

Review

Life History and Population Dynamics of Green Crabs (*Carcinus maenas*)

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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. *Carcinus maenas* has been the subject of numerous papers, with over 1000 published in the past decade. This review provides an up-to-date account of the current published information on the life history and population dynamics of this very important species, including genetic differentiation, 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; life history

1. Introduction

1.1. Overview

The first extensive examination of *C. maenas* was J.H. Crothers’ “The Biology of the Shore Crab *Carcinus maenas*” Parts 1 and 2 published in 1967 and 1968 respectively [1,2]. At that time very few studies had been conducted on *C. maenas* [3–7] so much of Crothers’ paper presents original information. Many research studies followed but it was several decades before Sylvia Behrens Yamada published her review book “Global Invader: The European Green Crab” in 2001 [8], followed soon after by “A Biological Synopsis of the European Green Crab, *Carcinus maenas*” by Greg Klassen and Andrea Locke in 2007 [9]. The present review is an attempt to assimilate previous data with studies that have been published more recently, most notably involving the nonindigenous populations and the variable methods and conclusions relating to population genetics as a result of advancements in phylogenetic methods.

Due to the ease with which it can be collected, identified, sexed and measured, there have been many 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 extensive phenotypic plasticity of the species. *Carcinus maenas* is able to alter many aspects of its biology to fit particular environments, such flexibility and

adaptability making it an ideal invader. In addition, there are evolutionary differences in physiology among the various source populations such as from northern Europe or south-central European regions. It has not yet been determined if physiological differences in crabs from different areas is correlated with the three different genetic lineages in the native range (northern Europe, western Europe, and off-shelf of the Faroe Islands and Iceland) [10,11]. Genome-wide studies are exposing the complexity of the genetic background of this species [12–18]. Whenever possible this review will provide the consensus view on a particular topic, but in most cases there is so much variability in published data that no consensus is possible and we will instead present a variety of results from different studies.

Of the numerous studies on *C. maenas* (a literature search conducted by Darling 2011 revealed 1393 papers published in the first decade of the new millennium) the vast majority have involved three main populations—the native population in Europe and the two prominent nonindigenous populations in the northwestern Atlantic and northeastern Pacific. Studies of *C. maenas* populations in the native European population span most of the range but we are not aware of any published reports from Iceland aside from inclusion of some crabs from this area in genetics studies or from the northwestern Africa region of the native range other than a sample of 40 crabs from Morocco analyzed for DNA [13]. 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. In both the native and northwestern Atlantic populations, the numbers of crabs in the southern part of the ranges are greatly reduced, making collecting sufficient specimens for study difficult. Research in the northeastern Pacific has involved most of the range, including studies from British Columbia, Washington, Oregon and 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, where relevant studies from each major population will be discussed in appropriate sections to follow, with occasional mention of data from other populations when available and appropriate.

1.2. Native European Population

The native range of *Carcinus maenas* (where it is commonly known as the “shore crab”) is the northeast Atlantic coastline, from Mauritania in northern Africa to Norway, the British Isles and Iceland [2,10,11,19,20]. 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 [21,22]. 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 that a maintenance program might be needed to insure sustainability [22]. 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) [9,23–28]. It was the first marine organism to be designated as an aquatic nuisance species by the Aquatic Nuisance Species Task Force (ANSTF) [29]. The Latin name “*Carcinus maenas*” translates as “raving mad crab” and is known as “*le crab enragé*” in France. The common translation of *maenas* from Latin to English as “sprats” is not accurate. In Greek mythology, ‘maenads’ were the female followers of Dionysus and their name literally translates to “the raving ones” because of their frenzied state associated with rituals involving wild dancing and copious amounts of wine. Later, in Roman mythology the Latin feminine noun ‘*maenas*’ was used, meaning ‘frenzied or raging woman.’ Perhaps it is this meaning that Linnaeus had in mind when he named the crab *Carcinus maenas* (P. Sean McDonald, U. Washington, personal communication). 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 “European shore crab” [20,30–32].

1.3. Northwestern Atlantic Nonindigenous Population

Carcinus maenas was first discovered along the mid-Atlantic United States (location not given but assumed to be New Jersey or New York) in 1817, presumably carried from Europe in solid ballast or on the outside of wooden ship hulls, [10,20,33–37]. This part of the range now extends over approximately 1000–1200 kilometers of coastline [28,38,39]. The species 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* [40]. However, *C. maenas* has expanded mostly northward, arriving in northeastern Massachusetts, New Hampshire, and southern Maine waters in the 1890s or early 1900s, and eventually reaching southern Nova Scotia, Canada by the early 1950s, Prince Edward Island by 1997, and Newfoundland by 2007 [8,9,20,31,32,41–44]. The species' expansion northward from southern Nova Scotia was found to be associated with a second introduction, from northern Europe, probably Norway, around 1980, rather than being a northward expansion of the original introduction in the early 1800's that was derived from a source in south-central Europe [10,17,18,27,45–47]. A model of the invasion dynamics predicted that the two lineages would overlap only in the neighborhood of the invasion fronts, a region approximately 100–200 km wide [48] but in fact the original and later introductions have extensively interbred, leading to genetic admixture throughout much of the species' northwestern Atlantic range [10,14,17,45,46,49].

1.4. Northeastern Pacific Nonindigenous Population

In 1989–90 a well-established breeding population of green crabs was discovered on the northeastern Pacific coast, in San Francisco Bay in California [36]. Populations have become successfully established only 125 km to the south in Elkhorn Slough in the Monterey Bay area, but have spread over 1500 km northward in just 12 years, reaching the west coast of Vancouver Island, British Columbia, Canada by 1999 [31,50–52]. In Oregon and Washington estuaries, *C. maenas* continues to be found in low densities but the crabs are abundant in the inlets of the west coast of Vancouver Island [53]. More recently, crabs have been found in the Salish Sea (Sooke Basin in 2012, Westcott Bay and Padilla Bay in 2016), and Puget Sound (Dungeness Spit, Sequim and Whidbey Island in 2017) [53,54]. There have been occasional sightings of individual crabs elsewhere in the Puget Sound but they are rare and probably do not represent breeding populations [53,54]. The northeastern Pacific population is genetically depauperate and represents a secondary introduction from the initial northwestern Atlantic introduced population [10,12,55]. The likely transmission route was juvenile or adult crabs transported in seaweed packed around baitworm shipments and live lobsters shipped from New England to California restaurants [36,56,57], with subsequent range expansion by larval transport via ocean currents, especially after warm El Nino winters [50,51,53,58,59]. Movement into the Salish Sea has been slow due to two physical barriers: estuarine circulation normally moves water out of the Sea and water temperatures are typically less than the 10 °C lower thermal tolerance for larval development. Only during periods of El Nino does the current flow reverse and the temperature rise above 10 °C [53]. Several sites are areas of oyster aquaculture so it is possible that shellfish transplants may play a role in some range expansion [51,53]. By whatever means, further expansion northward along the northeastern Pacific coast is thought to be inevitable [59–62].

1.5. Other Nonindigenous Populations

The northwestern Atlantic and northeastern Pacific populations are the most-studied invasive populations. Additional secondary and tertiary introduced populations are now located in South Africa, Australia and Argentina [31,63]. 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 [64–68]. 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 in the late 1800's via solid ballast and hull fouling [69–80]. Occurrence outside its normal range in Tasmania is often in association with aquaculture activities [76]. 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 [81–83]. Although there have been reports of an established population of *C. maenas* in Japan, the Japanese population apparently represents hybridization between *C. maenas* and its congener in the Mediterranean, *C. aestuarii* (= *C. mediterraneus*) [8,10,27,63,76,84] and will not be included in this review.

1.6. Additional Introductions and Potential Invasion Sites

There are established 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 [9,20] because females require temperatures at or below 18 °C to successfully incubate their eggs [1,85]. Based on temperature and salinity information from both native and established invasive ranges of *C. maenas*, one study 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 [86] (see Figure 1). Perhaps all that is needed is a means of introduction into these new environments, especially of a lineage, possibly one from northern Europe, that is adapted for the conditions, such as colder waters, in these new regions [86] (Carlton [87] discusses the many possible vectors).

