46° N	89.76	76.44	21.3	28.66	[111]
Basin Head Lagoon, Prince Edward Island, Canada	46° N				42.7	[175]
Boothbay Harbor, Maine, US	44° N	82	70	34	34	[102]
Great Bay Estuary, New Hampshire, US	43° N	91	88			[149]
Hampton-Seabrook Estuary, New Hampshire, US	43° N				36	[165]
Salem Sound, Massachusetts, US	42° N	80.9	85.9			[76]
northeastern Pacific nonindigenous population						
Little Espinoza Inlet, British Columbia, Canada	50° N	80.3				[190]
Pipestem Inlet, Barkley Sound, British Columbia, Canada	49° N	113 (104)	89			[38]
Barkley Sound, British Columbia, Canada	49° N	101.1	85.4			[37]
British Columbia, Canada	49° N	106				[37]
Pipestem Inlet, Barkley Sound, British Columbia, Canada	49° N	95				[191]
Vancouver Island, British Columbia	49° N	98	76			[148]
Oregon/Washington, US	46-48° N	99.6				[189]
Yaquina Bay, Oregon, US	45° N	96	79			[29]
Oregon, US	45° N	99				[190]
Bodega Harbor, California, US	38° N				34	[29]
Argentina nonindigenous population						
Camaronas Bay, Patagonia	45° S	81.4	71.4		39.9	[52]
San Jorge Gulf, Patagonia	45° S	73.4	64.3		45.8	[54]
South Africa nonindigenous population						
Table Bay Docks, Cape Town	34° S	84	56			[44]

latitude of each sample site in the native range found that latitude explained 61% of the variation in CW [23]. Within the native range in Europe, crabs generally do not exceed 86 mm but a single male with a carapace width of 100 mm was collected in western Sweden [105] and a 92 mm male crab from Denmark was reported by Eriksson & Edlund [62]. The smallest maximum CW male within a population (71 mm) is from Portugal, nearest to the southern limit of the range [120]. The largest female reported in Europe is a crab from the

UK measuring 74.1 mm [37]; there are no data published for sizes of females north of Germany. It should be noted that researchers in Europe, the United States and Atlantic Canada measure carapace width as tip-to-tip of the fifth spines whereas the Pacific Canadian standard for measurement is from notch-to-notch between the 4th and 5th spines, excluding the spines themselves [10]. Gillespie et al. [148] has devised the following regression equation to convert between the two different width measurements:

$$CW_{\text{notch-to-notch}} = 0.9095 (CW_{\text{tip-to-tip}}) + 0.4816.$$

The largest male crab reported from the northwestern Atlantic population had a carapace width of 91 mm and the largest female measured 88 mm, found in New Hampshire [149]. In the northeastern Pacific population, crabs from near the northern range limit in British Columbia were significantly larger than those from near the southern limit in California [23, 75, 192]. The largest *C. maenas* on record to date is a 113 mm (converted from reported value of 104 mm) male from British Columbia [38]. Grosholz and Ruiz [15] suggest that crabs of size 110-115 mm CW may be attainable and, although not published, there is a report of a crab from British Columbia that measured 106 mm (presumably this is a notch-to-notch measurement so would be 116 mm when converted) [37].

6.2 Minimum Size at Sexual Maturity

The minimum sizes of sexually mature *C. maenas* varies considerably with no specific trend evident, despite the assertion that size decreases as latitude increases [29, 102, 176]. It also should be noted that physiological maturity precedes morphological maturity [155]. In the native range the greatest minimum size of sexually mature *C. maenas* males is given as 44 mm in Norway [169], South Wales [82], UK [172] and Belgium [168] whereas the smallest sexually mature males (27mm) have been reported from Portugal, many kilometers to the south [173, 174]. For females the data are much more variable, ranging from 38.6 mm in Ireland [155] to 21.5 mm in Portugal [173]. In the northwestern Atlantic, there are only three reports for male minimum size at maturity, 34 mm in Maine [102], 32 mm in Newfoundland [157], and 21.3 mm in PEI [111]. For females the minimum size at sexual maturity ranges from 40 mm in Nova Scotia [158] to 28.7 mm in PEI [111]. See Table 3 for additional data for the native European and nonindigenous northwestern Atlantic populations. For the northeastern Pacific population the only value reported is an estimated 34 mm for females in California [29]. In Argentina, Vinuesa [54] concluded that female

