Invasive alien Crustacea: dispersal, establishment, impact and control

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Abstract The subphylum Crustacea includes the most successful species among aquatic alien invaders. The impacts of invasive alien crustaceans (IAC) are often substantial, due to the complex trophic role of most of these species leading to cascading effects throughout the invaded ecosystems. IAC also have the potential to cause a shift in the 'keystone' ecosystem functions, changing energy flux and nutrient cycles which together affect critical ecosystem services such as biodiversity, fisheries yield and water quality. Although no individual trait appears to be a good predictor of invasion success, a combination of some characteristics such as eurytolerance, omnivory and certain *r*-selected life-history traits results in a high probability of alien crustacean species becoming invasive. Both environmental factors, such as habitat heterogeneity in the invaded ecosystems, and evolutionary factors, such as adaptations to new environmental conditions, also play important roles during establishment. Therefore, individual environmental niche models, including genetic algorithm, have the highest likelihood of providing useful predictive information about invasion success and spread of alien Crustacea. Attempts to control IAC through biocides or mechanical removal have had mixed success in the past but a strategic combination of different methods may lead to some success in the future.

Keywords Aquatic habitats · Genetic diversity · Prevention · Control · Ballast water · Invasions · Crustacea

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Introduction

Analyses on continental and regional scales confirm that the subphylum Crustacea Brünnich is the most successful taxonomic group of aquatic alien invaders (as defined by Engelkes and Mills 2011) across the globe (Devin et al. 2005; Karatayev et al. 2009). In European freshwater ecosystems, for example, 53% of invasive alien species are Crustacea, whereas the native fauna is dominated by insects with only 12% of crustacean species (Karatayev et al. 2009). A similar pattern appears in brackish waters (Olenin and

Leppakoski 1999; Ranasinghe et al. 2005) and in marine coastal environments (Galil 2008). Invasive alien crustaceans (hereafter referred to as IAC) can reach extremely high population densities outnumbering native competitors. For example, the North American spiny-cheek crayfish, *Orconectes limosus* (Rafinesque), and the signal crayfish, *Pacifastacus leniusculus* (Dana), can reach densities of 70 and 30 m^{-2} respectively in the invaded European countries, whereas population density of the native noble crayfish *Astacus astacus* (L.) is 14 m^{-2} on average (Gherardi 2007).

IAC are mostly Amphipoda and Decapoda, but other prominent examples include Cladocera, Copepoda and Mysida (Ricciardi 2011; Table 1). Although IAC are widespread (Vilá et al. 2010), there appear to be some geographic hotspots for their invasion. For example, Crustacea have played a major role in the mass invasions recently experienced by the Baltic Sea, California Bay and the Laurentian Great Lakes (Cohen and Carlton 1998; Olenin and Leppakoski 1999; Ricciardi and MacIsaac 2000). Conversely, the Ponto-Caspian region represents one of the most important sources of IAC to Europe and North America (Ricciardi and Rasmussen 1998; Table 1).

In this paper we review the literature on IAC and summarise our current knowledge about the drivers of their dispersal and establishment as well as their impact on native ecosystems. Recent developments in prevention and control are also reviewed. We exclude from our examples the few obligate herbivorous and detritivorous crustacean species. The large majority of Crustacea are in fact omnivorous collector-gatherers (Karatayev et al. 2009) that occasionally behave as predators. No geographic restriction was made, although most case studies come from Europe and North America due to the strong literature bias towards these regions. Since most Crustacea are aquatic, the focus of our analysis will be freshwater and marine ecosystems. Our intention was to highlight the relevance of the theories on invasion ecology to IAC. We refer to specific theoretical chapters of this special issue of BioControl for more in depth discussion of the theoretical framework (Engelkes and Mills 2011; Lawson Handley et al. 2011; Roy et al. 2011). In line with Engelkes and Mills (2011), the three stages of the invasion process of arrival, establishment and spread will be analysed.