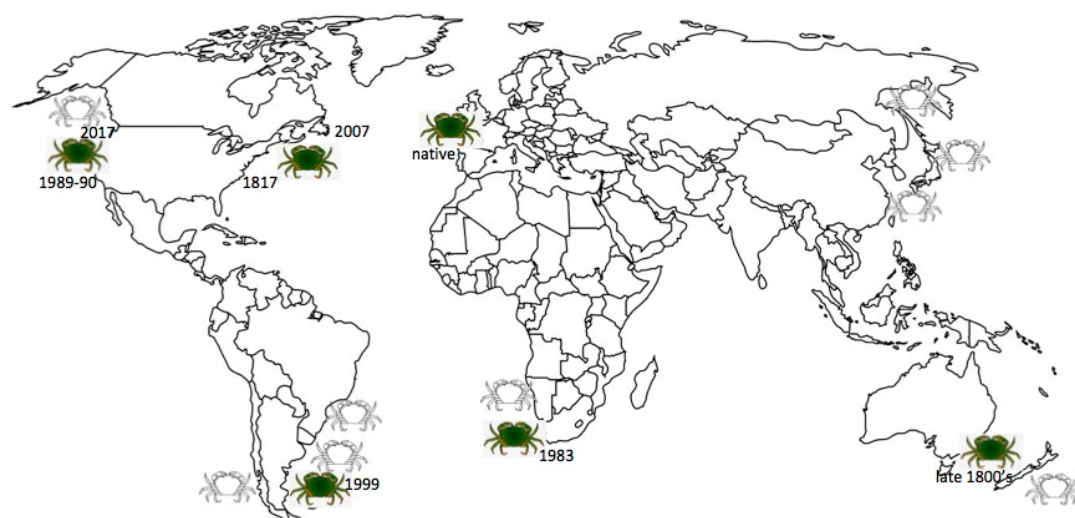


Figure 1. Worldwide distribution of green crab (*Carcinus maenas*) populations as of 2019. Solid icons represent established populations with dates of introduction. Open icons indicate potential locations for future invasions.

2. Population Genetics

One of the newest research frontiers is the advancement in the use of genetic markers to elucidate population affinities and differences. An early goal of using molecular methods in the study of green crabs was to provide insight into the differences within the native range between *C. maenas* along the Atlantic coast and *C. aestuarii* (formerly *C. mediterraneus*) in the Mediterranean Sea, differences that had been well characterized morphologically [8], and genetically [27]. Over the years, *Carcinus* populations have been studied with an evolving suite of genetic markers including allozymes [88], mitochondrial 16S [89] and cytochrome c oxidase I (COI) genes [11,46,90], microsatellite markers [10,12,14,63,91,92], and SNPs [15,16,18,49]. Increasingly high resolution studies of population genetics have led to a greater understanding of intraspecific and interspecies diversity. For example, an initial analysis of 19 allozyme loci led to the conclusion that the genetic differentiation between *C. maenas* and *C. aestuarii*

was insufficient to warrant independent species status and a designation of two subspecies of *C. maenas* was recommended [88]. However, later work identified species-diagnostic differences in partial sequences of the 16S small subunit rRNA gene [89], supporting the now accepted idea that *C. maenas* and *C. aestuarii* indeed are separate species, although they can hybridize.

A more comprehensive study based on the mitochondrial cytochrome c oxidase subunit I (COI) gene revealed considerable divergence between northwestern Atlantic populations and a single Mediterranean population, confirming a species-level taxonomic distinction, as well as significant intraspecific differentiation between populations from Iceland and the Faeroe Islands and those from continental Europe [11]. Within continental Europe, the COI data supported weak but significant differentiation between crabs from northern Europe (Norway, Sweden, Finland, Denmark, Germany, and Poland) and those from southwestern Europe (the Netherlands, Belgium, France, Spain and Portugal [11]. This divide is not clear-cut, and the United Kingdom population contains a mix of haplotypes from both the northern Europe and southwestern Europe groups [93]. Using microsatellite markers in the native European population, *C. maenas* from Faeroe Islands and Iceland were found to be genetically differentiated from continental populations when using microsatellite markers, and like earlier mitochondrial markers, also showed a significant partitioning of genetic variance between northern Europe (including Germany and Scandinavian populations) and western Europe (including the Netherlands, England, and Atlantic Iberian populations) [10].

Along the northeastern Pacific coast, microsatellite markers were used to assess the genetic diversity in 1040 *C. maenas* samples from 21 sites representing the major episodes of population establishment and expansion in that region [12]. It was concluded that *C. maenas* in this population likely derived from a single introduction of a small number of founders to San Francisco Bay, California, from the western Atlantic, supporting an early conjecture based on observations of crabs in live seafood shipments arriving in the western US from the northeastern US [36]. The use of both mitochondrial and nuclear markers in reconstructing invasion pathways for *Carcinus* serves as a valuable illustration of the utility of multiple genetic markers and multiple analytical methods in genetic studies of biological invasions [27].

An updated genetic analysis of seven populations from the native European, northwestern Atlantic, and northeastern Pacific ranges, using a panel of 10,809 transcriptome-derived nuclear SNPs, identified significant population structure that was previously undifferentiated with earlier markers [15]. This SNP panel represented a considerably larger portion of the genome than previous approaches, covering at least 1673 regions, and identified both neutral and non-neutral mutations in the SNP panel in an attempt to predict what genes may support a successful invasion. By all measures, genetic diversity was highest in the European native range and lowest on the northeastern Pacific coast [15], consistent with serial bottlenecks caused by introduction from Europe to the US east coast, and from the east coast to the US west coast. The data revealed significant genetic structure between all locations, even between invasive populations that appeared undifferentiated when using mitochondrial DNA and microsatellites [10].

There have been several attempts to reconstruct introduction histories for invasive *Carcinus* populations using population genetics [27] (see “Introduction” section). The first introduction of green crabs outside of Europe was to the northwestern Atlantic in the early nineteenth century [36], where they spread northwards along the coastline, eventually reaching a stable northern range limit near Halifax, Nova Scotia by the 1970s [32]. In the late 1980s, a second introduction of green crabs from northern Europe to northern Nova Scotia occurred in concert with a rapid expansion of the species up the coast, where it achieved high densities by the 2000s [45]. This second invasion in the northwestern Atlantic was derived from a native northern European source that was genetically distinct from the earlier invasion [45].

The introgression cline of east coast US has been most extensively studied with a number of markers being used. The first such investigation used only the COI marker, and reported a strong genetic cline along the Scotian Shelf with a prominent Mid-Atlantic haplotype that diminished in

frequency from south to north [45]. The structure of the cline was attributed to differentiation through selection in the northern part of the eastern US range and/or contact of two invasion fronts through a more recent invasion of new genetic lineages in Nova Scotia [45]. The aforementioned microsatellite markers [92] yielded a slightly different result. Although analyses of both mitochondrial and nuclear genetic loci indicated admixture between the two invasion fronts, two marker systems disagreed in the geographic extent of the admixture zones [46]. While COI data suggested that genetic introgression from the more recently introduced northern *C. maenas* population has extended well into the western Bay of Fundy [45], microsatellite data show very little evidence of admixture at northern Bay of Fundy sites, and introgression of northeastern Nova Scotian alleles is low even at sites along the southern Bay of Fundy [46]. Still, vessel traffic and shipping were considered the most likely vector candidates for the Newfoundland introduction [46], agreeing with previous conclusions [45].