sexual maturity seems to be attained at about 40 to 50 mm CW based on a small sample size of 25 females collected, where the smallest mature crab measured 45.8 mm.

7. Ecosystem Dynamics

In addition to physical parameter tolerances (eg., temperature, salinity, oxygen), the other major determinant of whether or not a population can be successfully established and/or expanded involves ecosystem dynamics (eg., diet, competitors, predators and parasitic infections).

7.1 Diet

Juvenile *C. maenas* feed primarily on detritus and interstitial meiofauna and then become more carnivorous as they age [65]. Green crab adults are opportunistic omnivores, whose diet varies with season, composition of the community, size of prey, availability of prey and the energy expenditure / energy gained [78, 152, 193]. Green crabs are known to feed on organisms from at least 158 genera in five plant and protist and fourteen animal phyla [10, 12, 20, 194], with members of all populations showing a strong preference for molluscs, especially bivalves such as clams, mussels and cockles [10, 14, 28, 45, 99, 136, 195-204]. Additional preferred prey items include gastropod molluscs such as periwinkles [21, 29, 200, 205], other crustaceans, such as the common brown shrimp, *Crangon crangon* [152] and recently settled small juvenile lobsters, *Homarus americanus* [206], as well as members of their own species [61, 66, 71, 136], polychaetes [207] and amphipods [14]. In addition to being predators of a large variety of organisms, *C. maenas* are also scavengers of any dead material along the shore [7, 63, 65].

In the native European population, there are regional differences in diet composition. In the temperate Mondego estuary in Portugal, *C. crangon*, polychaete worms and teleost fish were the most abundant stomach items by occurrence, numbers, and [152]. In the Menai Strait, North Wales and in the Rance Basin, France, green crabs were reported to eat mostly other crustaceans, polychaetes and algae [208, 209]. Jensen and Jensen [198] found that younger *C. maenas* in the Danish Wadden Sea favor the common cockle, *Cerastoderma edule*, over other prey items. Scherer & Reise [136] found that older males continue to feed on molluscs but older females feed primarily on annelid worms, although Baeta et al. [152] found that different age classes and sexes of *C. maenas* showed no difference in diet when

they occurred in the same area of an estuary in Portugal. In the nonindigenous population in South Africa the most important prey items, based on gut contents, were gastropods, isopods and polychaetes (see [44] for a list of over 30 organisms known to be consumed by *C. maenas*), whereas in Australia, crabs preyed predominantly on bivalves such as cockles and mussels and native crab species [47, 210]. The authors are not aware of any published information on food eaten by *C. maenas* in Argentina.

For a more extensive list of prey organisms, see discussions in [1, 10, 29, 44].

Herbivory in larger crabs may be by accidental ingestion [152], but there is evidence that some portunid crabs feed selectively on plant material or algae [44, 65, 85, 209]. In the northwestern Atlantic population, *C. maenas* alters its diet from bivalves, its preferred prey, to consume more algae in the presence of a competitor species, the Asian shore crab *Hemigrapsus sanguineus* [211]. The wide variety of prey items that *C. maenas* consumes indicates that they are resilient, and can survive on whatever food is available [29]. Green crabs can even survive three months of starvation [212].