Vectors of introduction and invasion pathways

By definition, the arrival of IAC is aided by humans (Engelkes and Mills 2011). The three most important vectors for their introduction are ship transport as ballast water (Gollasch 2006; Ricciardi 2006), dispersal through canal systems (Galil 2008) and intentional introductions for aquaculture and stocking purposes (Savini et al. 2010; Table 1). The same pathways and associated processes are also often important during the secondary spread of IAC.

Ballast water transport allows for the long-distance dispersal of many IAC. Indeed, many Crustacea possess planktonic life stages that are easily taken up and released during ballasting/deballasting procedures, thus creating a high propagule pressure at the points of discharge. This introduction effort is theoretically a significant element of success at this stage (Engelkes and Mills 2011; Lockwood et al. 2005), although there are yet few empirical data to substantiate this claim. A large population of invaders is expected to be more resilient to extinction through demographic stochasticity and Allee effects. Furthermore, high propagule pressure may contribute to maintaining high levels of genetic variation and thus facilitate adaptation to the new environment (see below).

The first recorded example of intercontinental transport is probably the Chinese mitten crab *Eriocheir sinensis* (H. Milne-Edwards) from China to Europe in the early twentieth century. Ballast water might have played a role also for the dispersal of this species on a shorter geographical scale within Europe, as indicated by molecular data showing a significant correlation between rates of gene flow and shipping routes (Herborg et al. 2007c). Many other Crustacea, including amphipods, branchiopods, copepods, decapods, isopods, and mysids are regularly transported in the ships' ballast (Bailey et al. 2007; Table 1), including the fishhook waterflea *Cercopagis pengoi* (Ostroumov) (Grigorovich et al. 2000; Panov et al. 2004) and other Ponto-Caspian Crustacea which have invaded the Laurentian Great Lakes in North America (Ricciardi and MacIsaac 2000).

Artificial canals between previously isolated water bodies have contributed to intra-continental invasions of IAC (Table 1). By design, these artificial waterways provide shortcuts between water bodies, thus leading to a rapid expansion in the geographical range

Table 1 Examples of prominent IAC, their native and invasive ranges, most likely introduction vectors and potential traits and factors that might have facilitated their invasion process

Taxon	Native range	Invasive range	Main vectors of introduction	Facilitating traits	References
Amphipoda					
Dikerogammarus villosus	Ponto–Caspian basin	Baltic and North Sea drainages, Rhône, Loire	Canal, ballast water, hull fouling	Euryhaline, eurytherme omnivorous, r-selected traits	DAISIE (2009), Füreder and Pöckl (2007), and Pöckl (2009)
Echinogammarus ischnus	Ponto–Caspian basin	Baltic and North Sea drainages	Canal, ballast water	Euryhaline, omnivorous	DAISIE (2009), Bij de Vaate et al. (2002), and Jazdzewski (1980)
Echinogammarus trichiatus	Ponto–Caspian basin	Baltic and North Sea drainages, Dnjepr reservoirs	Canal, intentional	Euryhaline, omnivorous	Bij de Vaate et al. (2002), DAISIE (2009), and Füreder and Pöckl (2007)
Echinogammarus warpachowskyi	Ponto–Caspian basin	Baltic drainage, reservoirs and lakes in Ukraine	Intentional	Euryhaline, omnivorous	Bij de Vaate et al. (2002)
Gammarus tigrinus	Atlantic coast of North America	British Isles, Baltic and North Sea drainages, Baltic Sea, Great Laurentian Lakes	Ballast water	Euryhaline	DAISIE (2009), Grigorovich et al. (2000), Holdich and Pöckl (2007), and USGS (2005)
Gmelinoides fasciatus	Lake Baikal	Baltic drainage, lakes of North-western and Central Russia	Intentional, fisheries trade accidental		DAISIE (2009)
Obesogammarus crassus	Ponto–Caspian basin	Baltic drainage, lakes and reservoirs in Western Russia	Intentional, canal	Euryhaline, omnivorous	Bij de Vaate et al. (2002), DAISIE (2009), and Jazdzewski (1980)
Decapoda					
Carcinus maenas	Europe	Atlantic and Pacific coasts of North America	Ballast water, fisheries and trade—accidental	Euryhaline, enemy release hypothesis	Carlton (1985), DAISIE (2009), Torchin et al. (2001), and USGS (2005)
Orconectes limosus	North America	Africa, Europe, North America	Intentional	Commercial importance	DAISIE (2009), Holdich and Black (2007)
Pacifastacus leniusculus	North America	Asia, Europe, North America	Intentional	Commercial importance	Gherardi (2007, 2011a)
Portunus pelagicus	Red Sea	Mediterranean	Canal	Euryhaline, r-selected traits	DAISIE (2009)
Procambarus clarkii	North America	Africa, Asia, Europe, Americas	Intentional	Tolerant to anoxic conditions and high turbidity, r-selected traits	Gherardi (2006, 2007, 2011a), and Lindqvist et al. (2004)
Eriocheir sinsensis	China	Europe, North America	Ballast water, intentional	Euryhaine, eurytherme, omnivorous	André (1954), DAISIE (2009), Dittel and Epifanio (2009), and Herborg et al. (2005)