Over time, it was predicted that continued patterns of dispersal and connectivity would result in a persistent southward shift [90], however this would later be found to be incorrect with an advance in genetic markers [49]. The original hypothesis was that larval dispersal alone could not explain the displacement of *C. maenas* clines, where introgression occurred more rapidly for mitochondrial DNA relative to nuclear markers, suggesting demographics (e.g., gene surfing) or natural selection (e.g., thermal tolerance) may be influencing invasion dynamics [14,45]. Although an analysis of SNPs revealed that there was not a southward shift in genetic cline as previously predicted [90] both neutral and selective processes were attributed as drivers of introgression and all marker types resolved a common spatial genetic pattern, where current clines for COI, microsatellites, and SNP allele frequencies overlapped in cline center and width [16,18,49]. The application of multiple genetic markers to elucidate invasion history is well supported from the study of the introgression cline of the eastern US coast, as the understanding of green crab invasion dynamics has changed with increasingly high-resolution markers.

Molecular genetics methods offer new insight into the population dynamics of *C. maenas*, and have proved to be a very useful tool in understanding genetic lineages in many marine invasive species. With advancements and improvements in the extent of the genome that can be characterized using high-throughput sequencing, further genomic research may help to elucidate the species' invasion history and, most importantly, shed light on the species' potential future expansion.

3. 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 [8,83,94]. 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 [8,95–106]. Juvenile crabs frequently display striking colors and mottling patterns that may help to camouflage them in geometrically complex habitats with variable substrates [107,108]. 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 [109–111] and avoid open sandy areas that do not offer any refuge, although adults are common in muddy sands where they can burrow for concealment [112–114]. Mussel beds on mudflats offer optimal refuge from predators such as large crabs, fishes and birds [109]. 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 [101]. 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 [8]. Adult crabs forage over extensive areas of their habitat, travelling as much as 2 km in 6 h [115], but do not return to a home shelter after excursions [116].

Adult *C. maenas* can be found to depths of 10 m or greater [117–119] but they are most commonly found at depths not exceeding 6–7 m and their numbers diminish greatly below this depth [2,5,9,75,113,120–124]. 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 [113,125]. Following a colder than normal winter the density of the population is reduced [113,126,127] and many crabs can be found dead inside their *Spartina* bank burrows (M. Fregeau, Salem State U., pers com), 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.

4. Tolerances

4.1. 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 [128]. For example, *C. maenas* is eurythermal, able to survive short-term exposure to temperatures between 0 and 33–35 °C [3,8,9,96,126,129]. 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* [130]. A critical thermal maximum (CTMax) of 35.1 °C was estimated for crabs collected in Portugal [131] and of 35.8 °C for North Sea crabs caught in the fall and acclimated to 22 °C [132]. Crabs from California near the southern part of the northeastern Pacific range had higher thermal tolerance (36.2 °C) than those near the northern limit in British Columbia (34.7 °C) [39]. Green crabs, like many species that inhabit variable hot environments such as estuaries and intertidal zones, have high levels of heat shock proteins (e.g., HSP70) that are important components in the cellular defense against proteotoxic stress [131]. The abundance of green crabs has declined after harsh winters in their native range [98,133,134] as well as in nonindigenous populations [113,126,135,136]. Adult *C. maenas* from British Columbia survived an 18-week duration period in the lab at temperatures at or below 5 °C [137]. The maximum temperature tolerated for breeding is 26 °C [138] and for brooding eggs, 18 °C [8], 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 [20,36,39]. There are no populations of *C. maenas* in tropical or sub-tropical environments, despite introductions in many such locations [20]. This likely 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 [8,139]. The lower temperature limit for feeding is generally considered to be 7 °C [8], although Ropes [112] 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 [2,4,5,125,140–146]. Audet et al. [147] 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. [96] indicates that feeding may occur below 7 °C but almost ceases below 3–4 °C for crabs in Sweden [96]. The lower temperature limits reported for the Sweden population may represent the more cold-tolerant Scandinavian lineage identified by Roman [45] 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. [147] 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 [85,148] and juveniles are more tolerant of temperature variations than older individuals [28,107,149,150]. deRivera

et al. [85] 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 only 32 days at 18 °C for a crab to complete its early development to where it is considered an adult [151].

4.2. Salinity

Carcinus maenas is also euryhaline, with the long-term adult survival minimum salinity variously reported as 11‰ [8], 9‰ [152], 5‰ [96,140] or 4‰ [3]. At high salinity the crab is an osmotic conformer but becomes an osmotic regulator at a critical low salinity [153]. 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 [3] 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. [154] 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 h 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 maenas* does not acclimate rapidly to reduce salinity and still exhibits an increase in oxygen consumption after 3–4 days of immersion [155]. 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 [140,146,156–159] although Himes et al. [125] found that females in a Maine population 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 *C. maenas*, making the green morphotype more tolerant than red [125]. 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 [2,150,160]. Bessa et al. [111] 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 [2,146,150,157]. 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 [125]. Adult *C. maenas* can tolerate short-term exposure to high salinities of up to 54‰ [1,3,8,96] but the preferred salinity range based on laboratory choice experiments performed with Isle of Man crabs is reported to be 27–40‰ [115,161], and Broekhuysen [3] 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 [28,149,150,158,159,162]. Anger et al. [163] 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 [152,164].

4.3. 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 [2,165]. 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 exhalant openings and exit through the normally inhalant Milne-Edwards openings, a process referred to as “bubbling” [2,9,166–168]. Perhaps this ability allowed green crabs to be introduced from New England into California by transport in shipments of live bait worms and seafood packed in wet seaweed [20,27]. 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 [167,169] 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 [169]. 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 [170]. 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 [171]. Large numbers of crabs move into the intertidal to forage during high tide [2,118,167] and some remain in the intertidal during low tide [2] 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 (see McMahon [172]).

5. Reproduction and Development

5.1. Molting

During its life cycle, *C. maenas* molts about 18 times, four during the zoea and megalopa larval stages and 14 after the larval stages [173]. The molting cycle consists of an intermolt period (termed diecdysis if short, anecdysis 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 h [3], 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 [3]. 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 molting and growing much less) [2,113,125,158,174–177]. Many red crabs are in a terminal anecdysis and will not molt again. Those that do molt usually become pale green or yellow in color but some females have been reported occasionally to remain red immediately after ecdysis [178,179]. Red morphotypes generally present a heavier and thicker carapace while green morphotypes are lighter and thinner [173]. It is likely that a crab's energy allocation shifts once it molts but that has not been examined. It is believed that molting occurs throughout the year for *C. maenas* in all populations, although Queiroga [180] 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 [150]. Several studies describe peak molting times for populations in the Netherlands, South Wales and France as between May and June [3,5,7], but in Mondego estuary, Portugal, the peak is April to June for males, and July to October for females [150].

For the western Atlantic population molting in male *C. maenas* in Prince Edward Island, Canada, occurs in a synchronized molting window during July [181]. 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 [113,182]. In British Columbia within the northeastern Pacific range mature and older males with new shells were found from January through November, being most common from April through July and again in September and least common in August; numbers of new shell mature and older female crabs peaked in June and July, decreased in August and peaked again in September [59]. A recent molt of a large male crab (74 mm CW) was collected in August 2016 in Roche Harbor, Wescott Bay, Washington [8].

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) [82]. 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 [9].

Whatever the true peak time of molting is for each regional population, age is always inversely proportional with molting frequency [9]. 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. Limb autotomy is essential for survival in juvenile *C. maenas* but is a rare event in sexually mature crabs [183]. Regeneration of autotomized limbs in first year crabs may be completed in one molt [1] but takes at least two or three molts after the first year [183,184].

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 [3]. Males can mate repeatedly over a long period of time [185] without molting, and therefore typically molt earlier in the year in comparison to females [2,186]. They wait in shallow water closer to the shore for females to arrive [22]. Males locate receptive females by sensing pheromones that females release just prior to molting [9]. 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 [187]. The seasonality of mating varies among populations. In the native European population, *C. maenas* mating behavior is reported to occur between June and October [188], with a peak in August [3]. Studies in both Prince Edward Island [147] and Maine [139] 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 & Locke [9] 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 [82].

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 [3]. As noted previously by Baeta, et al. [150] seasonality of ovigerous females differs considerably with study and region due to latitude (temperature) and other factors (see Table 1).

