Environ Sci Pollut Res (2014) 21:9129–9144
DOI 10.1007/s11356-014-2979-4

REVIEW ARTICLE

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

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Received: 11 February 2014 / Accepted: 23 April 2014 / Published online: 6 May 2014

Abstract Green crabs (*Carcinus*, Portunidae) include two species native to Europe—*Carcinus aestuarii* (Mediterranean species) and *Carcinus 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 invasiveness 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

Responsible editor: Philippe Garrigues

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Introduction

Description of *Carcinus* species

In 1814, Leach defined the *Carcinus* genus, including a unique species *Carcinus maenas*, previously described as *Cancer maenas* (Linneaus 1758), and sometimes written as *Carcinoides maenas* or *Carcinides 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. mediterranae* 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,

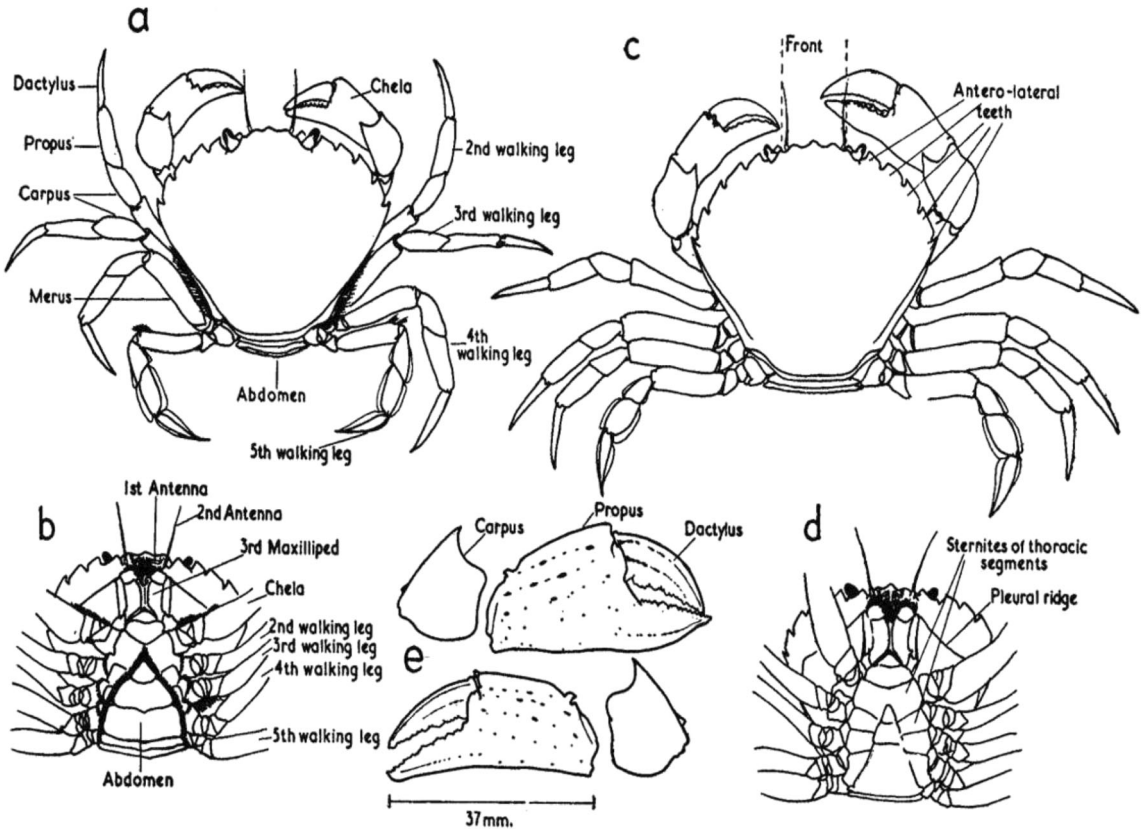

Fig. 1 Anatomy and morphological criteria of *Carcinus maenas*, published by Crothers (1967). *a*, *b* Female, dorsal, and ventral view; *c*, *d* male, dorsal, and ventral view, *e* chelae of the male

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 (premolt crab) to red indicating sexual maturation (Styrishave et al. 2004). Molting 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 (Harms 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). Megalopal cohorts are localized along coasts with high dispersal capacity, estimated from 57 to 198 km (Domingues 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 annelids, 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).

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). 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 acclimatization 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 acclimation. 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

Acclimation Temperature (°C)	Summer caught CTMax	Autumn caught CTMax	Winter caught CTMax
8	31.8±0.27	33.5±0.50	31.3±0.24
15		34.2±0.12	32.5±0.20
22	35.4±0.26	35.8±0.11	

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) (Matozzo et al. 2011b). Disruption of homeostasis in multiple physiological pathways can lead to an increased mortality rate in these crabs (Legeay and Massabuau 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).

Table 2 Critical thermal maxima of *Carcinus maenas* according to the geographic localization and acclimation (modified from Kelley et al. 2011)

	CTMax	
	Acclimation 6 °C	Acclimation 23 °C
California	34.7 °C	36.2 °C
British Columbia	31.7 °C	35.5 °C

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). Zoeae larvae tolerate salinity ranges from 20 to 35 psu (Edgell and Hollander 2011). *Carcinus* development is directly influenced by salinity. For example, *C. maenas* zoea 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.

(2008). Increase of a Na^+/K^+-ATPase α-subunit and carbonic anhydrase mRNA synthesis was also confirmed during salt stress (15 and 32 psu) by Jillette et al. (2011).

Hypoxia effects in *Carcinus*

Shore crabs are tolerant to low oxygen conditions and can survive at least 1 week out of water (Darbyson 2006). Anoxia induces acid–base disturbances, and these crabs use metabolic depression as a survival strategy (Durand and Regnault 1998) as evidenced by hemolymph urate increasing drastically in response to hypoxic exposure (Lallier et al. 1987). Alanine and fumarate were accumulated in *C. maenas* tissues during anoxia, and L-lactate appears as the major end-product of anaerobic metabolism (Hill et al. 1991). This observation confirms the importance of anaerobic glycolysis for energy production in crabs during environmental hypoxia (Hill et al. 1991). Hypoxia decreased competitive ability and increased mortality during combat between crabs (Legeay and Massabuau 2000a). Hypoxia may induce high embryonic mortality even though females actively aerate their broods by balancing on two periopods and flapping the abdomen, allowing accumulation of air bubbles around the egg mass (Wheatly 1981). Legeay and Massabuau (2000b) studied variation in *C. maenas* gill hemolymph pO_2 across an annual cycle of environmental oxygen variability. *C. maenas* appeared less tolerant to hypoxia during winter as water temperature is lowest, and pO_2 ranged from 0.7 to 6 kPa, following a seasonally physiological-dependent pattern. Reid and Aldrich (1989) also demonstrated a variation in response to water oxygenation between green and red crabs. They showed that red individuals start to escape a water body in which pO_2 is below 6 kPa whereas green crabs tolerate down to pO2 of 3.5 kPa. Martin (1977) (cited in Legeay and Massabuau 2000a) suggested that the network of phycomycetes on the gill cuticles of red morphs impaired O_2 diffusion.

In *C. aestuarii*, two aggregation forms of the respiratory protein hemocyanin exist—dodecameric 24S accounting for 90 % of total hemocyanin and hexameric 16S accounting for 10 % (Dainese et al. 1998). The hemocyanin of *C. aestuarii* shows a high carbohydrate moiety (1.6 % of protein mass). This carbohydrate content is higher than other arthropod hemocyanins (Dolashka-Angelova et al. 2001). In *C. maenas*, however, only the 24S form has been found (Markl et al. 1979). Truchot (1980) showed that lactate increased the O_2 affinity of crab hemocyanin as confirmed by Weber et al. (2008). Before any appearance of lactate in the blood, the switch from postprandial acidification to postprandial alkalinisation is a preliminary alarm showing that the intracellular medium is becoming hypoxic (Legeay and Massabuau 2000b).

