Overview on the European green crab *Carcinus* spp. (Portunidae, Decapoda), one of the most famous marine invaders and ecotoxicological models

V. Leignel · J. H. Stillman · S. Baringou · R. Thabet · I. Metais

Received: 11 February 2014 / Accepted: 23 April 2014 / Published online: 6 May 2014
© Springer-Verlag Berlin Heidelberg 2014

**Abstract** Green crabs (*Carcinus*, Portunidae) include two species native to Europe—*C. aestuarii* (Mediterranean species) and *C. maenas* (Atlantic species). These small shore crabs (maximal length carapace, approximately 10 cm) show rapid growth, high fecundity, and long planktonic larval stages that facilitate broad dispersion. *Carcinus* spp. have a high tolerance to fluctuations of environmental factors including oxygen, salinity, temperature, xenobiotic compounds, and others. Shipping of *Carcinus* spp. over the past centuries has resulted in its invasions of America, Asia, and Australia. Classified as one of the world’s 100 worst invaders by the International Union for Conservation of Nature, *Carcinus* spp. are the most widely distributed intertidal crabs in the world. Their voracious predatory activity makes them strong interactors in local communities, and they are recognized as a model for invastiveness in marine systems as well as a sentinel species in ecotoxicology. This review shows an exhaustive analysis of the literature on the life cycle, diversity, physiological tolerance, genomic investigations, ecotoxicological use, historical invasion, control programs, and putative economical valorization of shore crabs.

**Keywords** *Carcinus* · Ecotoxicology · Indicator · Invader · Review · Pollution

**Introduction**

Description of *Carcinus* species

In 1814, Leach defined the *Carcinus* genus, including a unique species *Carcinus maenas*, previously described as *Cancer maenas* (Linnaeus 1758), and sometimes written as *Carcinoïdes maenas* or *Carcinoides maenas*. The morphological characters of *C. maenas* that allows easy identification include five teeth on the anterolateral margin of the carapace, a slight projection of the front of the carapace with a rounded rostral area, orbit with a dorsal fissure, and a fifth leg with a wider unspatulated dactyl (Fig. 1). The abdomen has three to five fused somites; its form is triangular for males, but circular for females (Squires 1990). Two major color morphs exist—green and red (Crothers 1968)—which represents different stages in the molt cycle. Though *C. maenas* are commonly observed in estuary and rocky zones, they are able to colonize a broad range of habitat types (salt marshes, woody debris, rocky substrate, and seagrass). Postlarval and adult crabs are abundant in the intertidal and subtidal zones, occurring as deep as 60 m (Elner 1980). *C. maenas* is distributed from Northern Europe (Baltic Sea, Iceland, and Central Norway) to the North African coasts (Morocco and Mauritania) and the Mediterranean Sea.

Nevertheless, in 1847, Nardo established morphological distinction between Atlantic and Mediterranean green crabs, describing the species *Carcinus aestuarii* (also known as *C. mediterranea* or *C. mediterranius*) which presents a restrictive geographical distribution in the Mediterranean and Black Seas (Behrens Yamada and Hauck 2001). Although the two species are highly similar, Cohen et al. (1995) and Behrens Yamada and Hauck (2001) confirmed the discrimination of *C. aestuarii/C. maenas* using morphological criteria. Characters used to differentiate these species include carapace parameters as follows: width/length ratio, width/depth ratio,
appearance of dorsal surface, margin of frontal area between the eyes, and segmentation of first and second antennae; for C. maenas, pleopods of male are crescent-shaped and curves outward with the center of the crescents touching, whereas for C. aestuarii, they are straight and parallel. For C. aestuarii, the frontal area is flat without distinct bumps that are not protruding, and it is bordered by three scalloped-shaped lobes with bumps that are not protruding (Behrens Yamada and Hauck 2001). In contrary, based on crabs (n=20) from the Atlantic, Mediterranean, and Pacific collection sites, Clark et al. (2001) found morphological overlap of individuals among Atlantic and Mediterranean sites suggesting lack of complete separation of European shore crabs, with potential hybridization zone in southwestern Iberian which was confirmed by Carlton and Cohen (2003).

Analyses of ribosomal (16S) and mitochondrial (cytochrome oxidase subunit I) gene sequences confirmed the status of the two species (Geller et al. 1997; Roman and Palumbi 2004) with hybridization in Japan and South Africa (Darling 2011a). This genetic distinction was also demonstrated in the plankton larvae (Darling and Tepolt 2008). Cytochrome oxidase I (COI) sequence variation revealed the existence of three genetic C. aestuarii groups (Adriatic, Ionian, and Tyrrhenian and West Mediterranean Sea), explained by Mediterranean Sea topography, convection, and counterclockwise circulations that form physical barriers, favoring local larval retention (Patarnello et al. 2007; Marino et al. 2011). In C. maenas, COI sequence also revealed three genetic groups (off-shelf, Northern Europe, and Western Europe) according to regional current patterns causing local larval retention associated with seasonal circulation in the North Sea (Roman and Palumbi 2004; Darling et al. 2008; Domingues et al. 2010; Marino et al. 2011).

Sexual dimorphism exists in both Carcinus species. The length, convexity, and width of the carapace are clearly distinct between the two sexes of C. maenas where female carapaces are more convex to accommodate gonadal tissue (Ledesma et al. 2010; Ozbek et al. 2012). It was also demonstrated that the number of eggs is correlated with the carapace width of the C. aestuarii females (Ozbek et al. 2012). Adult males are always larger than females in both Carcinus species (Koçak et al. 2011; Matozzo et al. 2013).

Life cycle of Carcinus spp.