Table 1 continued

Taxon	Native range	Invasive range	Main vectors of introduction	Facilitating traits	References
Atyaephyra desmaresti	Southern Europe	Central Europe	Canal	Omnivorous	van der Velde et al. (2000)
Cladocera					
Bosmina coregoni maritima	Ponto–Caspian basin	Laurentian Great Lakes	Ballast water	Diapausing eggs, tolerant of eutrophic conditions	Grigorovich et al. (2000), Panov et al. (2004), and USGS (2005)
Bosmina longirostris	Ponto–Caspian basin	Laurentian Great Lakes	Ballast water	Diapausing eggs	Grigorovich et al. (2000) and Panov et al. (2004)
Cercopagis pengoi	Ponto–Caspian basin	Laurentian Great Lakes, Baltic Sea	Ballast water		DAISIE (2009), Grigorovich et al. (2000), Panov et al. (2004), and USGS (2005)
Branchiura					
Argulus japonicus	East Asia	Worldwide	Fisheries and trade—accidental		DAISIE (2009), Lester and Roubal (1999), and USGS (2005)
Sessilia					
Balanus improvisus	North America Atlantic coast	Atlantic coast of Europe, Baltic and Black seas, African coast, Japan, Australian East Coast, New Zealand, Pacific coast of USA, Mexico, Columbia, Peru	Hull fouling, fisheries and trade—accidental, ballast water	Self-fertilisation	DAISIE (2009)
Mysida					
Hemimysis anomala	Ponto–Caspian basin	Baltic and North Sea drainages, Laurentian Great Lakes	Canal, ballast water	Euryhaline, omnivourus	Bij de Vaate et al. (2002), DAISIE (2009), Füreder and Pöckl (2007), Pöckl (2009), Pothoven et al. (2007), Stubbington et al. (2008), and USGS (2005)
Limnomysis benedeni	Ponto–Caspian basin	Baltic and North Sea drainages, Baltic Sea	Intentional, canal	Euryhaline, omnivourus	Bij de Vaate et al. (2002) and DAISIE (2009)
Isopoda					
Jaera istri Veuille	Ponto–Caspian basin	North Sea drainages	Canal	Euryhaline, omnivourus	Bij de Vaate et al. (2002) and DAISIE (2009)