Table 1. Seasonality of *C. maenas* reproductive events in different populations. Empty cells indicate no data are available for that location.

Location	Copulation	Females Ovigerous	Larvae Released
Native European Population			
Norway		January [189]	
Scotland		All year (Peaks October to Spring Months) [190]	April to end of July [190]
Denmark	May and June [191]		
Baltic Germany	August [142]		
United Kingdom	July–September [192]	November to December [192]	May–June [192]
Wales	August to September [5]	February to June (Peak in March and April) [5]	February to July [5]
The Netherlands	July to September (Peaks in August) [3]	November and December, and during the spring and early summer [3]	After winter season and in June [3]
Belgium	June to October [188]	December to August [188]	March to mid-October [188]

Table 1. Cont.

Location	Copulation	Females Ovigerous	Larvae Released
France	May to November (Peak in August and September) [7]	November to July (Peak in April) [7]	
Portugal	April-May and September-December [193]	All year [150]; October to June (Peaks in January-February) [193]	All year [150]; October through May [194]; February to June [195]
Northwestern Atlantic Nonindigenous Population			
Newfoundland, Canada	Spring and Late Summer [196]	July and August [196]	Late May or Early June to August (Peak in June and July) [196]
Prince Edward Island, Canada	Peak from mid-August to September [147]	July to mid-September; (Peak in early July) [147,197]	August to December [147,197]
Maine, US	July to October (Peaks in August) [139]	April to August (Peaks from May to June) [139]; December to August, peak in summer months [125]	Peaks in September [139]
Massachusetts, US		November to January, and May to August [113]	
Northeastern Pacific Nonindigenous Population			
British Columbia, Canada	July [9,198]	April and May [9,198]	May [9,198]
South Africa Nonindigenous Population			
Bloubergstrand and Sea Point		July to December [65]	
Table Bay		June to January, peak in October [199]	
Argentina Nonindigenous Population			
San Jorge Gulf, Patagonia, Argentina		May to September [82]	

Studies from the Netherlands and Wales independently observed the appearance of ovigerous females between March and April [3,5], 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 [3]. 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 [200]. 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* [3] and because females carry their eggs for several months, depending on the water temperature [8]. In Massachusetts, 79% of ovigerous females were caught between May and August, and all others were caught between November and January [113], similar to the seasonality of the native European population. In British Columbia, female *C. maenas* were reported to be ovigerous during April and May [9,147] but more recently ovigerous females have been found in every month sampled from January through October [59]. It is suggested that *C. maenas* may have one breeding season in adverse conditions but may have a continuous breeding season in favorable conditions such as in newly invaded areas [59]. Ovigerous females are most abundant from May to September (winter months) along the Argentina coast [82]. 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 [9,112,146,147,150,182]. 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 [147].

Depending on the persistence of colder temperatures ($<10^{\circ}$), ovigerous females produce one or two clutches per year in all populations [9,139]. The number of clutches and eggs per gravid female varies with the size of the female, resources availability, and temperature [106]. Larger females, in warmer water with high food availability, are the optimal variables for greatest number of eggs per clutch [147,201,202]. In the native European population, the earliest estimation of *C. maenas* clutch size is 200,000 eggs [203] and Broekhuysen [3] 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 4781 to 165,940 eggs, with a mean of $75,577 \pm 37,808$ eggs [204]. 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 [147]. Therefore, fecundity likely varies for the same ovigerous female during different stages of embryonic development.

Carcinus maenas employs diverse strategies for egg release [196], and the timing of egg extrusion can vary by region because females have the capacity to release eggs when conditions are optimal [3]. After reaching sexual maturity, *C. maenas* females migrate to downstream areas where eggs can be shed near the open ocean [150]. In the native European population, eggs are generally released between February and July [195]. 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 [205], most likely from the clutch carried in the winter [3]. In the Canal de Mira, Portugal, eggs generally were released between February and June, usually soon after a nighttime high tide [195].

In the northwestern Atlantic, the larval release window in Newfoundland is from late May or early June until August, peaking in June and July [196]. In Prince Edward Island the release occurs between the middle of July and the end of September [147], and the peak is in September in Maine [139]. Within the northeastern Pacific population, larval release peaks in British Columbia earlier, in May [9,198]. 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 [3,9,38]. Therefore, it is possible that longer periods of warmer waters could positively influence the success of invasions in the northeastern Pacific, especially during El Niño events [51]. However, Best et al. [196] suggests that temperature is not likely to be the sole cause of difference in larval release patterns, but rather a combination of temperature, salinity [152], photoperiod [195], and food abundance [1] may all influence the seasonality of various reproductive events in temperate latitudes [206].

5.4. Larval Development

The planktonic component of the green crab life cycle consists of four zoeal stages and one megalopal larval stage [86,151,207,208]. 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‰ [163], although the lower limit is reported as 19‰ by Rasmussen [209], 17‰ by Behrens Yamada [8] and 10‰ by Broekhuysen [3]. Broekhuysen [3] found that larvae at 10 °C require salinity $>26‰$ whereas those at 16–17 °C can develop at salinity as low as 20‰. Nagaraj [152] 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‰). Ovigerous females tend to congregate near the mouth of an estuary [111], 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 after four to six weeks as megalopae or juveniles [76]. 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 [210] to migrate offshore

where they develop [195,208]. Benthic recruitment of early life stages primarily occurs in the upstream area of estuaries so the megalopal stage reinvades the estuary on a spring flood tide to restart the cycle [195,211–213]. Megalopae choose complex substrates to settle in and habitat selection continues through early instars [1,102,107,214].

Interestingly, larvae exhibit higher physiological tolerance to temperature fluctuations than adults [85,148] but larvae are more susceptible to cold temperatures (below 12.5 °C), thereby limiting range expansion into higher latitudes [85]. Temperature is inversely proportional to the time needed to complete development of the five larval stages (Zoea 1 through Megalopa) of *C. maenas* [151]. 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 [151]. In nature, this early development can last for upward of 50 days or up to 82 days in laboratory experiments [85,215]. 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. At study sites in England it was determined that megalopae that settle in April reached sexual maturity in the same autumn whereas megalopae that settled in August reached maturity the following spring at a slightly smaller carapace width [7,183,216]. In contrast, it took crabs in western Sweden more than two years to reach sexual maturity [97].

Larval behavior has a significant influence on invasion success [13] 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 [151] and day length [208,212] and biological factors such as food availability [1], competition and predation [40].

5.5. Life Span

The life span of *C. maenas* in the native European and nonindigenous western Atlantic populations is 5–7 years [9,139,217] and of crabs from Oregon and Washington within the northeastern Pacific nonindigenous population, is reported to be around 4–6 years [8,218]. No data are available for life spans in the other nonindigenous populations.

6. Size

6.1. Adult Maximum Size

The maximum sizes (CW) reported for crabs from many European, northwestern Atlantic and northeastern Pacific sites are compiled in Table 2.

Table 2. Maximum size (CW) reported and minimum size at sexual maturity in various populations of *C. maenas*. When not stated in the reference, CW was estimated from graphs. (C) = combined sexes or sex not indicated. Empty cells indicate no data are available. No data are available for nonindigenous population in Australia. Latitude rounded to nearest whole degree.

Location	Latitude	Maximum Size (mm)		Sexual Maturity (mm)		Reference
		Male	Female	Male	Female	
Native European Population						
Herdla, NO	61° N	80		44	28–30	[189]
Herdla, NO	61° N	80			>20	[185]
west coast of Sweden	58° N	72				[219]
Western Sweden	58–59° N	100				Moksnes, unpublished data, cited in Behrens Yamada [218]

Table 2. Cont.