Response to hypercapnia

In the short term, hypercapnia, a rapid adjustment of osmo- and acid–base regulation, was noted. Fehsenfeld et al. (2011) used a 4,462-feature microarray to identify a significant effect of pCO_2 (53 vs 440 Pa) on gill transcripts, where changes occurred in 26 % of transcripts, including those involved in cellular stress and osmoregulation. Elevated seawater pCO_2 modified the membrane of gill epithelial cells, through gene expression changes of tetraspanin, integrin-alpha7, a calcium-activated chloride channel, and proteins included in a multispanning endomembrane protein of the transmembrane 9 superfamily (protein member 4=TM9SF4) (Fehsenfeld et al. 2011). Hammer et al. (2012) demonstrated that elevated pCO_2 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 (NH_3). To understand how *C. maenas* will acclimate at global climate change reflected by the predicted elevation of pCO_2, Fehsenfeld et al. (2011) studied transcriptome changes in gill epithelia cells following acclimation to 400 Pa pCO_2. After 1 week of exposure, significant changes were detected in a calcium-activated chloride channel, a hyperpolarization-activated nucleotide-gated potassium channel, a tetraspanin, an integrin and putative syntaxin-binding protein, a protein of the transmembrane 9 superfamily, and a Cl^-/HCO_3^- exchanger of the SLC 4 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), *Rickettsia* 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)), haplosporidians (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 tremadodes (e.g., the Digenean *Microphallus primas* 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 hepatopancras 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. carcini* 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 bactenecin) and 11.5 kDa protein (cf crustin)) (Chisholm and Smith 1992, 1995; Relf et al. 1999; Tincu and Taylor 2004). Chilsholm and Smith (1994) demonstrated antibacterial activity in the hemocyte lysate supernatants that was observed across all months, except February and August, following experimental infection with *Psydhrobacter 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 (osmolarity perturbation, muscle tissues reduced, discolouration 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 virus 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. Zetlmeisl 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) (Almaca 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), Hawaii (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*, *Transennella confuse*, *Transennella tantilla*, *Nutricola tantilla*, and *Nutricola 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 (sculpins, 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 sanguinaeus*), first discovered on the Atlantic coast in the 1980s, impacts *C. maenas* densities. Griffen et al. (2008) noted that *H. sanguinaeus* 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 carcinophila* (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-Diaz et al. 2004a, b, 2005; Bjerregaard 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, andPb), 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 ecotoxicants (Pedersen et al. 1997; Brown et al. 2004; Galloway et al. 2004, 2006; Martin-Diaz 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 biocids, dioxins, polychlorinated dibenzofurans, and hexachlorobenzene (Locatello et al. 2009) or benzo(*a*)pyrene (Fossi 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 xenoestrogen (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). Bjerregaard 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, ethoxyresorufine-*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-Khedher et al. 2013a; Rodrigues et al. 2013b). Hagger et al. (2008, 2009) and Jebali 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 Jebali 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 neuropeptidome 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 physiological genomics. Their recent and rapid expansion around the world makes them a central model for marine invasion.

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

References

Ahyong ST (2005) Range extension of two invasive crab species in eastern Australia: *Carcinus maenas* (Linnaeus) and *Pyromaia tuberculata* (Lockington). Mar Pollut Bull 50:460–462

Almaca C (1962) Sur la distribution géographique du genre *Carcinus* Leach (Crust. Dec. Brach.). Rev Fac Cienc Lisb 10:109–113

Ameyaw-Akumfi C, Hughes RN (1987) Behaviour of *Carcinus maenas* feeding on large *Mytilus edulis*. How do they assess the optimal diet? Mar Ecol 38:213–218

Anger K, Spivak E, Luppi T (1998) Effects of reduced salinities on development and bioenergetics of early larval shore crab, *Carcinus maenas*. J Exp Mar Biol Ecol 220:287–304

Atkinson D (1994) Temperature and organism size—a biological law for ectotherms? Adv Ecol Res 25:1–58

Baeta A, Cabral HN, Neto JM, Marques JC, Pardal MA (2005) Biology, population dynamics and secondary production of the green crab *Carcinus maenas* (L.) in a temperate estuary. Estuar Coast Shelf Sci 65:43–52

Baeta A, Cabral HN, Marques JC, Pardal MA (2007) Feeding ecology of the green crab, *Carcinus maenas* (L., 1758) in temperate estuary. Portugal Crustaceana 79(10):1181–1193

Bagley MJ, Geller JB (2000) Microsatellite DNA analysis of native and invading populations of European Green crabs. In: Pederson J (ed) Marine bioinvasions: Proceedings of the first national conference. MIT Seagrant College Program, Cambridge, MA, pp 241–243

Bamber SD, Depledge MH (1997) Evaluation of changes in the adaptive physiology of shore crabs (*Carcinus maenas*) as an indicator of pollution in estuarine environments. Mar Biol 129:667–672

Bateman KS, Tew I, French C, Hicks RJ, Martin P, Munro J, Stentiford GD (2012) Susceptibility to infection and pathogenicity of White Spot Disease (WSD) in non-model crustacean host taxa from temperate regions. J Invert Pathol 110:340–351

Behrens Yamada S, Becklund M (2004) Status of the European green crab invasion. J Shellfish Res 23:651

Behrens Yamada S, Hauck L (2001) Field identification of the European green crab species *Carcinus maenas* and *Carcinus aestuarii*. J Shellfish Res 20(3):905–912

Behrens Yamada S, Hunt C (2000) The arrival and spread of the European green crab, *Carcinus maenas* in the Pacific Northwest. Dreissena 11:1–7

Behrens Yamada S, Kosro PM (2010) Linking ocean conditions to year class strength of the invasive European green crab, *Carcinus maenas*. Biol Invasions 12:1791–1804

Behrens Yamada S, Dumbauld BR, Kalin A, Hunt CE, Figlar-Barnes R, Randall A (2005) Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the northeastern Pacific. Biol Invasions 7:309–321

Ben-Khedher S, Jebali J, Houas Z, Naweli H, Jrad A, Bousseta H (2013a) Metals bioaccumulation and histopathological biomarkers in *Carcinus maenas* crab from Bizerta lagoon, Tunisia. Environ Sci Pollut Res 21(6):4343–47357

Ben-Khedher S, Jebali J, Kamel N, Banni M, Rameh M, Jrad A, Bousseta H (2013b) Biochemical effects in crabs (*Carcinus maenas*) and contamination levels in the Bizerta Lagoon: an integrated approach in biomonitoring of marine complex pollution. Environ Sci Pollut Res 20:2616–2631

Berrill M (1982) The life cycle of the green crab *Carcinus maenas* at the northern end of its range. J Crust Biol 2:31–39

Bjerregaard P, Bjorn L, Norum U, Pedersen KL (2005) Cadmium in the shore crab *Carcinus maenas*: seasonal variation in cadmium content and uptake and elimination of cadmium after administration via food. Aquat Toxicol 72:5–15

Blakeslee AMH, McKenzie CH, Darling JA, Byers JE, Pringles JM, Roman JA (2010) Hitchhiker's guide to the Maritimes: anthropogenic transport facilitates long-distance dispersal of an invasive marine crab to Newfoundland. Divers Distrib 16:879–891