of alien Crustacea. In Europe, a number of canal systems such as the Rhine-Main-Danube Canal, the Mittelland Canal and the canal connecting the rivers Bug and Pripyat have facilitated the spread of Ponto-Caspian species including many IAC such as the bloody-red mysid *Hemimysis anomala* (G.O. Sars) and the amphipods *Echinogammarus trichiatus* (Martynov) and *Dikerogammarus villosus* (Sowinsky) to the North Sea and Baltic drainages (Bij de Vaate et al. 2002; Füreder and Pöckl 2007). The Suez Canal has been the pathway of introduction of 63% of the 95 IAC species recorded in the Mediterranean Sea (Galil 2009). Artificial canals facilitate the secondary spread of aquatic invaders. For example, *H. anomala* first arrived in the UK in ballast water but has dispersed further through the English Midlands using canals (Stubbington et al. 2008). After their first introduction to North America via ballast water, some Ponto-Caspian IAC, including freshwater and brackish-water amphipods, cladocerans, copepods, decapods and mysids, have spread quickly and irrepressibly, via drift and local boating through the systems of canals in the Hudson River catchment and the Laurentian Great Lakes (Mills et al. 1996). The canal that links Saint Malo to the River Loire and the Brest–Loire canal has been a possible pathway for the introduction of *E. sinensis* to the River Loire (André 1954). Crustacea may be also transported attached to ships' hulls, such as the acorn barnacle *Balanus improvisus* (Darwin), whilst other species burrow into softer materials such as wood, e.g. the isopod *Limnoria tripunctata* (Menzies). However, the number of individuals that survive during long-distance ship transport is low, making the risk of successful introductions via hull fouling relatively limited compared to ballast transport (Sylvester and MacIsaac 2010).

Stock translocation and aquaculture have been one of the most important intentional sources for IAC (Table 1). *Orconectes limosus*, introduced into Germany from North America in 1890, is probably the first documented example of a crustacean species being translocated for stocking purposes (Holdich and Black 2007). Many other crayfish species followed, such as *P. leniusculus* and the red swamp crayfish *Procambarus clarkii* (Girard), which were introduced to Europe in the 1960s and 1970s, respectively. Interestingly, 46% of all freshwater decapod species in Europe are today invasive aliens (Vilá et al. 2010) and some of these species have high

commercial importance (Gherardi 2011a). Secondary introductions of *E. sinensis* were likely associated with their use as a culinary delicacy accompanied by a market value of US$1.25 billion year^{-1} (Dittel and Epifanio 2009). Similarly, the experimental release of the red king crab *Paralithodes camtschaticus* (Tilesius) by Russian scientists to the southern Russian Barents Sea in 1961–1969 was aimed at developing commercial stocks (DAISIE 2009). Other motives for the introduction of IAC include their potential use as an industrial resource and the control of diseases and nuisance species. For example, *E. sinensis* was imported into several countries for the production of cosmetics and as agricultural fertilizer (Herborg et al. 2005), whereas *P. clarkii* was released, without success, to some African lakes to control freshwater snails that carry human schistosomiasis and to some European water bodies for weed clearance (Gherardi 2011a; Holdich and Pöckl 2007). Finally, the massive introduction of many amphipods and mysids to water bodies in North America and Europe were purposed to boost secondary production and increase yields for the fishing industry and recreational angling (Ricciardi 2011). The problems caused by these introduced species largely outweighed the desired benefits (*cf.* below).

Numerous alien Crustacea have been moved unintentionally for long distances outside their native ranges as "contaminants" of commodities. Amphipods, branchiurans, decapods, etc. may contaminate fish stocks or stocks of other taxa. For example, the branchiuran fish-louse *Argulus japonicus* (Thiele) has today a worldwide distribution having being moved with koi carp, *Cyprinus carpio* (L.) and other farmed fish from the Orient (Lester and Roubal 1999). The amphipod *Gmelinoides fasciatus* (Stebbing) was introduced accidentally into Lake Peipsi at the beginning of the 1970s during several attempts to enrich the native population of *Gammarus lacustris* (G.O. Sars) through stocking from Siberian populations, which contained a small proportion (1–2%) of *G. fasciatus*. Similarly, *B. improvisus* is a frequent epibiont on imported oysters and live American lobsters (*Homarus americanus* H. Milne-Edwards) shipped to restaurants on the west coast of the USA can contain the European green crab *Carcinus maenas* (L.) adults (Carlton 1985).