Location	Latitude	Maximum Size (mm)		Sexual Maturity (mm)		Reference
		Male	Female	Male	Female	
Kattegat, DK	57° N	71	62			[220]
Isefjord, DK	55–56° N	92				[209]
Millport, SL	56° N	80				[221]
Orensund, DK	56° N	80 (C)				[222]
Odense Fjord, DK	56° N	80				[223]
Clyde Sea Area, SL	56° N	80				[224]
Kerteminde Fjord, DK	55° N	81				[225]
Schlei Fjord, Baltic Sea, DE	54° N	75	60			[142]
Wadden Sea, DE	54° N	71				[174]
Whitby Harbor and Robin Hood's Bay, ENG	53° N	82.5	75		16–31	[226]
Boggle Hole, ENG	54° N	75				[227]
Isle of Man, UK	54° N				27	[207]
Llandudno and Conway, North WAL	53° N	75				[228]
Menai Straits, North WAL	53° N	83.1	74.1			[52]
Menai Straits, North WAL	53° N	75				[229]
Menai Straits, North WAL	53° N	74				[230]
Den Helder, NL	53° N	86	70		36–42	[3]
Essex, ENG	52° N	62				[231]
Dale Peninsula, SW WAL	51° N	86	70	25	15	[1]
Oosterschelde, NL	52° N	63				[232]
Bullens Bay, IE	52° N	86.5			38.6	[200]
Swansea, South WAL	52° N	86	70	44		[5]
Ostend, BE	51° N			44	23–45	[188]
Cornwall, ENG	50–51° N			21	28	[233]
Plymouth, ENG	50° N	57	65			[231]
Mountbatten, Plymouth, ENG	50° N	65 (C)				[234]
Baltic Germany	50° N	75	60			[8]
Luc-sur-Mer, FR	49° N				12	[7]
Minho Estuary, PT	42° N	65	56		30	[173]
Canal de Mira, PT	41° N			27		[195]
Mondego estuary, PT	41° N	71	65		29	[150]
Ericeira and Parede, PT	39° N			27	21.5	[193]
Northwestern Atlantic Nonindigenous Population						
Bras d'Or Lakes, Nova Scotia, CA	46° N	91	69		40	[235]
Placentia Bay, Newfoundland, CA	48° N	79	72	32	37	[196]
Newfoundland west coast, CA	48° N				30	McKenzie unpublished data, cited in Best et al. [196]

Table 2. Cont.

Location	Latitude	Maximum Size (mm)		Sexual Maturity (mm)		Reference
		Male	Female	Male	Female	
Basin Head, Prince Edward Island, CA	46° N	89.76	76.44	21.3	28.66	[147]
Basin Head, Prince Edward Island, CA	46° N	80				[236]
Basin Head Lagoon, Prince Edward Island, CA	46° N				42.7	[197]
Long Harbor, Placentia Bay, Newfoundland, CA	45° N	78				[237,238]
Boothbay Harbor, Maine, US	44° N	82	70	34	34	[139]
Days Cove, Damariscotta, Maine, US	44° N	82 (C)				[239]
Broad Cove, Yarmouth, Maine, US	44° N	85 (C)				[239]
Webhannet River, Wells, Maine, US	43° N	78 (C)				[239]
Great Bay Estuary, New Hampshire, US	43° N	91	88			[182]
Hampton-Seabrook Estuary, New Hampshire, US	43° N				36	[182]
Pavilion Beach, Ipswich, Massachusetts, US	42° N				22	A.M. Young, personal observation
Salem Sound, Massachusetts, US	42° N	80.9	85.9			[113]
Northeastern Pacific Nonindigenous Population						
Little Espinoza Inlet, British Columbia, CA	50° N	80.3	58.4			[240]
Pipestem Inlet, Barkley Sound, British Columbia, CA	49° N	113	87			[241]
Barkley Sound, British Columbia, CA	49° N	101.1	85.4			[52]
Barkley Sound, British Columbia, CA	49° N	114	93		41	[59]
British Columbia, CA	49 ° N	106				Therriault & DiBacco personal communication to Iain McGaw
Pipestem Inlet, Barkley Sound, British Columbia, CA	49° N	95 (C)				[242]
Vancouver Island, British Columbia, CA	49° N	98	76			[198]
Oregon/Washington, US	46–48° N	99.6	79			[218]
Tillamock Bay, Oregon, US	46° N	92	85			[241]
Netarts Bay, Oregon, US	45° N	98	89			[241]
Yaquina Bay, Oregon, US	45° N	96	83			[241]
Yaquina Bay, Oregon, US	45° N	96	79			[8]

Table 2. Cont.

Location	Latitude	Maximum Size (mm)		Sexual Maturity (mm)		Reference
		Male	Female	Male	Female	
Oregon, US	45° N	99 (C)				Behrens Yamada personal communication to Jamieson [240]
Coos Bay, Oregon, US	43° N	98	88			[241]
Bodega Harbor, California, US	38° N				40	[30]
Bodega Harbor, California, US	38° N				34	[8]
Bodega Bay, California, US	38° N	102	88			[241]
Tomales Bay, California, US	38° N	86	73			[241]
Sea Drift Lagoon, California, US	38° N	88	88			[241]
San Francisco Bay	38° N	83	80			[241]
Elkhorn Slough, California, US	37° N	89	89			[241]
Argentina Nonindigenous Population						
Camaronas Bay, AR	45° S	81.4	71.4		39.9	[243]
San Jorge Gulf, Patagonia, AR	45° S	73.4	64.3		45.8	[82]
South Africa Nonindigenous Population						
Table Bay Docks, Cape Town, ZA	34° S	84	56			[65]
Australia Nonindigenous Population						
Gulf St. Vincent, South Australia, AU	35° S	80	67			[244]

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 (P.-V. Mosnes, unpublished, cited in Behrens Yamada et al. [218]) and a 92 mm male crab from Denmark was reported by Rasmussen [209]. The largest reported female in the native range measured 75 mm from England [226]. The smallest maximum CW reported for males within the native European population is 62 mm from England [231] and more recently 63 mm from the Netherlands [232]; the smallest maximum female reported is a 56 mm crab from Portugal [173]. Based on an analysis of carapace width in 28 native European sites gleaned from a literature review, Kelly et al. [241] concluded that *C. maenas* appears to follow the temperature-size rule for ectotherms, whereby the largest individuals are found in the coldest parts of the range and a linear regression analyzing male maximum carapace width and the latitude of each sample site in the native range found that latitude explained 61% of the variation in CW [39]. A later study concluded that adult body size showed negative correlation with environmental temperature in both the native and invaded northeastern Pacific ranges [241]. However, several size data values for the native population included in Table S1 in [241] and attributed to various authors actually are not found in the papers therein cited (e.g., sites Ria de Aveiro and Mondego estuary, Portugal; Thurlestone, UK; Dutch Wadden Sea, Netherlands; and the 100 mm value for Gullmarsfjorden, Sweden). Furthermore, a large number of reported values were not included in that analysis, including reports of some of the largest (86 mm) crabs collected near the middle of the range for both latitude and temperature. Elimination of the unsubstantiated data and inclusion of all of the data in our Table 2 suggests that the temperature-size rule actually may not apply to the native population.

The largest size reported for a male crab in the northwestern Atlantic population is 91 mm from both the northernmost part of the range in Nova Scotia [235] and much farther south in New Hampshire [182]; the largest female crab measured 88 mm from New Hampshire [182]. The smallest maximum size for males (69 mm) is also found in Nova Scotia [235] and for females (70 mm) from Maine [139]. Unfortunately, no size data have been published for crabs between Massachusetts and Maryland so any examination of the temperature-size rule would be limited to a small portion of the northwestern Atlantic population at the current time.

In the northeastern Pacific population, crabs from near the northern range limit in British Columbia tend to be larger than those from near the southern limit in California [39,245,246]. In this population the temperature-size rule appears to apply, based on collections from ten sites [241]. The largest *C. maenas* on record is a 114 mm red male from Barkley Sound, British Columbia and a red female with CW 93 mm was found in the same location [241]; however, the second largest size reported for a female is 89 mm for crabs found in both Oregon and near the southern limit of the range in California [241].