Green crabs have planktonic larvae, and benthic adults inhabit estuaries and rocky shores. These iteroparous crabs live up to 7 years (Klassen and Locke 2007). Individual crabs can mate multiple times within a single year, but females probably produce eggs only once per year (Klassen and Locke 2007).
Histological analysis showed that the ovarian development occurred biannually, correlating to two seasonal breeding groups—a primary winter cycle and secondary summer cycle (Lyons et al. 2012). Color changes in Carcinus from green (pre molt crab) to red indicating sexual maturation (Styrishave et al. 2004). Melting occurs primarily in spring and summer; in Northern Hemisphere sites (e.g., Maine, USA), egg laying occurs between May and July (Berrill 1982). In comparison, male C. maenas in the Southern Hemisphere (e.g., Argentina) molt in November and females molt in January–March (Vinuesa 2007). After copulation, female crabs move to lower littoral levels where they remain through the fall and winter. Embryos develop from May to September along the Argentinean coasts (Vinuesa 2007). For C. aestuarii, the reproductive period seems to be from November to February, with maximum ovigerous females in January in the Homa Lagoon (Turkey) (Ozbek et al. 2012) whereas it was noted from November to early May, with maximum in February, in San Teodoro (Italy) (Mori et al. 1990).

Females produce up to 370,000 embryos/brood (Grosholz and Ruiz 2002; Lovell et al. 2007), which hatch during the summer or winter. The larval pelagic duration of ~90 days is comprised of four planktonic zoeal stages, which display vertical migration behavior in pelagic environments, and one megalopal stage, which settles into benthic habitats before metamorphosis to the first crab stage (Rice and Ingle 1975; Dos Santos et al. 2008). Larval growth and development depend upon temperature, salinity, and food availability. C. maenas larvae eat mainly phytoplankton (Harns et al. 1994; Gimenez 2010). The daily mortality rate of larvae was estimated at 7%, which is equivalent to that of other decapod larvae (Rumrill 1990). Megaporal cohorts are localized along coasts with high dispersal capacity, estimated from 57 to 198 km (Domínguez et al. 2010, 2011, 2012). Sexual maturity occurs within 1 or 2 years (3–4 cm carapace length), but exact times are variable among geographical regions (Berrill 1982; Mori et al. 1990; Grosholz and Ruiz 2002; Vinuesa 2007; Coelho et al. 2008; Lyons et al. 2012; Ozbek et al. 2012).

Carcinus adults are voracious omnivores, aggressive competitors, and have a high impact on the populations of amelids, gastropods, bivalves, fish, algae, and other crustaceans (shrimp, crab); cannibalism is also common (Moknes 2004; Baeta et al. 2007). Green crab adults consume at least 104 distinct families of marine organisms included in 14 animal phyla (Ameyaw-Akumfi and Hughes 1987; Klassen and Locke 2007; Mowles et al. 2011). Their primary mode of foraging is chemosensory, not visual (Robinson et al. 2011) and Hauck 2001). They are also tolerant to food deprivation. Starvation during molting periods (ecdysis) induced no major physiological performance decline in C. aestuarii, but did influence the crab immune system (Matozzo et al. 2011a). The ability for C. maenas adults to survive without food for over 3 months was also demonstrated by Wallace (1973). C. maenas shows acclimation responses in muscle membrane lipid composition and fluidity (Cuculescu et al. 1999) and modest plasticity in thermal tolerance.

Temperature acclimation

Temperature is one of the most important environmental factor affecting the physiology, behavior, phenotypic traits, reproduction, distribution, and metabolic rate of aquatic ectotherms (Somero 2002; Atkinson 1994). Temperature impacts an organism’s fitness through its pervasive effects on most biological processes. Green crabs are eurythermic, able to survive temperatures from freezing to 35 °C, and to mate from 18 to 26 °C (Klassen and Locke 2007; Tepolt and Somero 2013). Kelley et al. (2013) demonstrated that C. maenas may be maintained at or below 5 °C during 18 weeks of experiments without behavioral disturbance. In laboratory conditions, the critical thermal maximum (CTMax) of C. maenas has been estimated at 35.1±0.8 °C (Madeira et al. 2012), a heat tolerance higher than in most subtidal decapods (Hopkin et al. 2006; Tepolt and Somero 2013). CTMax values are influenced by collection time, collection location, and thermal history, including temperature acclimation or aclimatisation across thermal (latitudinal) gradients (Tepolt and Somero 2013). For example, Cuculescu et al. (1988) estimated that CTMax may be higher (35.8±0.11 °C) if the crabs were caught in autumn and pre-acclimated from 8 to 22 °C (Table 1). Winter-caught crabs had lower CTMax values than summer- and autumn-caught crabs that were acclimated to winter temperatures (Table 1; Hyde et al. 2012). Kelley et al. (2011) demonstrated that green crabs (C. maenas) collected in

Table 1 Critical thermal maxima of Carcinus maenas extracted from Cuculescu et al. (1988) demonstrating effects of season and aclimation. Mean values±SEM, significantly different groups (P<0.05) are denoted with different symbols. Crabs were acclimated for 3 weeks at 8 °C before their CTMax was determined. They were then transferred to 15 °C for a further week after which they were kept at 22 °C for 3 weeks and their CTMax was determined. Water was heated at a constant rate of 0.28 °C per min.

<table>
<thead>
<tr>
<th>Acclimation Temperature (°C)</th>
<th>Summer caught CTMax</th>
<th>Autumn caught CTMax</th>
<th>Winter caught CTMax</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>31.8±0.27</td>
<td>33.5±0.50</td>
<td>31.3±0.24</td>
</tr>
<tr>
<td>15</td>
<td>34.2±0.12</td>
<td>32.5±0.20</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>35.4±0.26</td>
<td>35.8±0.11</td>
<td></td>
</tr>
</tbody>
</table>

Physiological capacities of Carcinus spp. to cope with major environmental factors

Carcinus spp. are known for high tolerance to varying environmental abiotic conditions (Fehsenfeld et al. 2011), including air exposure, temperature, and salinity (Behrens Yamada

and Hauck 2001).
southern (Stinson Beach, California, CA, USA) and northern (Vancouver Island, British Columbia, BC) zones in North America did not show the same CTMax after experimental acclimation (Table 2), suggesting local population differentiation and/or developmental plasticity in heat tolerance. Variation in CTMax may be correlated to heat shock protein synthesis. Crabs (C. maenas) living in Southern USA (CA, California group) synthesized more heat shock protein 70 (HSP70) than Northern crabs (BC, British Columbia group) when they were acclimated to 6 °C (Kelley et al. 2011).