7.2 Competitors

Green crabs experience both intraspecific (within the species) and interspecific (between different species) competition within established populations. In South Wales, *C. maenas* is by far the most abundant of several crab species, suggesting that it wins most interspecific competition and therefore intraspecific competitions is probably much more important in determining distribution [1]. Intraspecific competition is not well documented nor its overall significance established, but it is assumed that as the density of a population increases, intraspecific competition for available resources also increases. *Carcinus maenas* is a very aggressive species so it is likely that there are many agonistic encounters with other members of the population. Observed higher rates of leg autotomy within higher density *C. maenas* populations in British Columbia, Canada, were attributed to intraspecific agonistic behaviors [148].

Interspecific competition is also difficult to document in the field so it generally is assumed that if two somewhat similar species are consuming the same foods and/or occupying similar habitat, they must be competing for those resources, but according to Gause's competitive exclusion principal, no two species can remain in direct competition indefinitely so either one will out-compete and eliminate the other or the niche will be

fragmented such that they are no longer in direct competition.

Within the native European population in South Wales, in 1966 there were 29 other crab species in localities where green crabs were found [213], many of which eat similar food, so *C. maenas* could be in competition with at least some of them [1], but they all have slightly different habitat preferences that serve to keep them apart (fragmentation of the niche) [214]. Crothers [81] argues that any competition among species would favor *C. maenas*, restricting the distribution of the other species. The European edible crab *Cancer pagurus* was able to consume larger bivalves than *C. maenas* because the species has stronger chelae [215]. The brush-clawed shore crab, *Hemigrapsus takanoi*, was unintentionally introduced to the Netherlands in the late 1990's and is now abundant in the Eastern Scheldt, where adults compete with juvenile *C. maenas* [216]. A sibling species, the Asian shore crab, *H. sanguineus*, is also found in European waters, having arrived by 2003 in the Mediterranean Sea [217], around 2007 on the coast of France [218] and then Helgoland, Germany, where it is now the second most abundant intertidal crab in the North Sea after *C. maenas* [132]. It is predicted that the Asian shore crab will assert competitive dominance over the green crab in this region [132].

The native rock crab, *Cancer irroratus* and *Carcinus maenas* coexist in southwestern Nova Scotia so they may compete for resources [85, 219, 220]. The rock crab is a larger species that is known to outcompete *C. maenas* in a lab setting [221, 222], and apparently competitively excludes green crabs from their preferred habitat and forces them to occupy the upper intertidal in Chignecto Bay, Bay of Fundy, Canada, resulting in habitat segregation between the two species [99]. On the Isles of Shoals, New Hampshire, green crabs were abundant in the intertidal while rock and Jonah crabs (*Cancer borealis*) were both more abundant in subtidal waters [223]. In Prince Edward Island green crabs and rock crabs seemed to avoid each other on mussel clumps, suggesting that the two species could coexist [224]. In the Bras d'Or Lakes, Nova Scotia, rock crabs consumed large numbers of juvenile green crabs [225]. In contrast, another study determined that rock crabs were being displaced or preyed upon by *C. maenas* in Newfoundland [204]. Juvenile American lobster, *H. americanus*, and two species of crabs native to the northwestern Atlantic, the blue crab, *Callinectes sapidus*, and the lady crab, *Ocellatus ovalipes*, all consume similar food (bivalves, gastropods, polychaetes and crustaceans) so are assumed to be competitors of *C. maenas* [65, 85, 199, 226]. In laboratory experiments adult green crabs were able to physically compete with and, in many cases dominate larger, heavier lobsters [226]. In

addition to consuming small juvenile lobsters green crabs curtail the overall foraging activity and shelter use by lobsters [159, 227, 228]. In Passamaquoddy Bay in the Bay of Fundy, St. George's Bay in the Northumberland Strait and Chedabucto Bay on the Scotian Shelf the magnitude of the predatory effect of green crabs on lobsters varies and is correlated with the genetic origins of the invasive populations [229].