Bonami JR, Pappalardo R (1980) Rickettsial infection in marine crustacean. Experientia 36(2):180–181

Boschma H (1972) On the occurrence of *Carcinus maenas* (Linnaeus) and its parasite *Sacculina carcini* Thompson in Burma, with notes on the transport of crabs to new localities. Zool Med 47(11):145–155

Brian JV (2005) Inter-population variability in the reproductive morphology of the shore crab (*Carcinus maenas*): evidence of endocrine disruption in a marine crustacean? Mar Pollut Bull 50:410–416

Briski E, Ghabooli S, Bailey SA, MacIsaac HJ (2012) Invasion risk posed by macroinvertebrates transported in ships' ballast tanks. Bio Invasions 14:1843–1850

Brockton V, Smith VJ (2008) Crustin expression following bacterial injection and temperature change in the shore crab, *Carcinus maenas*. Dev Comp Immunol 32(9):1027–1033

Brockton V, Hammond JA, Smith VL (2007) Gene characterisation, isoforms and recombinant expression of carcinin, an antibacterial protein from the shore crab, *Carcinus maenas*. Mol Immunol 44: 943–949

Brown RJ, Galloway TS, Lowe D, Browne MA, Dissanayake A, Jones MB, Depledge MH (2004) Differential sensitivity of three marine

invertebrates to copper assessed using multiple biomarkers. Aquat Toxicol 66:267–278

Camus L, Davies PE, Spicer JI, Jones MB (2004) Temperature-dependent physiological response of *Carcinus maenas* exposed to copper. Mar Environ Res 58:781–785

Carlton JT, Cohen AN (2003) Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. J Biogeogr 30:1809–1820

Chan HM, Bjerregaard P, Rainbow PS, Depledge MH (1992) Uptake of zinc and cadmium by two populations of shore crabs *Carcinus maenas* at different salinities. Mar Ecol Prog Ser 86:91–97

Chilsholm JR, Smith VJ (1994) Variation of antibacterial activity in the haemocytes of the shore crab, *Carcinus maenas*, with temperature. J Mar Biol Assoc U K 74:949–982

Chisholm JR, Smith VJ (1992) Antibacterial activity in the haemocytes of the shore crab *Carcinus maenas*. J Mar Biol Assoc UK 72:529–542

Chisholm JR, Smith VJ (1995) Comparison of antibacterial activity in the hemocytes of different crustacean species. Comp Biochem Physiol A 110(1):39–45

Clark PF, Neale M, Rainbow PS (2001) A morphometric analysis of regional variation in *Carcinus* Leach, 1814 (Brachyura: Portunidae: Carcininae) with particular reference to the status of the two species *C. maenas* (Linnaeus, 1758) and *C. aestuarii* (Nardo, 1847). J Crust Biol 21:288–303

Coelho JP, Reis AT, Ventura S, Pereira ME, Duarte AC, Pardal MA (2008) Pattern and pathways for mercury lifespan bioaccumulation in *Carcinus maenas*. Mar Pollut Bull 56:1104–1110

Cohen AN, Carlton JT, Fountain MC (1995) Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Mar Biol 122:225–237

Colautti RI, Bailey SA, van Overjijk CDA, Amundsen K, MacIsaac HJ (2006) Characterised and projected costs of nonindigenous species in Canada. Biol Invasions 8:45–59

Compton TJ, Leathwick JR, Inglis GJ (2010) Thermogeography predicts the potential global range of the invasive European green crab (*Carcinus maenas*). Div Distrib 16:243–255

Corbel V, Zuprisal Z, Shi C, Huang I, Sumartono C, Arcier JM, Bonami JR (2001) Experimental infection of European crustaceans with white spot syndrome virus (WSSV). J Fish Dis 24:377–382

Crothers JH (1967) The biology of the shore crab, *Carcinus maenas* (L.) 2. The life of the adult crab. Field Stud 2:579–614

Crothers JH (1968) The backround—anatomy, grot and life history. Field Stud 2(4):407–434

Cuculescu M, Hyde D, Bowler K (1988) Thermal tolerance of two species of marine crab, *Cancer pagurus* and *Carcinus maenas*. J Therm Biol 23(2):107–110

Cuculescu M, Pearson T, Hyde D, Bowler K (1999) Heterothermal acclimation: an experimental paradigm for studying the control of thermal acclimation in crabs. Proc Natl Acad Sci U S A 96:6501–6505

Dainese E, Di Muro P, Beltramini M, Salvato B, Decker H (1998) Subunits composition and allosteric control in *Carcinus aestuarii* hemocyanin. Eur J Biochem 256:350–358

Darbyson EA (2006) Local vectors of spread of the green crab (*Carcinus maenas*) and the clubbed tunicate (*Styela clava*) in the southern Gulf of St. Lawrence, Canada. M.Sc. Thesis, University of Halifax, NS

Dare PJ, Edwards DB (1976) Experiments on the survival, growth, and yield of relaid seed mussels (*Mytilus edulis* L.) in the Menai Strait, North Wales. J Cons Int Explor Mer 37:16–28

Darling JA (2011a) Interspecific hybridization and mitochondrial introgression in invasive *Carcinus* shore crabs. Plos ONE 6(3):e17828

Darling JA (2011b) More than one way to invade: lessons from genetic studies of *Carcinus* shore crabs. In: Galil BS et al. (eds). The wrong place—alien Marine Crustaceans: distribution, biology and impacts. Invading nature. New York. Springer. pp 25

Darling JA, Tepolt CK (2008) Highly sensitive detection of invasive shore crab (*Carcinus maenas* and *Carcinus aestuarii*) larvae in mixed plankton samples using polymerase chain reaction and restriction fragment length polymorphisms (PCR-RFLP). Aquat Invasions 3(2):141–152

Darling JA, Bagley MJ, Roman J, Tepolt CK, Geller JB (2008) Genetic patterns across multiple introductions of the globally invasive crab genus *Carcinus*. Mol Ecol 17:4992–5007

Dawirs RR (1985) Temperature and larval development of *Carcinus maenas* (Decapoda) in the laboratory; predictions of larval dynamics in the sea. Mar Ecol Prog Ser 24:297–302

Dawirs RR, Pueschel C, Schorn F (1986) Temperature and growth in *Carcinus maenas* L. (Decapoda: Portunidae) larvae reared in the laboratory from hatching through metamorphosis. J Exp Mar Biol Ecol 100:47–74

DeRivera CE, Ruiz GM, Hines AH, Jivoff P (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. Ecol 86:3364–3376

DeRivera CE, Gray Hitchcock N, Teck SJ, Steves BP, Hines AH, Ruiz GM (2006) Larval development rate predicts range expansion of an introduced crab. Mar Biol 10(6):1275–1288

Dissanayake A, Bamber SD (2010) Detecting polyaromatic hydrocarbon (PAH) exposure in the Bay of Gibraltar, using fluorescence spectrophotometry as a biomonitoring tool of environmental contamination. Mar Environ Res 70:65–72

Dissanayake A, Galloway TS, Jones MB (2008) Physiological responses of juvenile and adult shore crabs *Carcinus maenas* (Crustacea: Decapoda) to pyrene exposure. Mar Environ Res 66:445–450

Dissanayake A, Piggott C, Baldwin C, Sloman KA (2010) Elucidating cellular and behavioural effects of contaminant impact (polycyclic aromatic hydrocarbons, PAHs) in both laboratory-exposed and field-collected shore crabs, *Carcinus maenas* (Crustacea: Decapoda). Mar Environ Res 70:368–373