Larvae exhibited higher physiological tolerances to temperature fluctuations than adults (DeRivera et al. 2006). For example, successful metamorphosis from C. maenas larvae to juveniles occurred at temperatures between 9 and 22.5 °C (Dawirs et al. 1986), whereas molting, growth, and feeding of C. maenas adults are affected by seasonal temperature fluctuation (Berrill 1982; Cohen et al. 1995; Eriksson and Edlund 1977; Behrens Yamada et al. 2005). C. maenas juveniles were found to be more tolerant to temperature and salinity variations than older individuals, influencing their distribution in estuary and coastal zones (McKnight et al. 2000; Baeta et al. 2005; Todd et al. 2005). Thus, larvae and juveniles are the primary stages for geographic spread, suggesting that C. maenas has high capacity to establish populations in latitudinal ranges outside the geographical range where adults breed (DeRivera et al. 2006). Accordingly, temperature increases predicted in global climate change scenarios may promote the global spread of C. aestuarii and C. maenas (Compton et al. 2010).

Temperature variation alters response to an array of physiological performance parameters, including oxygen consumption rates, immunity, and digestion. McGaw and Whiteley (2012) showed that a temperature increase (from 10 to 20 °C) increased contraction in the foregut and food transit rate through the gut, and, as a result, reduced nutrient absorption efficiency for C. maenas. Truscott and White (1990) demonstrated in C. maenas that a gradual temperature variation (from 10 to 20 °C) after 5 days is related to an increase of circulating hemocytes which are involved in wound repair and defense mechanisms against parasites, viruses, and bacteria. This observation was confirmed in C. aestuarii, exhibited hemocyte proliferation when exposed to thermal stress (from 17 to 30 °C, salinity 35 psu, 5 days) (Mattozzo et al. 2011b). Disruption of homeostasis in multiple physiological pathways can lead to an increased mortality rate in these crabs (Legeay and Massabauu 2000a). Thus, sea surface temperature is likely a major limiting factor for the expansion of C. maenas around the world because it affects larval survival and alters the physiological performances of juveniles and adults (Vinuesa 2007; Tepolt and Somero 2013).

### Salinity acclimation

*Carcinus* spp. are euryhaline osmoregulators that inhabit a broad range of salinities (1.4–54 psu) during annual migration from estuaries (in spring) to marine zones (in summer) (Zanders 1980). Larval stages are less tolerant to salinity fluctuation than juveniles, which are in turn more tolerant than adults (McKnight et al. 2000; Reid et al. 1989; McGaw et al. 1992; Lee et al. 2003; Baeta et al. 2005). Zoae larvae tolerate salinity ranges from 20 to 35 psu (Edgell and Hollander 2011). *Carcinus* development is directly influenced by salinity. For example, *C. maenas* zoae larvae did not fully develop at salinities <15 psu (Anger et al. 1998; Dawirs 1985). Adults shift rapidly between osmoconforming and osmoregulating (Henry et al. 2003; Rainbow and Black 2005), though the kinetics may differ depending on environmental shifts in salinity. Jillette et al. (2011) reported that hemolymph osmolarity from *C. maenas* adults transferred from low (15 psu) to high (32 psu) salinity rapidly increased and stabilized twice as fast as during transitions from high to low salinity. Three posterior gills, numbers 7–9, have been found to be involved in osmotic and acid–base regulation, while the anterior six gill pairs function in respiratory gas exchange, as is the case in other decapod crustaceans (Fehsenfeld et al. 2011). The neurotransmission is also altered by both hypo- and hypersalinity (Rodrigues et al. 2012).

Molecular investigations identified distinct genes implicated in osmoregulation in gills. Towle et al. (1997, 2011) detected the global transcription responses during salinity stress (from 32 to 10 or 15 psu) on *C. maenas* gills. Their investigation showed that transcripts encoding Na+/K+-ATPase and cytoplasmic carbonic anhydrase were mainly upregulated between 6 and 24 h post-transfer. Transport proteins showing little transcriptional response included a Na+/H+-exchanger, a Na+/K+/2Cl− cotransporter, and a V-type H+-ATPase B subunit, all of which have been implicated in osmoregulatory ion transport across crustacean gills. Mitochondrial proliferation was noted, reflected by the upregulated expression of mitochondrial genes between 4 and 7 days post-transfer (Towle et al. 2011). Carbonic anhydrase, γ-amino butyric acid, dopamine receptors, sodium/glucose cotransporter, and chloride/bicarbonate exchanger upregulated expressions were also shown by Henry et al. (2003, 2006) and Towle et al.
Response to hypercapnia

In the short term, hypercapnia, a rapid adjustment of osmoregulation, was noted. Fehsenfeld et al. (2011) used a 4,462-feature microarray to identify a significant effect of pCO2 (53 vs 440 Pa) on gill transcripts, where changes occurred in 26% of transcripts, including those involved in cellular stress and osmoregulation. Elevated seawater pCO2 modified the membrane of gill epithelial cells, through gene expression changes of tetrastepain, integrin-alpha7, a calcium-activated chloride channel, and proteins included in a multistranded endomembrane protein of the transmembrane 9 superfamily (protein member 4=TM9SF4) (Fehsenfeld et al. 2011). Hammer et al. (2012) demonstrated that elevated pCO2 led to some disturbances in intracellular iso-osmotic regulation and a putative amino acid catabolism increase (glycine, proline) to supply the body fluids with proton-buffering ammonia (NH3). To understand how *C. maenas* will acclimate at global climate change reflected by the predicted elevation of pCO2, Fehsenfeld et al. (2011) studied transcriptome changes in gill epithelium cells following acclimation to 400 Pa pCO2. After 1 week of exposure, significant changes were detected in a calcium-activated chloride channel, a hyperpolarization-activated nucleotide-gated potassium channel, a tetrastepain, an integrin and putative syntaxin-binding protein, a protein of the transmembrane 9 superfamily, and a Cl-/HCO3- exchanger of the SLC family.