Although the temperature-size relationship is unclear, it does appear that *C. maenas* in both the northwestern Atlantic and northeastern Pacific nonindigenous populations tend to be larger overall than those in the native European population [198,241,247]. Furthermore, with only rare exceptions (see Young et al. [113]), males are larger than females. Grosholz and Ruiz [31] suggest that crabs of size 110–115 mm CW may be attainable; to date the largest *C. maenas* on record is the 114 mm male from British Columbia mentioned above [241].

6.2. Size at Sexual Maturity

The minimum size of sexually mature *C. maenas* varies considerably with no specific trend evident. It also should be noted that physiological maturity precedes morphological maturity [200]. In the native range the greatest minimum size of sexually mature *C. maenas* males is given as 44 mm in Norway [189], South Wales [5], UK [192] and Belgium [188] whereas the smallest sexually mature males (27 mm) have been reported from Portugal, many kilometers to the south [193,195]. For females the data are more variable, ranging from 38.6 mm in Ireland [200] to 21.5 mm in Portugal [193]. In the northwestern Atlantic, there are only three reports for male minimum size at maturity, 34 mm in Maine [139], 32 mm in Newfoundland [196], and 21.3 mm in PEI [147]. For females the minimum size at sexual maturity ranges from 40 mm in Nova Scotia [235] to 22 mm in Massachusetts (AM Young, personal observation). For the northeastern Pacific population the only value reported is an estimated 34 mm for females in California [8]. In Argentina, Vinuesa [82] 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. See Table 2 for additional data for the native European and nonindigenous northwestern Atlantic populations.

7. Population Characteristics

7.1. 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, owing to several factors, not the least of which is variability in time and space. The number of crabs in a particular area varies considerably with environmental factors such as temperature and salinity changes due to water depth and seasonal, diel and tidal movements, as well as internal variations attributed to sex, spawning, molting and life stage (juveniles versus adults) and biotic interactions with other species [93]. 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 Pihl & Rosenberg [98]. Individuals can be counted directly along a transect or within quadrats (see for example [52,105,125,145,248]) 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 [95,109,249,250]. 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 [113]. 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 trap design, 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) [2,113,124,143,251,252], crab state (newly molted and ovigerous females tend to burrow and do not feed) [2,112], and mobility (the population as a whole is very active, migrating many meters, even kilometers, in a matter of a few hours) [21,115]. Furthermore, there are concerns that the presence of large crabs or large numbers of crabs in a trap dissuades additional crabs from entering [251,253]. It is estimated that only 80% of a green crab population can be caught at any one time using traps [2]. Underwater video used to evaluate the effectiveness of Fukui traps to catch green crabs revealed only a 16% success rate out of 1226 entry attempts [254]. It has been shown recently that certain modifications to the Fukui traps can significantly increase productivity up to 59% [255]. 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. Trawling may be used if the bottom conditions are suitable [256] but often they are not due to the crab's preference for bivalve beds or other geometrically complex areas. 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 a *C. maenas* population in areas of the Kattegat in Denmark [220]. 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 [21] used a suture-tag method described by Edwards [257] 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 6800 or 0.7%), making any accurate determination of growth rate or population size impossible. Nearly 3000 crabs tagged with Floy tags inserted into the right gill chamber along the suture line yielded approximately a 15% recovery [258]. Crabs marked by branding a code on the dorsal carapace with a battery charged soldering bolt retained the marks after molting, although the marks changed color from red to white [187]. Due to the difficulty in 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.

7.2. Sex Ratios

Another aspect of *C. maenas* population dynamics is the male to female sex ratio determined by trapping or other survey methods. Sex 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 [113,150]. 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 [143,144,146,176]. Multiple studies in Europe [3,145,177,259] and the western Atlantic [113,149,182,198,260] 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 [125]. 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 [143–145,261] 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 [112,113,182,262].

Most of the sex ratios reported for the native European population show male bias (see Table 3) but in the Mondego estuary in Portugal (latitude 41° N) females outnumbered males caught (SR = 0.89) whereas the sex ratio of juvenile *C. maenas* in upstream areas favored males in the winter months [150], suggesting that females migrate to downstream areas when they are approaching maturity and will be ready to mate. In the northeastern Pacific nonindigenous population male biased ratios are more common in the higher latitude portion and female biased ratios are more common in the lower latitude portion of the range. 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 [241] (See Table 3 for details).

Table 3. Sex ratios (M:F) for various populations of *C. maenas*. Value > 1 indicates a higher proportion of males; value < 1 indicates a higher proportion of females.

Location	Latitude (to Nearest Degree)	Sex Ratio (M:F)	Reference
Native European Population			
Herdla, Norway	61° N	1.55; 1.48	[187]
Herdia, Norway	61° N	1.49	[185]
Kattegat, Denmark	57° N	51.63 * (shallow) 21.99 * (deeper)	[220]
Forth Estuary, Scotland	56° N	0.68	[259]
Firth of Forth, Scotland1	56° N	0.85	[107]
Kerteminde	55° N	2.99	[145]
Fjord, Denmark	55° N	2.99	[145]
Kerteminde	55° N	1.01	[225]
Fjord, Denmark	55° N	1.01	[225]
Menai Strait, Anglesey, UK	53° N	1.86	[263]
Whitby Harbor & Robin Hood's Bay, England	53° N	0.45	[226]
Ynys Faelog, Menai Strait, North Wales	53° N	2.33	[143]
Den Helder, Netherlands	53° N	0.62	[3]
Bullens Bay, Ireland	51° N	1.89	[200]
Looe Estuary, Cornwall, England	50° N	0.64	[233]
Mondego estuary, Portugal	41° N	0.89	[150]
northwestern Atlantic nonindigenous population			
Placentia Bay, Newfoundland, Canada	48° N	1.00 (September) > 1.00 (June) 1.76 (fall)	[264]
Placentia Bay, Newfoundland, Canada	48° N	1.33 (spring) 1.29 (summer)	[196]
Basin Head, PEI, Canada	46° N	1.63	[147]
Bras d'Or Lakes, Nova Scotia, Canada	46° N	2.70	[235]
Port L'Hebert, Nova Scotia, Canada	44° N	1.18 (May) 0.79 (August)	[122]
Boothbay Harbor, Maine	44° N	1.29	[139]
Days Cove, Damariscotta, Maine	44° N	1.57	[239]
Broad Cove, Yarmouth, Maine	44° N	0.60	[239]
Biddeford Pool, Maine	43° N	< 1.00 in 74.4% of samples	[125]
Webhannet River, Wells, Maine	43° N	0.94	[239]

Table 3. Cont.

Location	Latitude (to Nearest Degree)	Sex Ratio (M:F)	Reference
Great Bay Estuary, New Hampshire, US	43° N	1.00	[265]
Great Bay Estuary, New Hampshire, US	43° N	0.37	[182]
Houlton-Seabrook Estuary, New Hampshire, US	43° N	0.98	[182]
Plum Island Sound, Massachusetts, US	43° N	0.34 (upstream) 0.90 (downstream)	[112]
Great Marsh, Rowley, Massachusetts, US	43° N	0.73	[260]
Great Marsh, Rowley, Massachusetts, US	43° N	1.11	[266]
Salem Sound, Massachusetts, US	42° N	0.37	[113]
Nauset Marsh, Eastham, Massachusetts, US	42° N	0.26	[260]
northeastern Pacific nonindigenous population			
Nootka Sound, British Columbia, Canada	49° N	4.18	[198]
Clayoquot Sound, British Columbia, Canada	49° N	3.88	[198]
Barkley Sound, British Columbia, Canada	49° N	1.58	[198]
Barkley Sound, British Columbia, Canada	49° N	2.45	[263]
Barkley Sound, British Columbia, Canada	49° N	1.61	[59]
Pipestem Inlet, British Columbia, Canada	49° N	1.71	[241]
Tillamook Bay, Oregon, US	45° N	8.25	[241]
Netarts Bay, Oregon, US	45° N	4.04	[241]
Yaquina Bay, Oregon, US	44° N	6.00	[241]
Coos Bay, Oregon, US	43° N	3.45	[241]
Bodega Harbor, California, US	38° N	3.07	[241]
Tomales Bay, California, US	38° N	2.36	[241]
Seadrift lagoon, California, US	38° N	0.73	[241]
San Francisco Bay, California, US	37° N	0.63	[241]
Elkhorn Slough, California, US	36° N	0.72	[241]
Argentina nonindigenous population			
San Jorge Gulf, Patagonia, Argentina	45° S	2.36	[82]

* ratio calculated from percentages of males and females.