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

Dolashka-Angelova P, Beltramini M, Dolashki A, Salvato B, Hristova R, Voelter W (2001) Carbohydrate composition of *Carcinus aestuarii* hemocyanin. Arch Biochem Biophys 389:153–158

Domingues CP, Creer S, Taylor MI, Queiroga H, Carvalho GR (2010) Genetic structure of *Carcinus maenas* within its native range: larval dispersal and oceanographic variability. Mar Ecol Prog Ser 410: 111–123

Domingues 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

Domingues CP, Nolasco R, Dubert J, Queiroga H (2012) Model-derived dispersal pathways from multiple source populations explains variability of invertebrate larval supply. Plos ONE 7(4):e35794

Dos Santos A, Santos AMP, Conway DVP, Bartilotti C, Lourenco P (2008) Diel vertical migration of decapod larvae in the Portuguese coastal upwelling ecosystem: implications for offshore transport. Mar Ecol Prog Ser 359:171–183

Dunstone N, Birks JDS (1987) The feeding ecology of mink (*Mustela vison*). J Zool 212:69–83

Durand F, Regnault M (1998) Nitrogen metabolism of two portunid crabs, *Carcinus maenas* and *Necora puber*, during prolonged air exposure and subsequent recovery: a comparative study. J Exp Biol 201:2515–2528

Duve H, Johnsen AH, Maestro J-L, Scott AG, Jaros PP, Thorpe A (1997) Isolation and identification of multiple neuropeptides of the allatostatin superfamily in the shore crab *Carcinus maenas*. Eur J Biochem 250:727–734

Ebling FG, Kitching JA, Muntz L, Taylor CM (1964) The ecology of Lough Ine: XIII. Experimental observations of the destruction of Mytilus edulis and Nucella lapillus by crabs. J Anim Ecol 33:73–82

Eddy F, Powell A, Gregory S, Nunan LM, Lightner DV, Dyson PJ, Rowley AF, Shields RJ (2007) A novel bacterial disease of the European shore crab, *Carcinus maenas*—molecular pathology and epidemiology. Microbiology 153:2839–2849

Edgell C, Hollander J (2011) The evolutionary ecology of European green crab, *Carcinus maenas*, in North America. In: Galil BS et al. (eds.). The wrong place—alien Marine Crustaceans: distribution, biology and impacts. Invading nature. New York: Springer. pp 25

Elner RW (1980) The influence of temperature, sex and chela size on the foraging strategy of the shore crab, *Carcinus maenas* (L.). Mar Behav Physiol 7:15–24

Elumalai M, Antunes C, Guilhermino L (2007) Enzymatic biomarkers in the crab *Carcinus maenas* from the Minho River estuary (NW, Portugal) exposed to zinc and mercury. Chemosphere 66:1249–1255

Eriksson S, Edlund A-M (1977) On the ecological energetics of group *Carcinus maenas* (L.) from a shallow sandy bottom in Gullmar Fjord, Sweden. J Exp Mar Biol Ecol 30:233–248

Fehsenfeld S, Kiko R, Appelhnsa Y, Towle DW, Zimmer M, Melner F (2011) Effects of elevated seawater pCO_2 on gene expression patterns in the gills of the green crab, *Carcinus maenas*. BMC Genomics 12(488):2–17

Finger J (1998) Concerns for the molluscan shellfish industry. Green crab workshop sponsored by Oregon/Washington Sea Grant, Vancouver, WA

Fossi MC, Casini S, Savelli C, Corbelli C, Franchi E, Mattei N, Sanchez-Hernandez JC, Corsi I, Bamber S, Depledge MH (2000) Biomarker responses at different levels of biological organization in crabs (*Carcinus aestuarii*) experimentally exposed to benzo(*a*)pyrene. Chemosphere 40:861–874

Galloway T, Brown RJ, Browne M, Dissanayake A, Lowe D, Jones M, Depledge M (2004) A multibiomarker approach to environmental assessment. Environ Sci Technol 38:1723–1731

Galloway T, Brown RJ, Browne MA, Dissanayake A, Lowe D, Depledge MH, Jones MB (2006) The ECOMAN project: a novel approach to defining sustainable ecosystem function. Mar Pollut Bull 53:186–194

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by Xow. Am Nat 155:769–789

Geller JB, Walton ED, Grosholz ED, Ruiz GM (1997) Cryptic invasions of the crab *Carcinus* detected by molecular phylogeography. Mol Ecol 6:901–906

Gimenez L (2010) Relationship between habitat conditions, larval traits, and juvenile performance in a marine invertebrate. Ecology 91(5): 1401–1413

Glenner H, Hoeg JT (1995) A new motile, multicellular stage involved in host invasion by parasitic barnacles (Rhizocephala). Nature 377: 147–149

Glude JB (1955) The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. Trans Am Fish Soc 84:13–26

Goddard JHR, Torchin ME, Kuris AM, Lafferty KD (2005) Host specificity of *Sacculina carcini*, a potential biological control agent of the introduced European green crab *Carcinus maenas* in California. Biol Invasions 7:895–912

Griffen BD, Guy T, Buck JC (2008) Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator. J Anim Ecol 77:32–40

Griffiths CL, Hockey PAR, Van Erkom SC, LeRoux PJ (1992) Marine invasive aliens on South Australian shores: implications for community structure and trophic functioning. S Afr J Mar Sci 12:713–722

Grosholz ED (1996) Contrasting rates of spread for introducted species in terrestrial and marine systems. Ecology 77:1680–1686

Grosholz ED (2002) Ecological and evolutionary consequences of coastal invasions. Trends Ecol Evol 17:22–27

Grosholz ED (2005) Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. Proc Natl Acad Sci U S A 102:1088–1091

Grosholz ED, Ruiz GM (1995) Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in Central California. Mar Biol 122:239–247

Grosholz ED, Ruiz GM (1996) Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biol Conserv 78:59–66

Grosholz ED, Ruiz GM (2002) Management plan for the European green crab. Submitted to the Aquatic Nuisance Species Task Force November 13, pp 55

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206–1224

Hagger JA, Jones MB, Lowe D, Leonard DRP, Owen R, Galloway TS (2008) Application of biomarkers for improving risk assessments of chemicals under the Water Framework Directive: a case study. Mar Pollut Bull 56:1111–1118

Hagger JA, Galloway TS, Langston WJ, Jones MB (2009) Application of biomarkers to assess the condition of European Marine Sites. Environ Pollut 157:2003–2010

Hamilton KM, Shaw PW, Morritt D (2010) Physiological responses of three crustacean species to infection by the dinoflagellate like protest *Hematodinium* (alveolata: Syndinea). J Invertebr Pathol 105(2): 194–196

Hammer KM, Pedersen SA, Storseth TR (2012) Elevated seawater levels of CO_2 change the metabolic fingerprint of tissues and hemolymph from the green shore crab *Carcinus maenas*. Comp Biochem Physiol Part D 7:292–302

Harms J, Meyer-Harms B, Dawirs RR, Anger K (1994) Growth and physiology of *Carcinus maenas* (Decapoda, Portunidae) larvae in the field and in laboratory experiments. Mar Ecol Prog Ser 108:107–118

Hart JL (1955) The green crab—a shellfish enemy. Fisheries Research Board of Canada, Report of the Atlantic Biological Station, St. Andrews, N.B. pp 11

Hauton C, Williams JA, Hawkins LE (1997) The effects of a live in vivo pathogenic infection on aspects of the immunocompetence of the common shore crab, *Carcinus maenas* (L.). J Experiment Mar Biol Ecol 211:115–128

Henry RP, Gehnrich S, Weihrauch D, Towle DW (2003) Salinity-mediated carbonic anhydrase induction in the gills of the euryhaline green crab, *Carcinus maenas*. Comp Biochem Physiol Part A 136: 243–258