In the northeastern Pacific population few native species appear to compete with *C. maenas* for food. In laboratory experiments, juvenile *C. maenas* were able to out-compete equal-sized *Cancer magister* (Dungeness crab) whereas adult *C. magister* could out-compete adult green crabs, but they do not currently share the same habitat so are actually not in direct competition [230]. Limb autonomy was more common in *C. maenas* in areas of Bodega Bay, California that were inhabited by red rock crabs *Cancer productus* and brown rock crabs *C. antennarius*, suggesting that competitive interactions with these rock crabs directly resulted in green crab injuries or the green crabs were forced out of protected habitats into areas where they were then injured by predators [10, 231].

Two species of grapsid crabs, the Asian shore crab, *H. sanguineus* in the northwestern Atlantic and a sibling species with several common names (yellow shore crab, hairy shore crab, mud-flat crab, Oregon shore crab), *H. oregonensis*, in the northeastern Pacific, have relatively recently invaded the areas occupied by *C. maenas* and are direct competitors [75, 202, 232-234]. Under controlled experimentation *H. sanguineus* was overwhelmingly dominant over *C. maenas* whereas *C. maenas* dominated over *H. oregonensis* [75]. In the wild, *C. maenas* in the presence of *H. sanguineus*, shifts its habitat use, abandoning otherwise preferred habitat under rocks in the cobble of intertidal areas [75]. Along the southern New Jersey, Long Island and southern New England coastlines, *H. sanguineus* has essentially eliminated *C. maenas* in the rocky intertidal zone where it formerly was extremely abundant [134, 233, 235-240] and apparently the same thing happened along the Delaware coastline [241]. In the presence of *H. sanguineus*, *C. maenas* not only occupies a less-desirable habitat but also alters its diet from bivalves, its preferred prey, to consume more algae [211]. In laboratory experiments green crabs were superior competitors to both blue crabs and Asian shore crabs [234], but that does not seem to be the case in the wild.

The authors are not aware of any published information on *C. maenas* competitors in the other nonindigenous populations in Australia, South Africa or Argentina.

7.3 Predators

The major predators of *C. maenas* include many species of birds, fish, and other crustaceans (for more in-depth discussion of various predators and lists of predators, see [1, 10, 20, 242]. Cannibalism among green crabs, especially juveniles, is common and often proportional to the population density, so *C. maenas* must be considered as a predator of itself [65, 66, 71, 152, 243]. Predators other than in those three groups include a few mammals such as mink, *Mustela vison* and otters, *Lutra lutra* [244, 245] and harbor seals, *Phoca vitulina* [246]. The southern limit of the nonindigenous northwestern Atlantic population apparently is determined by the native predator *Callinectes sapidus* that provides biotic resistance to invasion and prevents the southward spread and establishment of *Carcinus maenas* within and south of Chesapeake Bay, despite the fact that the temperature regime in those areas falls within the acceptable temperature distribution seen in green crab populations elsewhere in the world [24]. In laboratory studies juvenile green crabs are superior competitors to juvenile blue crabs [234] but adult blue crabs are more than twice the size of green crabs and readily prey on them [24].

The authors are not aware of any published information on *C. maenas* predators in the other nonindigenous populations in Australia, South Africa or Argentina, but one could assume that species of gulls and other shorebirds and fish and perhaps other crustacean species would be the major predators, as they are in the other populations.

Perhaps the most significant *C. maenas* predator is *Homo sapiens* (humans). In the native population, there are established fisheries for green crabs in several European countries, where they are caught to be fried as a soft-shell crab delicacy or as an ingredient for soups and fish pastes [7]. In Canada, a green crab fishery for food is being explored [247, 248] but the difficulty of removing meat from the carapace by conventional methods and the relatively small size of *C. maenas* poses challenges for a traditional “hard-shell” fishery [249]. A pilot commercial fishery was attempted in 2014, but its long-term practicality was deemed questionable because of the lack of suitable markets for the harvested crabs [164]. There currently is considerable interest in the Atlantic Canada and New England region for development of a variety of green crab based food products [247, 250-253]. The variable colors (green, yellow, orange, red) seen on the ventral surface of *C. maenas* are potential indicators for various physiological processes [76, 102, 121, 161, 254]. Color as an indicator of when a green crab is about to molt is of interest to any potential soft-shell crab food business modeled on the lucrative *moleche* (fried soft-shell crab)