Response to pathogens/infections

*Carcinus* are susceptible to infection by viruses (Vlak et al. 2005), bacteria (e.g., *Vibrio anguillarum* in *C. maenas* (Hauton et al. 1997), *Ricketsia* like-organism in *C. aestuarii* (Bonami and Pappalardo 1980) or in *C. maenas* (Eddy et al. 2007)), dinoflagellates (e.g., *Hematodinium perezi* in *C. maenas* (Hamilton et al. 2010)), haptosporidians (e.g., *Haplosporidium littoralis* in *C. maenas* (Stentiford et al. 2013)), helminths (Zetlmeisl et al. 2011), nemerteans (e.g., *Carcinonemertes epialti* in *C. maenas* (Torchin et al. 1996)), and trematodes (e.g., the Digenean *Microphallus primus* in *C. maenas* (Saville and Irwin 2005)). The most famous parasite studied in *Carcinus* spp. is an endoparasitic barnacle, *Sacculina carcini*, which possess a planktonic cyprid larva (*C. aestuarii* (Boschma 1972); *C. maenas* (Thresher et al. 2000)). Female cyprids parasites the molting crabs and metamorphoses into kentrogon and vermigon that are localized in the hemolymph (Glenner and Hoeg 1995). No host immune response to *S. carcini* infection is noted, but a significant reduction in serum proteins and hepatopancreas necrosis was commonly observed (analysis done for *C. aestuarii* (Sanviti et al. 1981); examination of *C. maenas* (Powell and Rowley 2008)). Since 1982, two fractions were identified in the blood of infested crabs demonstrating rapid molecular responses...
against *S. carcki* infection (Herberts 1982). Several studies demonstrated that *C. maenas* possess hemocytes containing factors able to attenuate or neutralize the pathogen effects (i.e., 6.5 kDa protein (cf bactericin) and 11.5 kDa protein (cf crustin)) (Chisholm and Smith 1992, 1995; Relf et al. 1999; Tincu and Taylor 2004). Chisholm and Smith (1994) demonstrated antibacterial activity in the hemocyte lyase supernatants that was observed across all months, except February and August, following experimental infection with *Psychrobacter immobilis*.

*Carcinus* seems to possess physiological properties to be most tolerant than other decapod crustaceans for various parasites. For example, *Hematodinium* (protist, dinoflagellate) reduces the osmoregulatory capacity of *C. maenas*, but any macroscopical alteration of functionality of gills cells is detected. In comparison, *Cancer pagurus* showed many physiological perturbations (osmolality perturbation, muscle tissues reduced, discoloration of exoskeleton, and hemolymph pH increased) (Hamilton et al. 2010). Chisholm and Smith (1995) also showed that *C. maenas* is most tolerant than *Galathea strigosa, Nephrops norvegicus*, and *Crangon crangon*, during *Psychrobacter immobilis* infection. Therefore, *C. maenas* revealed a lower susceptibility to viral infection like white spot disease when it compared to others European decapods tissues (Bateman et al. 2012; Corbel et al. 2001). So, several authors suggested that their invasion success may be related to minor pressure of the parasites, and probably competitors and predators, in invaded environments. For example, Torchin et al. (2001) demonstrated that the parasite load on *C. maenas* was higher in their native regions than in invaded area. Zetmeisl et al. (2011) also analyzed the parasite prevalence in distant geographical populations of *C. maenas* in the native (Europe) and invasive localizations (South Africa, Australia) confirming that the invasive populations had lower parasite infections than native populations.

### Carcinus spp. is a marine invader

At present, the shore crab is considered as one of the world’s 100 worst invaders by the IUCN Species Survival Commission Invasive species specialist group (Lafferty and Kuris 1996; Grosholz 2005; Towle and Smith 2006; Klassen and Locke 2007; Darling 2011b).

**Historical invasion of Carcinus spp.**

In natural conditions, larvae have the potential to disperse over considerable distances given that green crab larval stages must develop in open waters. Thus, green crabs can rapidly expand their range once becoming established (Grosholz 1996). For example, Behrens Yamada and Becklund (2004) estimated that larval stages migrated over 50 km during the strong El Niño event of 1997/1998. Effectively, in September 1997 to April 1998, coastal currents were strong (up to 50 km/day) and seawater temperature was unusually warm (Hickey 2001; Behrens Yamada et al. 2005). A strong New Year cohort of *C. maenas* appeared in Oregon and Washington coastal estuaries as well as in northern California and on the west coast of Vancouver Island, British Columbia, as a result from this recent colonization event (Behrens Yamada and Hunt 2000).

Thus, these long planktonic larval stages with large dispersion capabilities facilitate their rapid expansion (Shanks et al. 2003; Roman and Palumbi 2004). However, the vast majority of green crab invasions throughout the world have been mainly attributed to transport by human agents. In the last two centuries, *Carcinus* specimens have been accidentally introduced into several regions outside their native range as a result of ship hulls, drilling platforms, aquarium releases, and ballast transport and maritime commerce (for example, juvenile crabs may be unintentionally transported with fishery products such as mussels, oysters, clams, and sediments) (Almecas 1962; Geller et al. 1997; Behrens Yamada and Hauck 2001; Carlton and Cohen 2003; Briski et al. 2012).