Henry RP, Thomason KL, Towle DW (2006) Quantitative changes in branchial carbonic anhydrase activity and expression in the Euryhaline green crab, *Carcinus maenas*, in response to low salinity exposure. J Exp Zool 305A:842–850

Herberts C (1982) Host-parasite relation between the shore crab *Carcinus maenas* and *Sacculina carcini* (Rhizocephala): identification and characterization of a specific fraction correlated with parasitism. J Invert Pathol 39:60–65

Hickey BM (2001) Coastal ocean-estuary coupling. In: Parrish JK and Little K (eds) PNCERS 2000 Annual Report, pp 77–84. Coastal Oceans Program, NOAA

Hidalgo FJ, Barón PJ, Orensanz JM (2005) A prediction comes true: the green crab invades the Patagonian coast. Biol Invasions 7:547–552

Hill AD, Taylor AC, Strang RHC (1991) Physiological and metabolic responses of the shore crab *Carcinus maenas* L. during environmental anoxia and subsequent recovery. J Exp Mar Biol Ecol 150:31–50

Høeg JT (1995) The biology and life cycle of the rhizocephala (cirripedia). J Mar Biol Assoc UK 75:517–550

Hopkin RS, Qari S, Bowler K, Hyde D, Cuculescu M (2006) Seasonal thermotolerance in marine crustacean. J Mar Biol Ecol 331:74–81

Hunt CE, Behrens Yamada S (2003) Biotic resistance experienced by an invasive crustacean in a temperate estuary. Biol Invasions 5:33–43

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 neuromusculary system to temperature? J Therm Biol 37:164–170

Jamieson GS (2000) European green crab, *Carcinus maenas*, introductions in North America: differences between the Atlantic and Pacific experiences. Proceedings of the 10th International Aquatic Nuisance Species and Zebra Mussel Conference, Toronto. pp. 307–312

Jamieson GS, Armstrong DA, Grosholz ED, Elner RW (1998) Potential ecological implications from the introduction of the European green crab, *Carcinus maenas*, to British Columbia, Canada, and Washington, USA. J Nat Hist 32:1587–1598

Jamieson GS, Foreman MGG, Cherniawsky JY, Levings CD (2002) European green crab (*Carcinus maenas*) dispersal: The Pacific experience. In: Paul AJ, Dawe EG, Elner R, Jamieson GS, Kruse GH, Otto RS, Sainte-Marie B, Shirley TC and Woodby D (eds.). Crabs in cold water regions: Biology, management and economics. University of Alaska Sea Grant College Program AK-SG-02-01. pp. 561–576

Jebali J, Ben-Khedher SB, Ghedira J, Kamel N, Boussetta H (2011) Integrated assessment of biochemical responses in Mediterranean crab (*Carcinus maenas*) collected from Monastir Bay, Tunisia. J Env Sci 23(10):1714–1720

Jebali J, Chicano-Galvez E, Fernandez-Cisnal R, Banni M, Chouba L, Boussetta H, Lopez-Barea J, Alhama J (2014) Proteomic analysis in caged Mediterranean crab (*Carcinus maenas*) and chemical contaminant exposure in Teboulba Harbour. Tunisia Ecotoxicol Environ Saf 100:15–26

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

Jensen GC, McDonald PS, Armstrong DA (2007) Biotic resistance to green crab, *Carcinus maenas*, in California bays. Mar Biol 151: 2231–2243

Jillette N, Cammack L, Lowenstein M, Henry RP (2011) Down-regulation of activity and expression of three transport-related proteins in the gills of the euryhaline green crab, *Carcinus maenas*, in response to high salinity acclimation. Comp Biochem Physiol Part A 158:189–193

Joska MAP, Branch GM (1986) The European shore-crab—another alien invader? Afr Wildlife 40:63–65

Kelley DF (1987) Food of bass in U.K. waters. J Mar Biol Assoc UK 67: 275–286

Kelley A, De Rivera CE, Buckley BA (2011) Intraspecific variation in thermotolerance and morphology of the invasive European green crab, *Carcinus maenas*, on the west coast of North America. J Exp Mar Biol Ecol 409:70–78

Kelley A, De Riviera CE, Buckley BA (2013) Cold tolerance of the invasive *Carcinus maenas* in the east Pacific: molecular mechanisms and implications for range expansion in a changing climate. Biol Invasions. doi:10.1007/s10530-013-0454-7

Kimbro DL, Grosholz ED, Baukus AJ, Nesbitt N, Travis N, Attoe S, Coleman-Hulbert C (2009) Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. Oecologia 160:563–575

Klassen G, Locke A (2007) A biological synopsis of the European green crab, *Carcinus maenas*. Can Manuscr Rep Fish Aquat Sci no 2818, pp. 75

Koçak C, Acarli D, Katagan T, Ozbek M (2011) Morphometric characters of the Mediterranean green crab (*Carcinus aestuarii* Nardo, 1847) (Decapoda, Brachyura), in Homa Lagoon, Turkey. Turk J Zool 35: 551–557

Koike F, Iwasaki K (2011) A simple range expansion model of multiple pathways: the case of nonindigenous green crab *Carcinus aestuarii* in Japanese waters. Biol Invasions 13:459–470

Kulhanek SA, Ricciardi A (2011) Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species? Ecol Appl 21(1):189–202

Kuris A (1997) Nemertean egg predators as potential biocontrol agents for *Carcinus maenas*. In: Thresher RE (ed) Proceedings the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests. CSIRO Marine Laboratories, Hobart, pp 88–90

Kuris AM, Torchin ME, Lafferty KD (2002) *Fecampia erythrocephala* rediscovered: prevalence and distribution of a parasitoid of the European shore crab, *Carcinus maenas*. J Mar Biol Assoc UK 82: 955–960

Lafferty KD, Kuris AM (1996) Biological control of marine pests. Ecology 77:1989–2000

Lallier F, Boitel F, Truchot JP (1987) The effect of ambient oxygen and temperature on haemolymph L-lactate and urate concentrations in the shore crab *Carcinus maenas*. Comp Biochem Physiol Part A 86: 255–260

Le Roux PJ, Branch GM, Joska MAP (1990) On the distribution, diet and possible impact of the invasive European shore crab *Carcinus maenas* (L.) along the South African coast. Afr J Mar Sci 9:85–92

Ledesma FM, Van Der Molen S, Baron PJ (2010) Sex identification of *Carcinus maenas* by analysis of carapace geometrical morphometry. J Sea Res 63:213–216

Lee KT, McKnight A, Kellogg K, Juanes F (2003) Salinity tolerance in color phases of female green crabs *Carcinus maenas* (Linnaeus, 1758). Crustaceana 76:247–253

Legeay A, Massabuau JC (2000a) Effect of salinity on hypoxia tolerance of resting green crabs, *Carcinus maenas*, after feeding. Mar Biol 136:387–396

Legeay A, Massabuau J-C (2000b) The ability to feed in hypoxia follows a seasonally dependent pattern in shore crab *Carcinus maenas*. J Exp Mar Biol Ecol 247:113–129

Legras S, Mouneyrac C, Amiard JC, Amiard-Triquet C (2000) Changes in metallothionein concentrations in response to variation in natural factors (salinity, sex, weight) and metal contamination in crabs from a metal-rich estuary. J Exp Mar Biol Ecol 246:259–279

Locatello L, Matozzo V, Marin MG (2009) Biomarker responses in the crab *Carcinus aestuarii* to assess environmental pollution in the Lagoon of Venice (Italy). Ecotoxicology 18:869–877