industry with *C. aestuarii* in Venice, Italy. Male *C. maenas* exhibit three external characteristics that are indicative of an imminent molt: presence of a halo or greying circle on the episternites, darkening of the apex line, and looseness of the ecdysial line (where abdomen meets posterior carapace) [164]. Beyond predation for food consumption, humans also collect green crabs for other uses, such as fish or conch bait [7] and fertilizer, as well as utilizing chitin in the production of self-healing car paints [255] and in inexpensive antiviral drugs [256], or just to reduce the density of invasive populations [10, 204, 257].

7.4 Epibionts

In the native European and nonindigenous northeastern Atlantic populations, *C. maenas* can become fouled with epibionts, primarily rock barnacles, slipper shells, serpulid tube worms, bryozoans, and occasionally tunicates during an extended intermolt period, the number of epibionts increasing as the crabs age without molting [1, 240], so red crabs are the most heavily fouled [1, 76, 258]. In the native European population *C. maenas* infected with the rhizocephalan parasite *Sacculina carcini* are much more likely to be fouled than non-infected crabs [258, 259]. The authors are not aware of any published information on *C. maenas* epibionts in any of the other nonindigenous populations.

7.5 Pathogens and Parasites

Green crabs are susceptible to a wide range of pathogens including bacteria, viruses, dinoflagellates, haplosporidians, helminths, nemerteans and trematodes (see review in [12]). There are a number of parasites that infect green crabs (see lists in [1, 10, 29, 260]), the most famous and well-studied being the rhizocephalan barnacle, *Sacculina carcini*. Rhizocephalans are morphologically modified crustacean parasites such that the main body of the parasite is a root-like system of branches that extends into most of the host's tissue. Red phase *C. maenas* are externally parasitized by *S. carcini* to a higher degree than green phase crabs in the Mondega estuary in Portugal [261], and the Dutch Wadden Sea [262]. The youngest developmental stages of the barnacle predominantly occur when the crabs are green, the intermediate stages when they are orange, and the oldest when they are red [258]. Infected crabs are castrated by the parasite and cease molting [259, 263, 264]. As is the case with many species, green crabs in non-native populations are substantially less infected by parasites than in the native population, which is another reason why *C. maenas* is such a successful invader [260]. In Europe, approximately 16% of green crabs are infected with *S. carcini* but the parasite is not found in any of the nonindigenous populations. Non-native

crabs in some populations (not South Africa) are infected with some of the other parasitic worms, including trematodes, nematodes, acanthocephalans and nemerteans [10, 260]. Several parasitic species, including *S. carcini*, have been proposed as potential biological control agents of invasive green crabs [12, 29, 265, 266] but any intentional introduction of another species into an environment is risky and could result in the death of native crab species [267].