Green crabs (*C. maenas*) were first observed on the east coast of North America in Massachusetts in 1817, and now occur from Newfoundland to Virginia (Grosholz and Ruiz 1996). The range in eastern North America extends over approximately 1,000–1,200 linear kilometer of coast (Jamieson 2000; Kelley et al. 2011). In 1989–1990, green crabs (*C. maenas*) have been described in San Francisco Bay, California, on the Pacific coast of the USA (Grosholz and Ruiz 1996). This founding population, which probably arrived in the 1980s, likely had no more than 48 individuals (Tepolt et al. 2009). This population started extending its range in 1993 and reached Oregon in 1995–1996, Washington and British Columbia in 1998 (Jamieson 2000; See and Feist 2010; Behrens Yamada and Kosro 2010). Thus, the western North America green crab invasion has undergone a rapid range expansion of over 1,500 km in less than 12 years since the initial colonization (Jamieson et al. 2002). Genetic studies have shown that the west coast populations belong to the lineage that has been present on the east coast of North America since the 1800s (Bagley and Geller 2000). The first report of green crabs (*C. maenas*) in Canadian waters was in 1950 at the Bay of Fundy (Hart 1955). Now, they occupy the five Atlantic Canadian provinces (Rossong et al. 2012).

*C. aestuarii* have also been reported in Australia since the nineteenth century, in Port Phillip Bay, Victoria, and have since spread along the coast of Victoria, reaching New South Wales in 1971, South Australia in 1976, and Tasmania in 1993 (Thresher et al. 2003; Ross et al. 2004; Ahyong 2005).

*C. maenas* reached South Africa in 1983, near Cape Town (Joska and Branch 1986; Le Roux et al. 1990). Green crabs (*C. aestuarii* and *C. maenas*) invaded the Japanese coast in 1984 from Atlantic and Mediterranean Europe (Darling
2011b), and a simulation predicted that they will be present all over the country by 2205 (Koike and Iwasaki 2011). In 1999 and 2003, green crabs were also recorded from the Atlantic coast of South America in Patagonia (Argentina); these mostly likely arrived from Australia via ballast water (Hidalgo et al. 2005; Vinuesa 2007; Darling 2011b).

Green crabs (C. aestuarii and C. maenas) have also been recorded, but apparently did not successfully establish populations, in waters of the Red Sea (before 1817), Brazil (Rio de Janeiro in 1857 and Pernambuco before 1899), Panama (Pacific coast, 1866), Sri Lanka (1866–1867), Hawai‘i (1873), Madagascar (1922), Myanmar (1933), Australia (Perth, 1965), and Pakistan (1971) (Boschma 1972; Carlton and Cohen 2003).

Impact of the Carcinus invaders

Green crabs have high fecundity, rapid growth, and predate upon many organisms (e.g., bivalves, gastropods, and crustaceans). It is evident that they have multiple significant effects on the alteration of community and ecosystem processes. Their impacts on natural ecosystems and commercial fisheries have been well established (Ruiz et al. 1997; Grosholz 2002; Kulhanek and Ricciardi 2011). C. maenas was the first marine organism to be designated as an aquatic nuisance species by the Aquatic Nuisance Species Task Force (ANSTF) (Grosholz and Ruiz 2002). Lafferty and Kuris (1996) have estimated that the potential losses due to green crab (C. maenas) predation on commercial fisheries species in the USA could be as high as $44 million per year (all values in USD). However, The Oregon Dungeness Crab Commission defined the potential impact of C. maenas on Dungeness crab population in 2005 at $50 million, whereas the annual values in sales of farmed bivalves just in Washington State were $77 million (PCSGA 2003). On the East Coast, Lovell et al. (2007) showed that the estimated average annual losses to shellfisheries attributed to green crab predation are $22.6 million. The potential economic impact of green crabs (C. maenas) on bivalve and crustacean fisheries and aquaculture in the Gulf of St. Lawrence was estimated between $42 and $109 million (Colautti et al. 2006). A wide range of commercial bivalves species along the North American coast are clearly at risk since Carcinus colonization (Jamieson et al. 1998). In eastern North America, green crabs have been shown to significantly reduce populations of commercial shellfish species including soft shell clams (Mya arenaria; Glude 1955; Ropes 1968; Whitlow et al. 2003) and scallops (Argopecten irradians; Morgan et al. 1980). MacPhail et al. (1955) reported mortalities of planted soft shell clams (M. arenaria) as high as 57% over a 3-day period following the arrival of green crabs, compared to estimated background mortalities of ~10% per month. Crab predation on scallops (A. irradians) in Connecticut was as high as 70% (Morgan et al. 1980). In California, C. maenas significantly reduces densities of the most abundant taxa, including the bivalves Ostreola conchaphila, Transsabella confusa, Transsabella tantilla, Nutricula tantilla, and Nutricula confusa, the crab Hemigrapsus oregonensis, the cumacean Cumella vulgaris, and the amphipod Corophium sp. (Grosholz and Ruiz 1995; Grosholz et al. 2000; Kimbro et al. 2009). C. maenas is a potential competitor of native crabs including the estuarine blue crab Callinectes sapidus (American native species) and Cancer irroratus (indigenous rock crab from Newfoundland and Labrador, Canada) (MacDonald et al. 2007; Ramey et al. 2009; Roudez et al. 2007; Matheson and Gagnon 2012a, b).