Lohrer AM, Whitlatch RB (2002) Interactions among aliens: apparent replacement of one exotic species by another. Ecology 83:710–732

Lovell S, Besedin E, Grosholz E (2007) Modeling economic impacts of the European green crab. Paper presented at American Agricultural Economics Association annual meeting, Portland, July 29–Aug 1. pp. 40

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the Global Invasive Species database. The Invasive Species Specialist Group (ed). A specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN). Pp. 12

Luschen W, Buckt F, Willig A, Jaros PP (1991) Isolation, sequence analysis, and physiological properties of enkephalins in the nervous tissue of the shore crab *Carcinus maenas* L. (crustacean neuropeptides/release-inhibiting neurohormone/neurosecretion/opioids). Proc Natl Acad Sci U S A 88:8671–8675

Lyons LJ, O'Riordan RM, Cross TF, Culloty SC (2012) Reproductive biology of the shore crab *Carcinus maenas* (Decapoda, Portunidae): a macroscopic and histological view. Invert Reprod Dev 56:144–156

Ma M, Bors EK, Dickinson ES, Kwiatkowski MA, Sousa GL, Henry RP, Smith CM, Towle DW, Christie AE, Li L (2009) Characterization of the *Carcinus maenas* neuropeptidome by mass spectrometry and functional genomics. Gen Comp Endocrinol 161(3):320–334

MacDonald JA, Roudez R, Glover T, Weis JS (2007) The invasive green crab and Japanese shore crab: behavioral interactions with a native crab species, the blue crab. Biol Invasions 9:837–848

MacPhail JS, Lord EI, Dickie LM (1955) The green crab—a new clam enemy. Fish Res Board Can Progr Rep Atl Biol Sta 1:1–16

Madeira D, Narciso L, Cabral HN, Vinagre C, Diniz MS (2012) HSP70 production patterns in coastal and estuarine organisms facing increasing temperatures. J Sea Res 73:137–147

Maria VL, Santos MA, Bebianno MJ (2009) Contaminant effects in shore crabs (*Carcinus maenas*) from Ria Formosa Lagoon. Comp Biochem Physiol Part C 150:196–208

Marino IAM, Pujolar JM, Zane L (2011) Reconciling deep calibration 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

Markl J, Hofer A, Bauer G, Markl A, Kempter B, Brenzinger M, Linzen B (1979) Subunit heterogeneity in arthropod hemocyanins. II. Crustacea J Comp Physiol 133:167–175

Martin JL (1977) Relations entre le développement d'un phycomycète et l'accumulation de fer sur la surface branchiale de *Carcinus maenas* (Crustacé Décapode) au cours du cycle d'intermue. Vie Milieu 27: 91–100

Martin-Diaz ML, Bamber S, Casado-Martinez C, Sales D, Del Valls TA (2004a) Toxicokinetics of heavy metals from a mining spill using *Carcinus maenas*. Mar Environ Res 58:833–837

Martin-Diaz 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

Martin-Diaz ML, Villena-Lincoln A, Bamber S, Blasco J, DelValls TA (2005) An integrated approach using bioaccumulation and biomarker measurements in female shore crab, *Carcinus maenas*. Chemosphere 58:615–626

Martin-Diaz ML, Sales D, DelValls TA (2008) Toxicokinetic approach for the assessment of endocrine disruption effects of contaminated dredged material using female *Carcinus maenas*. Ecotoxicology 17: 495–503

Martin-Diaz ML, Blasco J, Sales D, DelValls TA (2009) The use of a kinetic biomarker approach for in situ monitoring of littoral sediments using the crab *Carcinus maenas*. Mar Environ Res 68:82–88

Mason CF, MacDonald SM (1980) The winter diet of otters (*Lutra lutra*) on a Scottish sea loch. J Zool 192:558–561

Matheson K, Gagnon P (2012a) Temperature mediates non-competitive foraging in indigenous rock (*Cancer irroratus* Say) and recently introduced green (*Carcinus maenas* L.) crabs from Newfoundland and Labrador. J Exp Mar Biol Ecol 414–415:6–18

Matheson K, Gagnon P (2012b) Effects of temperature, body size, and chela loss on competition for a limited food resource between indigenous rock crab (*Cancer irroratus* Say) and recently introduced green crab (*Carcinus maenas* L.). J Exp Mar Biol Ecol 428: 49–56

Matozzo V, Gallo C, Marin MG (2011a) Can starvation influence cellular and biochemical parameters to the crab *Carcinus aestuarii*? Mar Environ Res 71:207–212

Matozzo V, Gallo C, Marin MG (2011b) Effects of temperature on cellular and biochemical parameters in the crab *Carcinus aestuarii* (Crustacea, Decapoda). Mar Environ Res 71(5):351–356

Matozzo V, Boscolo A, Marin MG (2013) Seasonal and gender related differences in morphometric features and cellular and biochemical parameters of *Carcinus aestuarii* from lagoon of Venice. Mar Environ Res 89:21–28

McGaw IJ, Whiteley NM (2012) Effects of acclimation and acute temperature change on specific dynamic action and gastric processing in the green shore crab, *Carcinus maenas*. J Therm Biol 37:570–578

McGaw IJ, Kaiser MJ, Naylor E, Hughes RN (1992) Intraspecific morphological variation related to the moult-cycle in colour forms of the shore crab *Carcinus maenas*. J Zool 228:351–359

McKnight A, Mathews LM, Avery R, Lee KT (2000) Distribution is correlated with color phase in green crabs, *Carcinus maenas* (Linnaeus, 1758) in southern New England. Crustaceana 73:763–768

Mesquita SR, Guilhermino L, Guimarães L (2011) Biochemical and locomotor responses of *Carcinus maenas* exposed to the serotonin reuptake inhibitor fluoxetine. Chemosphere 85:967–976

Minchin D (1997) The influence of the parasitic cirripede *Sacculina carcini* on its brachyuran host *Carcinus maenas* within its home range. In: Thresher, R.E. (ed.) Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab, *Carcinus maenas*. CRIMP Tech. Rep. 11. Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratories, Hobart, Australia. p 81–86

Moknes P-O (2004) Self-regulating mechanisms in cannibalistic populations of juvenile shore crabs *Carcinus maenas*. Ecology 85(5): 1343–1354

Moksnes P-O (2002) The relative importance of habitat-specific settlement, predation, and juvenile dispersal for distribution and abundance of young juvenile shore crabs *Carcinus maenas* L. J Exp Mar Biol Ecol 271:41–73

Montes Nieto R, Garcia-Barrera T, Gomez-Ariza JL, Lopez-Barea J (2010) Environmental monitoring of Domingo Rubio stream (Huelva Estuary, SW Spain) by combining conventional biomarkers and proteomic analysis in *Carcinus maenas*. Environ Pollut 158: 401–408

Morales-Caselles C, Martin-Diaz ML, Riba I, Sarasquete C, DelValls TA (2008) Sublethal responses in caged organisms exposed to sediments affected by oil spills. Chemosphere 72:819–825

Moreira SM, Moreira-Santos M, Guilhermino L, Ribeiro R (2006) An in situ postexposure feeding assay with *Carcinus maenas* for estuarine sediment-overlying water toxicity evaluations. Environ Pollut 139: 318–329

Morgan DE, Goodsell J, Mathiessen GC, Garey J, Jacobson P (1980) Release of hatchery-reared bay scallops (*Argopecten irradians*) onto a shallow coastal bottom in Waterfor, Connecticut. Proc World Mariculture Soc 11:247–261