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 3). Male biased ratios appear to be more common in the higher latitude (colder) portion of a range 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 [147], but female-biased in the more southerly area of southern Maine [125], New Hampshire [182] and Massachusetts [113,260]. Although sex ratio appears to be correlated with latitude, it is quite possible that other factors may in fact influence the ratio, such as when (both seasonal and daily variations) and how (type of traps or seining) crabs were collected. 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 [112] 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 [126]. Similarly, in Placentia Bay, Newfoundland, the overall proportion of sexes was reported to be 60% male and 40% female (exact SR = 1.48) but the sex ratio varied from a high of 1.76 in the fall to a low of 1.29 in the summer [196].

8. Ecosystem Dynamics

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

8.1. Diet

Juvenile *C. maenas* feed primarily on detritus and interstitial meiofauna and then become more carnivorous as they age [97,99,267,268]. Green crab adults are opportunistic omnivores, whose diet varies with season, composition of the community, size of prey, availability of prey and energy expenditure versus energy gained [116,262,269]. Green crabs are known to feed on organisms from at least 158 genera in five plant and protist and fourteen animal phyla [9,28,36,270], with members of all populations showing a strong preference for molluscs, especially bivalves such as clams, mussels and cockles [9,30,44,66,99,136,228,249,271–278]. Additional preferred prey items include gastropod molluscs such as periwinkles [8,37,275,279], other crustaceans such as the common brown shrimp *Crangon crangon* [262] and recently settled small juvenile lobsters *Homarus americanus* [280] as well as members of their own species [101,105,106,205,249], polychaetes [281] and amphipods [30]. There appears to be no difference in foraging between males and females, suggesting that the two sexes are probably ecological equivalents [234]. In addition to being predators of a large variety of organisms, green crabs are also scavengers of any dead material along the shore [22,112].

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 weight [262]. In the Menai Strait, North Wales and in the Rance Basin, France, green crabs were reported to eat mostly other crustaceans, polychaetes and algae [122,282]. Jensen & Jensen [273] found that younger *C. maenas* in the Danish Wadden Sea favor the common cockle, *Cerastoderma edule*, over other prey items. Scherer & Reise [249] found that older males continue to feed on molluscs but older females feed primarily on annelid worms, although Baeta et al. [262] 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. More research should be done in the topic of differential feeding by different size classes, as it could be utilized for selective removal of certain size classes when trapping.

In the nonindigenous population in South Africa the most important prey items, based on gut contents, were gastropods, isopods and polychaetes (see Le Roux et al. [65] 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 [78,244,283]. 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 Crothers [2]; Le Roux et al. [65]; Behrens Yamada [8]; Klassen & Locke [9].

Herbivory in larger crabs may be by accidental ingestion [262], but there is evidence that some portunid crabs feed selectively on plant material or algae [65,112,122,282]. 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* [284]. The wide variety of prey items that *C. maenas* consumes indicates that they are resilient, and can survive on whatever food is available [8]. Green crabs can even survive three months of starvation [285].

8.2. 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 [2]. 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 [198].

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. Within the native European population in South Wales, there were 29 other crab species in localities where green crabs were found [286], many of which eat similar food, so *C. maenas* could be in competition with at least some of them [2], but they all have slightly different habitat preferences that serve to keep them apart (fragmentation of the niche) [287]. Crothers [2] 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 [288]. 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* [289]. A sibling species, the Asian shore crab, *H. sanguineus*, is also found in European waters, having arrived by 2003 in the Mediterranean Sea [290], around 2007 on the coast of France [291] and then Helgoland, Germany, where it is now the second most abundant intertidal crab in the North Sea after *C. maenas* [171]. It is predicted that the Asian shore crab will assert competitive dominance over the green crab in this region [171].

The native rock crab, *Cancer irroratus*, and *Carcinus maenas* coexist in southwestern Nova Scotia so they may compete for resources [122,292,293]. The rock crab is a larger species that is known to outcompete *C. maenas* in a lab setting [294], 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 [136]. 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 [295]. In Prince Edward Island green crabs and rock crabs seemed to avoid each other on mussel clumps, suggesting that the two species could coexist [296]. In the Bras d'Or Lakes, Nova Scotia, rock crabs consumed large numbers of juvenile green crabs [297]. In contrast, another study determined that rock crabs were being displaced or preyed upon by *C. maenas* in Newfoundland [278]. 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 with *C. maenas* [99,112,122,298]. In laboratory experiments adult green crabs were able to physically compete with and, in many cases, dominate larger, heavier lobsters [298]. In addition to consuming small juvenile lobsters green crabs curtail the overall foraging activity and shelter use by lobsters [265,299,300] and may be able to locate and consume a food source before the lobsters can get to it [238]. 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 [301].

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 *Metacarcinus* (formerly *Cancer*) *magister* (Dungeness crab) whereas adult *M. magister* could out-compete adult green crabs, but they do not currently share the same habitat so are actually not in direct competition [302]. Limb autonomy was more common in adult *C. maenas* in areas of Bodega Bay, California that were inhabited by red rock crabs *Cancer productus* and brown rock crabs *Cancer antennarius*, likely due to predation by adult rock crabs [9,303]. At Pipestem Inlet, British Columbia, Gillespie et al. [198] noted mixed catches of *C. maenas* and the smaller graceful rock crab, *Cancer gracilis*. Both of these species are likely using this low salinity area as a refugium from the larger adult red and brown rock crabs so these two species may be in direct competition. However, green crabs were common and *C. gracilis* absent in traps set high in the intertidal but the reverse was true for traps set in the low intertidal and subtidal areas, suggesting that these two species are showing niche segregation to avoid interactions [304].

The Asian shore crab, *H. sanguineus* has recently invaded parts of the northwestern Atlantic where it competes with established *C. maenas*, and a native northeastern Pacific sibling species, *H. oregonensis*,

that has several common names (yellow shore crab, hairy shore crab, mud-flat crab, Oregon shore crab), is now in direct competition with recently invasive *C. maenas* [114,276,304–306]. Under controlled experimentation *H. sanguineus* was overwhelmingly dominant over *C. maenas* whereas *C. maenas* dominated over *H. oregonensis* [114]. 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 [114]. Along the southern New Jersey, Long Island and southern New England coastlines, *H. sanguineus* has essentially eliminated juvenile *C. maenas* in the rocky intertidal zone where it formerly was extremely abundant [248,306–312] and apparently the same thing has happened along the Delaware coastline [313]. In southern New England juvenile *C. maenas* were the numerically dominant species in the rocky intertidal zone [314] but *H. sanguineus* is now the numerically dominant (90%) crab species [310,315] while *C. maenas* densities have declined 40–90% [306]. *Hemigrapsus sanguineus* can outcompete *C. maenas* for food and shelter resources, forcing *C. maenas* to not only occupy a less-desirable habitat but also alter its diet from bivalves, its preferred prey, to more algae [114,284]. In laboratory experiments green crabs were superior competitors to both blue crabs and Asian shore crabs [308], but that does not seem to be the case in the wild, where *H. sanguineus* adults either prey on or displace *C. maenas* recruits [306,316].

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

8.3. Predators

The major predators of *C. maenas* include many species of birds, fish, and other crustaceans, such as the rock crabs and lobsters discussed above (for more in-depth discussion of various predators and lists of predators, see Crothers [2]; Cohen et al. [36]; Klassen & Locke [9]; Wong and Dowd [317]). 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 [101,105,106,112,262,318]. Predators other than in those three groups include a few mammals such as mink, *Mustela vison* and otters, *Lutra lutra* [319,320] and harbor seals, *Phoca vitulina* [321]. 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 [40]. In laboratory studies juvenile green crabs are superior competitors to juvenile blue crabs [304] but adult blue crabs are more than twice the size of green crabs and readily prey on them [40]. As *C. maenas* has expanded northward into Canadian waters, interactions with native lobsters (*Homarus americanus*) have increased. Usually adult green crabs retreat from encounters with the larger lobsters but some antagonistic responses result in the crabs being eaten [237,322].