MacPhail et al. (1955) stated: “It must be concluded that the green crab is one of the worst, if not the worst, clam predators that we know. Its ability to multiply rapidly, to feed on many varieties of shellfish other than commercial species, and its large appetite for commercially important shellfish, all suggest that it can do enormous damage” (Grosholz and Ruiz 2002). Finger (1998) has reported losses of cultured Ruditapes philippinarum as high as 50% in Tomales Bay, which he attributes to C. maenas. This heavy predation pressure exerted by green crabs was also observed on native mollusks and crabs from America, Tasmania, and South of Africa (Grosholz and Ruiz 1995, 2002; Griffiths et al. 1992). Thus, several native species have declined by more than 90% as the direct result of green crab predation (Grosholz et al. 2000). In Europe, predation by green crabs (C. maenas) is considered an important source of mortality for different commercial species (like Crassostrea gigas, C. crangon, Mercenaria mercenaria, Mytilus edulis, Ostrea edulis, Palaemon elegans, Ruditapes decussates, R. philippinarum) and also for noncommercial species (Ebling et al. 1964; Dare and Edwards 1976; Moksnes 2002).

Control of Carcinus populations

Control by management plan The European green crab (C. maenas) is now recognized as one of the most ecologically potent and economically damaging predators in coastal communities (Lowe et al. 2000). Following this designation in November 1998, the ANSTF called for development of a Management Plan to prevent, eradicate, and control C. maenas in the USA. Prior to colonization, prevention measures can be used to reduce the probability of transfer from any one of multiple transport vectors. Once a site is colonized, control measures, including a rapid response network (coordinated by professional and public outreach), are established to limit the invasion or to eradicate the population (Grosholz and Ruiz 2002). Control efforts including fencing, trapping, and poisoning have partially reduced the abundance of green crabs.

Control by predators Carcinus populations may be naturally limited by their predators like birds, crustaceans, fish, and
mammals. For example, some fish (scuppins, gobies, gadids, flatfish, ray, and shark) are predators of green crabs in the Atlantic (Kelley 1987; Cohen et al. 1995; Nelson et al. 2003). Predation pressure by native rock crabs (Cancer spp. and C. sapidus) may influence the habitat preference of Carcinus (Hunt and Behrens Yamada 2003; DeRivera et al. 2005; Jensen et al. 2007). Coastal mammals such as otters also consume green crabs in high quantity (Dunstone and Birks 1987; Mason and MacDonald 1980). Birds (sandpipers, heron, cormorants, and ducks) are likewise major predators of Carcinus (Cohen et al. 1995).

Control by other invasive species In the Gulf of Maine, Asian shore crab (Hemigrapsus sanguineus), first discovered on the Atlantic coast in the 1980s, impacts C. maenas densities. Griffen et al. (2008) noted that H. sanguineus predation on mussel populations altered C. maenas diet and induced a lower growth rate in the latter species. These observations confirmed those established along the Southern New England coast (Lohrer and Whitlatch 2002).

Control by parasites Several parasite species have been proposed as potential biological control agents of green crabs, such as S. carcini (parasitic crustacean castrator) (Minchin 1997), Portunion maenadis (isopoda) and Carcinonemertes carciniophila (nemertean), and Fecampia erythrocephala (flatworm) (Kuris 1997, 2002). The nemathelminth parasites do not induce significant effects on Carcinus population (Zetlmeisl et al. 2011). The parasitic barnacle S. carcini is considered as promising potential biological control agent because it impacts fitness (reducing spermatogenesis), inhibits molting and growth, and may induce mortality (Rubiliani 1983; Høeg 1995; Thresher et al. 2000; Goddard et al. 2005). Torchin et al. (2001) found that parasite load on green crabs (juvenile, young adult) was significantly higher in their native habitat than in invaded habitats (prevalence of 96 versus 8 %, respectively). The major problem for their control methods using parasites proposed for Carcinus spp. is that they could have negative consequences for native species too.

Is rapid evolution of Carcinus observed in invasive populations?

Carcinus spp. revealed a high genetic plasticity, and rapid modifications may be noted in recent invasive populations. Observable divergences in both morphology and physiological responses to heat stress have occurred in the invasive C. maenas populations on the west coast of North America within a relatively recent time span (~20 years) (Kelley et al. 2011). Temperature is a selective agent which affects morphological (body size) and physiological (metabolism, growth rate) characters in marine ectotherms (Atkinson 1994; Partridge and French 1996). In cold sites, the larvae show longer larval duration (Queiroga et al. 1994; Gaylord and Gaines 2000).