Mori M, Mancon R, Fancuilli G (1990) Notes on the reproductive biology of *Carcinus aestuarii* Nardo (Crustacea, Decapoda) from the lagoon of San Teodoro (Island of Sardinia, Italy). Riv Idrobiol 29:763–774

Mowles SL, Rundle SD, Cotton PA (2011) Susceptibility to predation affects trait-mediated indirect interactions by reversing interspecific competition. Plos ONE 6(8):e23068

Munari M, Matozzo V, Marin MG (2010) Vitellogenin induction in the clam, *Ruditapes philippinarum*, and the crab, *Carcinus aestuarii*, from the lagoon of venice: a comparative study. Freseanius Environ Bull 19:2312–2317

Nelson GA, Chase BC, Stockwell J (2003) Food habits of striped bass (*Morone saxatilis*) in coastal waters of Massachusetts. J Northw Atl Fish Sci 3:21–25

Ozbek M, Koçak C, Acarli D (2012) Reproductive biology of the Mediterranean Green Crab *Carcinus aestuarii* Nardo, 1847 (Crustacea, Brachyura, Portunidae) in Homa Lagoon, Aegean Sea, Turkey. Int J Oceanogr Hydrobiol 41:77–80

Partridge L, French V (1996) Thermal evolution of ectotherm body size: why get big in the cold? In: Johnston IA, Bennett AF (eds) Animals and temperature: phenotypic and evolutionary adaptation. Cambridge University Press, Cambridge, pp 265–292

Pascoal S, Creer S, Taylor MI, Queiroga H, Carvalho G, Mendo S (2009) Development and application of microsatellites in *Carcinus maenas*: genetic differentiation between Northern and Central Portuguese populations. Plos ONE 4(9):e7268

Patarnello T, Volckaert FAM, Castilho R (2007) Pillars of Hercules: is the Atlantic-Mediterranean transition a phylogeographical break? Mol Ecol 16:4426–4444

PCSGA (Pacific Coast Shellfish Growers Association) (2003) Shellfish economy: treasure of the tidelands. Olympia, WA. http://www.pcsga.org

Pedersen SN, Lundebye A-K (1996) Metallothionein and stress protein levels in shore crabs (*Carcinus maenas*) along a trace metal gradient in the Fal Estuary (UK). Mar Environ Res 42(1–4):241–246

Pedersen KL, Pedersen SN, Hojrup P, Andersen JS, Roepstorff P, Knudsen J, Depledge MH (1994) Purification and characterization of a cadmium-induced metallothionein from the shore crab *Carcinus maenas* (L.). Biochem J 297:609–614

Pedersen SN, Lundebye A-K, Depledge MH (1997) Field application of metallothionein and stress protein biomarkers in the shore crab (*Carcinus maenas*) exposed to trace metals. Aquat Toxicol 37:183–200

Pedersen SN, Pedersen KL, Hojrup P, Knudsen J, Depledge MH (1998) Induction and identification of cadmium-, zinc- and copper-metallothioneins in the shore crab *Carcinus maenas* (L.). Comp Biochem Physiol Part C 120:251–259

Pereira E, Abreu SN, Coelho JP, Lopes CB, Pardal MA, Vale C, Duarte AC (2006) Seasonal fluctuations of tissue mercury contents in the European shore crab *Carcinus maenas* from low and high contamination areas (Ria de Aveiro, Portugal). Mar Pollut Bull 52:1450–1457

Pereira P, De Pablo H, Dulce Subida M, Vale C, Pacheco M (2009) Biochemical responses of the shore crab (*Carcinus maenas*) in a eutrophic and metal-contaminated coastal system (Obidos lagoon, Portugal). Ecotoxicol Environ Saf 72:1471–1480

Powell A, Rowley AF (2008) Tissue changes in the shore crab *Carcinus maenas* as a result of infection by the parasitic barnacle *Sacculina carcini*. Dis Aquat Org 80:75–79

Queiroga H, Costlow JD, Moreira MH (1994) Larval abundance patterns of *Carcinus maenas* (Decapoda, Brachyura) in Canal de Mira (Ria de Aveiro, Portugal). Mar Ecol Prog Ser 111:63–72

Rainbow PS, Black WH (2005) Cadmium, zinc and the uptake of calcium by two crabs, *Carcinus maenas* and *Eriocheir sinensis*. Aquat Toxicol 72:45–65

Rainbow P, White SL (1989) Comparative strategies of heavy metal accumulation by crustaceans: zinc, copper and cadmium in a decapod, an amphipod and a barnacle. Hydrobiologia 174:245–262

Rainbow PS, Amiard-Triquet C, Amiard JC, Smith BD, Best SL, Nassiri Y, Langston WJ (1999) Trace metal uptake rates in crustaceans (amphipods and crabs) from coastal sites in NW Europe differentially enriched with trace metals. Mar Ecol Prog Ser 183:189–203

Ramey PA, Teichman E, Oleksiak J, Balci F (2009) Spontaneous alternation in marine crabs: invasive versus native species. Behav Process 82:51–55

Reid DG, Aldrich JC (1989) Variations in response to environmental hypoxia of different forms of the shore crab, *Carcinus maenas*. Comp Biochem Physiol Part A 29:535–539

Reid DG, Abelló P, McGaw I, Naylor E (1989) Differential tolerances of desiccation and hypo-osmotic stress in sub- and inter-tidal *Carcinus maenas*. In: Aldrich JC (ed) Phenotypic responses in aquatic ectotherms. Japaga, Dublin, pp 89–96

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

Ricciardi F, Matozzo V, Marin MG (2008) Effects of 4-nonylphenol exposure in mussels (*Mytilus galloprovincialis*) and crabs (*Carcinus aestuarii*) with particular emphasis on vitellogenin induction. Mar Pollut Bull 57:365–372

Ricciardi F, Matozzo V, Binelli A, Marin MG (2010) Biomarker responses and contamination levels in crabs (*Carcinus aestuarii*) from the Lagoon of Venice: an integrated approach in biomonitoring estuarine environments. Water Res 44:1725–1736

Rice AL, Ingle RW (1975) The larval development of *Carcinus maenas* (L.) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. Bull Br Mus (Zool) 28:103–119

Robinson EM, Smee DL, Trussell GC (2011) Green crab (*Carcinus maenas*) foraging efficiency reduced by fast flows. Plos ONE 6(6): e21025

Rodrigues AP, Oliveira PC, Guilhermino L, Guimaraes L (2012) Effects of salinity stress on neurotransmission, energy metabolism, and antioxidant biomarkers of *Carcinus maenas* from two estuaries of the NW Iberian Peninsula. Mar Biol 159:2061–2074

Rodrigues AP, Gravato C, Guimaraes L (2013a) Involvement of the antioxidant system in differential sensitivity of *Carcinus maenas* to fenitrothion exposure. Environ Sci Process Impacts 15:1938–1948

Rodrigues AP, Lehtonen KK, Guilhermino L, Guimaraes L (2013b) Exposure of *Carcinus maenas* to waterborne fluoranthene: accumulation and multibiomarker responses. Sci Total Environ 443:454–463

Roman J, Palumbi SR (2004) A global invader at home: population structure of the green crab, *Carcinus maenas*, in Europe. Mol Ecol 13:2891–2898

Ropes JW (1968) The feeding habits of the green crab *Carcinus maenas* (L.). J Exp Mar Biol Ecol 67:183–201

Ross DJ, Johnson CR, Hewitt CL, Ruiz GM (2004) Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. Mar Biol 144:747–756

Rossong MA, Quijo'N PA, Snelgrove PVR, Barrett TJ, McKenzie CH, Locke A (2012) Regional differences in foraging behaviour of invasive green crab (*Carcinus maenas*) populations in Atlantic Canada. Biol Invasions 14:659–669