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 [22]. In Canada, a green crab fishery for food is being explored [323] 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 [324,325]. 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 [181]. There currently is considerable interest and progress in the Atlantic Canada and New England region for development of a variety of green crab based food products [323,326–331], with whole books dedicated to the cooking of green crabs [332]. The variable colors (green, yellow,

orange, red) seen on the ventral surface of *C. maenas* are potential indicators for various physiological processes [1,113,139,174,333–335]. 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 *Carcinus 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) [181]. Beyond predation for food consumption, humans also collect green crabs for other uses, such as fish, conch and lobster bait [22,336] and fertilizer [327], as well as utilizing chitin as an intermediate material in the production of self-healing car paints [337], cosmetics [338], antimicrobial textile treatments [339], bioadhesive delivery gel [340], and inexpensive antiviral drugs [341], an affinity ligand for protein purification [342], or just to reduce the density of invasive populations [9,278,343].

8.4. Epibionts

In the native European and nonindigenous northwestern 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 increases as the crabs age without molting, so red crabs are the most heavily fouled [2,113,344]. 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 [344,345]. The authors are not aware of any published information on *C. maenas* epibionts in any of the other nonindigenous populations.

8.5. 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 Leignel et al. [28]). Green crabs have recently been identified as a carrier of novel pathogenic species, from viruses [346] to parasitic Metazoa [347]. While there are a number of parasites that infect green crabs (see lists in Crothers [2], Torchin et al. [348]; Behrens Yamada [8]; Klassen & Locke [9]), the most famous and well-studied is 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 [349], and the Dutch Wadden Sea [350]. 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 [344], and it has been shown most recently that the success of male green crab *S. carcini* acquisition is susceptible to both seasonal and regional variation in the native range [351]. Infected crabs are castrated by the parasite and cease molting [219,345,352]. As is the case with many species, green crabs in non-native populations are substantially less infected by parasites than in the native population [348]. In Europe, approximately 16% of green crabs are infected with *S. carcini* but the parasite is not found in any of the nonindigenous populations. Although the global success of *C. maenas* is attributable to multiple factors, the escape from *S. carcini* has been hypothesized to be a major reason for the success of green crabs in nonindigenous ranges [348]. Parasites such as *S. carcini* suppress *C. maenas* populations in many areas of Europe, and the escape from these natural enemies increases the performance where green crabs have invaded [353]. Non-native crabs in some populations are infected with some of the other parasitic worms, including trematodes, nematodes, acanthocephalans and nemerteans [9,348], but the parasite load in introduced regions generally amounts to only a fraction of that in the native region [353]. Furthermore, the parasites that are most commonly acquired in introduced regions (such as the trematode, *Microphallus similis*) do not have the same lasting effects on physiology and behavior as *S. carcini* [354]. Several parasitic species, including *S. carcini*, have been proposed as potential biological control agents for invasive green crabs [8,28,355,356] but any intentional introduction of another species into an environment is risky and could result in the death of native crab species [357].

9. Ecological Impacts

The green crab is considered an “ecosystem engineer” because it has the ability to modify entire ecosystems [9,358,359], including such habitats as mudflats [252], saltmarshes [112,360], eelgrass beds [361–363] and rocky shores [364]. Both native and nonindigenous populations of *C. maenas* have had impacts, mostly negative, on ecosystem components. For examples, in the Menai Straits it has had a devastating effect on commercial mussel beds [365], and has reduced the density of cockles, *Cerastoderma edule*, in the Danish Wadden Sea [273] and *C. edule* and *Macoma balthica* in Scotland [366]. 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 [367]. Negative impacts have been far greater in the invaded ranges, however. In the northwestern Atlantic, *C. maenas* has caused considerable damage to blue mussels [276], American oysters *Crassostrea virginica* [292], rock crabs *Cancer irroratus* and lobsters *H. americanus* [280] along the Atlantic Canada and New England coasts [278]. 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 [126], 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 [106]. It has been labeled a “moderate to high risk” species, both environmentally and economically, for both coasts of Canada [215].

Green crabs have had a devastating effect on the economically important soft-shell clam *Mya arenaria* industry in New England [44,112,271,272,274,277,368–370]. 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 [19,44,368]. 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 subsequent sharp declines in the commercial harvest of soft-shell clams [371] only do adult green crabs feed on juvenile and adult clams but postlarval and juvenile crabs prey heavily on newly settled clam larvae [369,372–375]. Green crabs also prey on juveniles as well as settling and newly settled postlarvae of another economically important species, American lobsters [280,298–300,376]. 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 [359,361–363,377–379]. Similarly, it has been concluded that green crabs indirectly caused a collapse in a unique strain of giant Irish moss (*Chondrus crispus*) in Prince Edward Island waters by consuming small blue mussels (*Mytilus edulis*), thereby depleting the mussel clumps required as attachment surfaces by the Irish moss [236].

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 but recent models project a potential loss of 2.8–64% in commercial shellfish harvest in Puget Sound as green crab densities increase [61]. 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* becomes abundant, those wading birds could be affected adversely [8,252]. Field experiments have also shown that green crab predation has facilitated the invasion of non-native clams in Bodega Harbor [25]. In laboratory experiments to evaluate competition for food, *C. maenas* out-competed juvenile Dungeness crabs *Metacarcinus magister* so increased numbers of green crabs could adversely affect that commercially important species [60,302]. 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 [8,380]. However, changes in outplant timing was found to mitigate these potential impacts [381]. 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 [8,75] but there is concern for the commercial cockle fishery in South Australia [244].

Another potential ecological impact is the transmission of parasites and other symbionts from *C. maenas* to commercially important native crustacean species. A recent histological survey for symbionts of *C. maenas* identified 19 separate symbiotic associations in crabs collected from 27 sites. These included a variety of metazoan parasites, microbial eukaryotes, bacteria, and viral pathogens, some of which may pose a risk of transmission to other decapods and native fauna via the use of green crabs as bait [382].

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 [8,34,383–385].

10. Conclusions

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 $-1\text{ }^{\circ}\text{C}$ or exceed $22\text{ }^{\circ}\text{C}$ 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 fall below 4‰ or exceed 31‰ for adults (20‰ for larvae) for extended periods. Geometrically complex habitats such as cobble or mussel beds 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, but also to non-standardized methods for collecting data. For example, there is considerable variability in sex ratios reported for different populations, depending upon geographic as well as within-site location, time of year, and other considerations. One variable that often is not considered is method of collection, whether various nets and traps yield different results in the same study site. Part of a recent study [113] compared several different style traps and baits for their ability to catch crabs but more extensive comparisons are needed to determine if trap or net type affects not just the overall numbers but the size, age and sex data of crabs caught. In some cases the lack of information is simply due to few studies being conducted within certain portions of a population's range. For example, there are almost no data on crabs found south of Massachusetts in the northwestern Atlantic population. Knowledge of population density in an area is of considerable interest and importance for understanding population dynamics but turns out to be a very difficult value to measure, especially by the traditional tag & recapture method for mobile animals, due to the potential loss of tags during molting as well as the large numbers of crabs that travel extensively over wide areas in short amounts of time. There even is lack of agreement on whether crabs move offshore during the cold winter months or stay near shore, perhaps in tunnels or burrows made by other organisms or the crabs themselves.

The nonindigenous populations in the northeastern Pacific, South Africa and Argentina have been established much more recently than that in the northwestern Atlantic and have been the subject of fewer studies, as has the long-established populations in Australia. Little has been published concerning some important aspects of the biology of *C. maenas* in these populations (e.g., size at sexual maturity, reproductive periods, longevity) and especially ecosystem functions (e.g., 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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