Carcinus as a model organism in ecophysiology

Carcinus as a model in ecotoxicology

Presently, Carcinus species are the most widely studied intertidal crabs in the world. Bamber and Depledge (1997) and Stewart et al. (2010) showed that green crabs may be used as biological monitors to test the impact of toxicants, and they were recommended as indicator species especially in the monitoring of heavy metal contaminations (Jennings and Rainbow 1979; Chan et al. 1992; Pedersen et al. 1994, 1998; Rainbow et al. 1999; Brown et al. 2004; Camus et al. 2004; Martin-Díaz et al. 2004a, b, 2005; Bjерregaard et al. 2005; Brian 2005; Stentiford and Feist 2005; Moreira et al. 2006; Klassen and Locke 2007; Ben-Khedher et al. 2013a). Indeed, C. maenas has demonstrated its ability as a physiological model crustacean to assess the potential impact of metals (Cd, Cu, Co, Hg, Zn, and Pb), industrial contaminants such as polyaromatic hydrocarbon (PAH) (Locatello et al. 2009; Dissanayake et al. 2008, 2010; Dissanayake and Bamber 2010; Ben-Khedher et al. 2013a, 2013b; Rodrigues et al. 2013a), and pesticide ecotoxics (Pedersen et al. 1997; Brown et al. 2004; Galloway et al. 2004, 2006; Martin-Díaz et al. 2004a, b, 2008; Elumalai et al. 2007; Coelho et al. 2008; Maria et al. 2009; Montes Nieto et al. 2010; Rodrigues et al. 2013a). C. aestuarii was also used for ecotoxicological investigations to detect the impacts of various environmental toxicants such as tributyltin/dibutyltin biocides, dioxins, polychlorinated dibenzo-furans, and hexachlorobenzene (Locatello et al. 2009) or benzo(a)pyrene (Foss et al. 2000). This species, along with clams, was a useful biomonitor in multispecies approaches to assess the impact of potential exposure to xenoestrogens on animals from different sites of the Lagoon of Venice (Munari et al. 2010) or exposed to 4-nonylphenol, a well-known xenooestrogen (Ricciardi et al. 2008). An integrated biological-chemical approach was also evaluated by Ricciardi et al. (2010) on C. aestuarii demonstrating its value to detect environmental pollution stress. As with other decapod crustaceans, C. maenas maintains its tissue concentrations of the essential metal zinc at approximately constant levels upon exposure to a wide range of ambient dissolved zinc concentration, whereas non-essential metals (e.g., cadmium (Cd)) are accumulated in proportion to dissolved metal exposure (Rainbow and White 1989). Bjерregaard et al. (2005) and Pereira et al. (2006) demonstrated high Cd concentration specifically in muscle and hepatopancreas tissues. Thus, C. maenas is commonly used for characterization and study of molecular biomarkers to give an integrated view of the toxic effects of single or multiple contaminant exposure on the organism at biochemical, cellular, and physiological levels (Pedersen and
Lundebye 1996; Pedersen et al. 1994, 1997; Vedel and Depledge 1995; Legras et al. 2000; Rainbow and Black 2005; Hagger et al. 2009. Biomarkers have been therefore investigated to study C. maenas-specific contamination of zinc (Legras et al. 2000), cadmium (Pedersen et al. 1994, 1998), and copper (Brown et al. 2004). Living on sediments and eating prey that burrow into sediments, C. maenas has been described as a suitable sentinel to assess the quality of estuary ecosystems. Bioaccumulation and bioamplification are the main processes which could transform C. maenas as a vector of contamination between polluted marine ecosystems and humans through consumption. Gills and hepatopancreas are the most significant tissues from the ecotoxicological viewpoint (Maria et al. 2009). As the primary organs in contact to environmental contamination, gills are the main entrance site of contaminants, particularly metals, and operate as a temporary store for metal accumulation. Traits including locomotion, heart rate, molt-related N-acetyl-β-glucosaminidase (NAGase), immune function (hemocyte phagocytic capability), endocrine systems (vitellogenin), and biochemical biomarkers, including combined defense and damage molecular biomarkers (i.e. acetylcholinesterase for exposure to neurotoxic compounds, catalase for antioxidant response, ethoxysresorufine-O-deethylase glutathione peroxidase, glutathione reductase, and glutathione-S-transferase for detoxification of organic compounds, isocitrate dehydrogenase and lactate dehydrogenase for energy metabolism, metallothioneins for detoxification of metal contamination, DNA damages) were successfully used on C. maenas showing its sensitivity to contaminants and its suitability to classify sites in relation to contamination levels (Legras et al. 2000; Galloway et al. 2004, 2006; Martin-Diaz et al. 2004a, b; Morales-Caselles et al. 2008; Martin-Diaz et al. 2008, 2009; Hagger et al. 2009; Maria et al. 2009; Pereira et al. 2009; Montes Nieto et al. 2010; Munari et al. 2010; Dissanayake et al. 2011; Mesquita et al. 2011; Ben-Khaled et al. 2013a; Rodrigues et al. 2013b). Hagger et al. (2008, 2009) and Jeblali et al. (2011) demonstrated that biomarker-based indices may be useful in coastal health monitoring using C. maenas as a sentinel species. Recently, the search of new biomarkers led Jeblali et al. (2014) to use proteomics approach to assess the toxic effects of contaminants in C. maenas. Proteins implied in different biological functions (chitin catabolism, proteolysis, exoskeleton biosynthesis, protein folding, stress response, and transport) were presented as new biomarkers that may be combined to the present battery of molecular biomarkers to develop for C. maenas an integrative tool for biomonitoring aquatic environment contamination.

New molecular tools to study diversity and ecophysiology in Carcinus

Microsatellite loci have provided useful genetic markers (Bagley and Geller 2000), allowing evaluation of C. maenas diversity in Portugal (Pascoal et al. 2009), in Canada (Blakeslee et al. 2010), in the USA (Tepolt et al. 2006), or for the global structure populations (Darling et al. 2008). Combinations of microsatellite and classical DNA markers (mitochondrial, ribosomal genes) will be useful for studying population genetic parameters at a range of spatial scales of Carcinus throughout its expanding species range.

A transcriptome developed by Towle and Smith (2006) identified 12,401 C. maenas expressed sequence tags (ESTs). This study allowed the characterization of several genes implicated in distinct mechanisms—antioxidant activity (12), binding activity (395), catalytic activity (578), chaperone activity (35), enzyme regulatory activity (55), motor activity (16), nutrient reservoir activity (5), signal transduction activity (89), structure activity (141), transcription regulatory activity (91), translation regulatory activity (30), and transporter activity (148) (Towle and Smith 2006).