Roudez RJ, Glover T, Weis JS (2007) Learning in an invasive and a native predatory crab. Biol Invasions 10:1191–1196

Rubiliani C (1983) Action of a rhizocephalan on the genital activity of host male crabs: characterization of a parasitic secretion inhibiting spermatogenesis. Int J Invertebr Reprod 6:137–147

Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. Am Zool 37:621–632

Rumrill SS (1990) Natural mortality of marine invertebrate larvae. Ophelia 32:163–198

Sanviti G, Romestand B, Trilles JP (1981) Les sacculines (*Sacculina carcini* Thompson, 1836) de *Carcinus mediterraneus* et *Pachygraspus marmoratus*: comparaison immunochemique: étude comparée de leur influence sur la composition protéique de l'hémolymphe des deux hôtes. Parasitol Res 64:243–251

Saville DH, Irwin SW (2005) A study of the mechanisms by which the cercariae of *Microphallus primas* (Jag, 1909) Stunkard, 1957 penetrate the shore crab, *Carcinus maenas* (L). Parasitology 131(Pt4): 521–529

Schnapp D, Kemp GD, Smith VJ (1996) Purification and characterization of a proline-rich antibacterial peptide, with sequence similarity to bactenecin-7, from the haemocytes of the shore crab, *Carcinus maenas*. Eur J Biochem 240:532–539

See KE, Feist BE (2010) Reconstructing the range expansion and subsequent invasion of introduced European green crab along the west coast of the United States. Biol Invasions 12:1305–1318

Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecol Appl 13(1):S159–S169

Smith VJ, Chisholm JRS (2001) Antimicrobial proteins in crustaceans. In: Beck G, Sugurmaran M, Cooper EL (eds) Advances in experimental medicine and biology, vol 484. Kluwer, Netherlands, pp 95–112

Somero GN (2002) Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. Integr Comp Biol 42: 780–789

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 littoralis* sp. nov. a crustacean pathogen within

the Haplosporida (Cercozoa, Ascetosporea). Dis Aquat Org 105: 243–252

Stewart SC, Dick JTA, Laming PR, Gerhardt A (2010) Assessment of the multispecies freshwater biomonitor (MFB) in a marine context: the Green crab (*Carcinus maenas*) as an early warning indicator. J Environ Monit 12:1566–1574

Styrishave B, Rewitz K, Andersen O (2004) Frequency of moulting by shore crabs *Carcinus maenas* (L.) changes their colour and their success in mating and physiological performance. J Exp Mar Biol Ecol 313:317–336

Tepolt CK, Somero GN (2013) Master of all trades: thermal acclimation and adaptation of cardiac function in a broadly distributed marine invasive species, the European green crab, *Carcinus maenas*. J Exp Biol 217:1129–1138

Tepolt CK, Bagley MJ, Geller JB, Blum MJ (2006) Characterization of microsatellite loci in the European green crab (*Carcinus maenas*). Mol Ecol 6:343–345

Tepolt CK, Darling JA, Bagley MJ (2009) European green crabs (*Carcinus maenas*) in the northeastern Pacific: genetic evidence for high population connectivity and current mediated expansion from a single introduced source population. Divers Distrib 15:997–1009

Thresher RE, Werner M, Høeg T, Svane I, Glenner H, Murphy NE, Wittwer C (2000) Developing the options for managing marine pests: specificity trials on the parasitic castrator, *Sacculina carcini*, against the European crab, *Carcinus maenas*, and related species. J Exp Mar Biol Ecol 25:37–51

Thresher RE, Proctor C, Ruiz G, Gurney R, MacKinnon C, WaltonW RL, Bax N (2003) Invasion dynamics of the European shore crab, *Carcinus maenas*, in Australia. Mar Biol 142:867–876

Tincu JA, Taylor SW (2004) Antimicrobial peptides from marine invertebrates. Antimicrob Agents Chemother 48:3645–3654

Todd PA, Ladle RJ, Briers RA, Brunton A (2005) Quantifying two-dimensional dichromatic patterns using a photographic technique: case study on the shore crab (*Carcinus maenas* L.). Ecol Res 20: 497–501

Torchin ME, Lafferty KD, Kuris AM (1996) Infestation of an introduced host, the European green crab, *Carcinus maenas*, by a symbiotic nemertean egg predator, *Carcinonemertes epialti*. J Parasitol 82(3): 449–453

Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biol Invasions 3:333–345

Towle DW, Smith CM (2006) Gene discovery in *Carcinus maenas* and *Homarus americanus* via expressed sequence tags. Integr Comp Biol 46(6):912–918

Towle DW, Rushton ME, Heidysch D, Magnani JJ, Rose MJ, Anstutz A, Jordan MM, Shearer DW, Wu WS (1997) Sodium/proton antiporter in the euryhaline *Carcinus maenas*: molecular cloning, expression and tissue distribution. J Exp Biol 200:1003–1014

Towle DW, Terwilliger NB, Henry RP (2008) Hypotonic stress alters expression of genes encoding transcription factors, protein homeostasis enzymes, mitochondrial proteins, and transport proteins in gills of the euryhaline green crab (*Carcinus maenas*). Comp Biochem Physiol Part A 151:S37–S43

Towle DW, Henry RP, Terwilliger NB (2011) Microarray-detected changes in gene expression in gills of green crabs (*Carcinus maenas*) upon dilution of environmental salinity. Comp Biochem Physiol Part D 6: 115–125

Truchot JP (1980) Lactate increases the oxygen affinity of crab hemocyanin. J Exp Zool 214:205–208

Truscott R, White KN (1990) The influence of metal and temperature stress on the immune system of crabs. Funct Ecol 4:455–461

Vedel GR, Depledge MH (1995) Stress-70 levels in the gills of *Carcinus maenas* exposed to copper. Mar Pollut Bull 31(1–3):84–86

Vinuesa JH (2007) Molt and reproduction of the European crab *Carcinus maenas* (Decapoda: Portunidae) in Patagonia, Argentina. Rev Biol Trop 55:49–54

Vlak JM, Bonami JR, Flegel TW, Kou GH, Lightner DV, Lo CF, Loh PC, Walker PW (2005) Nimaviridae. In: Fauquet CM, Mayo J, Maniloff J, Desselberger U, Ball LA (eds) Virus Taxonomy Eighth report of the International Committee on Taxonomy of Viruses. Elsevier, Amsterdam, pp 187–192

Wallace JC (1973) Feeding, starvation and metabolic rate in the shore crab *Carcinus maenas*. Mar Biol 20(4):277–281

Weber RE, Behrens JW, Malte H, Fago A (2008) Thermodynamics of oxygenation-linked proton and lactate binding govern the temperature sensitivity of O_2 binding in crustacean (*Carcinus maenas*) hemocyanin. J Exp Biol 211:1057–1062

Wheatly MG (1981) The provision of oxygen to developing eggs by female shore crabs (*Carcinus maenas*). J Mar Biol Assoc UK 61: 117–128

Whitlow WL, Rice NA, Sweeney C (2003) Native species vulnerability to introduced predators: testing an inducible defense and a refuge from predation. Biol Invasions 6:23–31

Zanders IP (1980) Regulation of blood ions in *Carcinus maenas* (L.). Comp Biochem Physiol Part A 65:97–108

Zetlmeisl C, Hermann J, Petney T, Glenner H, Griffiths C, Taraschewski H (2011) Parasites of the shore crab *Carcinus maenas* (L.): implications for reproductive potential and invasion success. Parasitology 138:391–401