8. Ecological Impacts

The green crab is considered an “ecosystem engineer” because it has the ability to modify entire ecosystems [10, 268]. Both native and nonindigenous populations of *C. maenas* have had impacts, mostly negative, on ecosystem components. For example, in the Dutch Wadden Sea, mass mortalities of common eider ducks, *Somateria mollissima*, were attributed in part to the transmission of the acanthocephalan parasite *Polymorphus botulis* for which the green crab is an intermediate host [269]. Negative impacts have been far greater in the invaded ranges, however. In the northwestern Atlantic, *C. maenas* has caused considerable damage to blue mussels [202], American oysters *Crassostrea virginica* [219], rock crabs *Cancer irroratus* and lobsters *H. americanus* [204] and eelgrass *Zostera marina* along the Atlantic Canada and New England coasts [204, 270-274]. As of now, there has been no decline in *C. irroratus* as a result of the emergence of green crabs in the Upper Bay of Fundy, Canada [88], but the situation merits monitoring. In Atlantic Canada green crabs recently have expanded into areas populated by native mud crabs (*Dyspanopeus sayi*), and *C. maenas* may threaten the sustainability of this native species [71]. Green crabs have had a devastating effect on the economically important soft-shell clam *Mya arenaria* industry in New England [28, 65, 195, 196, 201, 203, 275]. Some of the poorest clam harvest years in Massachusetts and Maine have followed high population levels of *C. maenas* and, conversely, some of the biggest clam harvests have followed declines in the *C. maenas* population, which were probably due to environmental factors such as extremely cold winters [2, 28, 275]. The early part of this decade has seen a large increase in the *C. maenas* population in Maine, New Hampshire, and northeastern Massachusetts, followed by a subsequent sharp decline in the commercial harvest of soft-shell clams in 2013 and 2014 [276].

In the northeastern Pacific nonindigenous population *C. maenas* has been present for a much shorter period of time so its ecological effects are not yet apparent. Green crabs feed on clams (*Nutricula* spp.) that are a major food source for wading shore birds so it is feared

that if *C. maenas* become abundant, those wading birds could be affected adversely [29, 138]. In laboratory experiments to evaluate competition for food, *C. maenas* out-competed Dungeness crabs *Cancer magister* so increased numbers of green crabs could adversely affect that commercially important species [75, 230, 277]. In 1993 *C. maenas* larvae settled in mesh bags where Manila clams (*Venerupis philippinarum*) were being aquacultured and the subsequent crabs preyed on a wide size range of clams, reducing the harvest considerably [29, 278]. In Tasmania, shellfish growers are not concerned that *C. maenas* will affect their economically important oyster (*Crassostrea gigas*) or mussel (*Mytilus edulis*) industries because the shellfish are grown in racks and on longlines off the bottom and out of reach of green crabs [29, 46].

Green crabs generally do not feed on eelgrass *Zostera marina* but their foraging activity digging in the soft substrate dislodges the grasses and has contributed to considerable loss of eelgrass beds along the New England coast [270-274].

It is interesting to note that the morphological features of some species have been altered due to interactions with *C. maenas*. The blue mussel *Mytilus edulis* and the snails *Littorina saxatilis*, *L. obtusata* and *Nucella lapillus* all possess thicker shells in sites where *C. maenas* is abundant [19, 29, 205, 279-282].

9. Conclusions and Future Research

Due to its phenotypic plasticity, wide tolerances and omnivorous diet, *C. maenas* is a very successful invasive species, having established populations in all continents except Antarctica. It is an ecosystem engineer and can have many adverse effects on ecological components within its settled region. Established population ranges are primarily determined by temperature and are restricted to temperate coastlines, where water temperatures do not drop below -1°C or exceed 22°C for extended periods. Within this suitable temperature band around the world, suitable habitat is further restricted to wave-protected sheltered bays and estuaries in which salinity does not exceed 31‰ or fall below 4‰ for adults, 20‰ for larvae, for extended periods. Rocky areas that offer protection from predators are preferred by both juveniles and adults, but adults also thrive on soft muddy sand substrates where they are able to burrow for shelter.

Despite the long history of this species as the subject of hundreds of studies there still are aspects of the biology that are not known conclusively, at least partly due to the genetic variability in different populations. The nonindigenous populations in the

northeastern Pacific, South Africa and Argentina have been established much more recently and have been the subject of many fewer studies. Little has been published concerning some important aspects of the biology of *C. maenas* in these populations (eg., size at sexual maturity, reproductive periods) and especially ecosystem functions (eg., diet, competition, predation, epibionts, parasitism). This information would be very helpful to evaluate the global population dynamics of green crabs and it is hoped that scientists in those areas will provide a better understanding of this important invasive species.

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