The role of peptides in ecophysiology

Peptides have been isolated from C. maenas displaying antimicrobial proprieties and/or neuropeptide functions. In 1996, Schnapp et al. (1996) isolated a protein of 11.53 kDa produced by circulating hemocytes in C. maenas. Purified and characterized by Relf et al. (1999), this protein is similar to defensin of other invertebrates. This peptide, designated “Carcinin” by Smith and Chisholm (2001), presents antimicrobial activity against Gram-positive bacteria (Chisholm and Smith 1992; Relf et al. 1999). Carcinin is included in “crustin” groups because homologous sequences have been found in various crustaceans such as shrimp (Macrobrachium rosenbergii, ACL15396), prawns (Fenneropenaeus chinensis, EU500912; Marsupenaeus japonicas, BAD15066...), lobster (Pacifastacus leniusculus, ABP88043; Palinurus japonicas, ACU25385), and other crabs (Hyas araneus, ACJ06764; Scylla paramamosain, ABY20727...). The first complete carcinin cDNA (AJ427538, 333 bp) and genomic sequences (four exons and three introns) have been described by Brockton et al. (2007). At least six putative isoforms exist resulting from the transcription of different alleles and/or single-point mutations of the transcript at up to four loci in the gene (AJ237947, AJ427538, AJ821886, AJ821887, AJ821888, and AJ821889) (Brockton et al. 2007). The expression of carcinin was evaluated by real-time PCR during Gram-positive bacterium challenge in C. maenas and it appeared that its expression was modulated by temperature, especially when the animal is close to the edges of its physiological-tolerated thermal range (Brockton and Smith 2008).

In 1991, Leu- and Met-enkephalin from thoracic ganglia of the shore crab C. maenas have been purified (Luschen et al. 1991). Enkephalins in C. maenas confirmed the presence of an opioid system in crustaceans which has been reported for pigment regulation, locomotion and escape responses, and glucose mobilization (Luschen et al. 1991). In 1997, 20 neuropeptides included in allatostatin superfamily (regulatory
substances that inhibit the biosynthesis of juvenile hormone and may indirectly influence muscular activity) were isolated from extracts of cerebral and thoracic ganglia of the shore crab *C. maenas*. These substances designated carcinustatins are the shortest and longest allatostatins characterized from arthropods (Duve et al. 1997). More recently, global peptidomic analysis allowed the identification of 122 peptides and paracrines/hormones from the *C maenas* central nervous system and neuroendocrine organs. This neuuropeptidome obtained by mass spectrometry revealed notably high variability of allatostatins (25 peptides) and 42 new peptides *de novo* sequenced (e.g., the pyrokinins TSFAFSPRlamide and DTGFAFSPRlamide) (Ma et al. 2009). These authors suggested that this study extended our understanding of hormonal control in *C. maenas*, including factors that contribute to its extreme adaptability.

**Conclusion**

This review shows that *Carcinus* species (*C. aestuarii* and *C. maenas*) are good models for ecotoxicological investigations. These small common shore crabs (maximal size, 10 cm), are easily identified, and are highly tolerant to various environmental changes (temperature, salinity, xenobiotics…). Their broad tolerance combined with the genomics resources already available makes them an attractive model for physio-logenomics. Their recent and rapid expansion around the world makes them a central model for marine invasion.

**Acknowledgments** Kali Esaney (University of Washington, USA) and Sylvia Anton (Université d’Angers, France) are gratefully acknowledged for English corrections on this article.

**References**


mixed plankton samples using polymerase chain reaction and restriction fragment length polymorphisms (PCR-RFLP). Aquat Invasions 3(2):141–152
Dissanayake A, Galloway TS, Jones MB (2011) Seasonal differences in the physiology of Carcinus maenas (Crustacea: Decapoda) from estuaries with varying levels of anthropogenic contamination. Estuar Coast Shelf Sci 93:320–327
Domínguez CP, Creer S, Taylor MI, Queiroga H, Carvalho GR (2011) Temporal genetic homogeneity among shore crab (Carcinus maenas) larval events supplied to an estuarine system on the Portuguese northwest coast. Heredity 106:832–840


Hyde D, Qari S, Hopkin RS, Bowler K (2012) Thermal acclimation, heat shock and photoperiod: do these factors interplay in the adaptive
responses of crab neuromuscular system to temperature? J Therm Biol 37:164–170
Jennings JR, Rainbow PS (1979) Studies on the uptake of cadmium by the crab Carcinus maenas in the laboratory. I. Accumulation from seawater and a food source. Mar Biol 50:131–139
Mariño IAM, Pujolar JM, Zane L (2011) Reconciling deep clade and demographic history: Bayesian inference of post glacial colonization patterns in Carcinus aestuarii (Nardo, 1847) and C. maenas (Linnaeus, 1758). Plos ONE 6(12):e28567
Martin-Díaz ML, Sales D, DelValls TA (2004b) Influence of salinity in hemolymph vitellogenin of the shore crab Carcinus maenas, to be used as a biomarker of contamination. Bull Environ Contam Toxicol 73:870–877
Mowles SL, Rundle SD, Cotton PA (2011) Susceptibility to predation affects trait-mediated indirect interactions by reversing interspecific competition. Plos ONE 6(8):e23068
Powell A, Rowley AF (2008) Tissue changes in the shore crab Carcinus maenas as a result of infection by the parasitic barnacle Saccodinia carunci. Dis Aquat Org 80:75–79
Relf JM, Chisholm JRS, Kemp GD, Smith VJ (1999) Purification and characterization of a cysteine-rich 11.5 kDa antibacterial protein from the granular haemocytes of the shore crab, Carcinus maenas. Eur J Biochem 264:350–357
Schamp D, Kemp GD, Smith VJ (1996) Purification and characterization of a proline-rich antibacterial peptide, with sequence similarity to bactecin-7, from the haemocytes of the shore crab, Carcinus maenas. Eur J Biochem 240:532–539
Squires HJ (1990) Decapod Crustacea of the Atlantic Coast of Canada. Department of Fisheries and Oceans. pp 22
Stentiford GD, Feist SW (2005) A histopathological survey of shore crab (Carcinus maenas) and brown shrimp (Crangon crangon) from six estuaries in the United Kingdom. J Invertebr Pathol 88:136–146
Stentiford GD, Bateman KS, Stokes NA, Carnegie RB (2013) Haplosporidium littorale sp. nov. a crustacean pathogen within
the Haplosporida (Cercozoa, Ascetosporae). Dis Aquat Org 105: 243–252