Other dispersal vectors include the translocation, either intentional or not, through recreational fishing

and aquarium trade. *Carcinus maenas* juveniles are common in the New England rockweed *Fucus* spp. and in the kelp *Ascophyllum nodosum* (L.), which are both used to pack live worms shipped to bait shops (Carlton 1992). Some crayfish species, such as *O. limosus*, the rusty crayfish *Orconectes rusticus* (Girard) and the crab *E. sinensis*, have been commonly used as live fish bait (Dittel and Epifanio 2009; Holdich and Black 2007; Lodge et al. 2000). The aesthetic characteristics of marbled crayfish *Procambarus* sp., a parthenogenetic form of *Procambarus fallax* (Hagen), led to its introduction into Europe and Madagascar through the pet trade, which was followed by its release to the wild (Nonnis Marzano et al. 2009). Finally, some crustacean species are used as biological supply or as research material, such as *O. rusticus* and *C. maenas* in North America: living specimens can be readily ordered and air-shipped in large quantities from several biological supply houses and are often accidentally or intentionally released to the wild from school or research aquaria.

Characteristics of successful Crustacea

The invasiveness of species is often imputed to a number of characteristics of their life history, physiology and behaviour. However, particularly in Crustacea, the relative importance of these characteristics may vary among different invasion events of the same species as well as among stages of the invasion process. Furthermore, as discussed below, the fitness value of certain traits varies across environments. Thus, we can only depict an ideal crustacean invader and assume that the probability of a given species' invasive success increases with the number of characteristics it shares with such an ideal invader.

Passive and active dispersal capacity

High dispersal capacity, either passive or active, facilitates the arrival of IAC, their initial colonization and their secondary spread. The passive human-mediated dispersal, including the so-called "saltation dispersal" through ballast water (Smith et al. 1999), is made effective by a suite of traits. Successful IAC are euryhaline, i.e. tolerate fluctuating salinities, such

as the ones encountered in ballast tanks during transoceanic voyages, typically ranging between 4 and 30‰ (Ellis and MacIsaac 2009). Pothoven et al. (2007) refer to a salinity tolerance range of 0.1–18‰ for *H. anomala* and Jazdzewski (1980) reports values up to 23‰ for the amphipod *Echinogammarus ischnus* (Stebbing), these two species having invaded the Laurentian Great Lakes Basin from the Ponto-Caspian in ballast water. Long-term climate change scenarios predict greater fluctuations in salinity: the potential of alien Crustacea to adapt to these changes will increase their invasive potential. Indeed, Reid and Orlova (2002) attribute the successful invasion of the Laurentian Great Lakes by Ponto-Caspian Crustacea to euryhaline tolerance traits that evolved with salinity fluctuations over evolutionary times.

Planktonic Crustacea also possess diapausing eggs (Bailey et al. 2003). Due to this characteristic, the cladocerans *Bosmina coregoni maritima* P. E. Müller and *Bosmina longirostris* (O. F. Müller), both Laurentian Great Lakes invaders, were able to survive periods of unfavourable salinity in ballast water, which would have otherwise killed them (Johannsson et al. 1991). Diapausing eggs occur commonly in the bottom sediments of the ships' ballast tanks in numbers that reach tens of millions per ship (Ricciardi 2011). A large pool of resting eggs of *C. pengoi* has facilitated its jump from the eastern Baltic Sea to the Laurentian Great Lakes (Grigorovich et al. 2000; Panov et al. 2004).

An ideal crustacean invader should also possess the ability to actively disperse for short (diffusion dispersal) and long distances (secondary spread) after its establishment (Smith et al. 1999). Quantitative data of active spreading rate are available for *E. sinensis* in Europe. During the peak time of range expansion in Continental Europe (1927–1931), *E. sinensis* spread with a mean rate of 441 km year^{-1}. In the United Kingdom, mitten crabs dispersed along the coast at a rate of 78 km year^{-1} on average (1976–1999), with a recent sharp increase to 448 km year^{-1} (1997–1999) (Herborg et al. 2005). The upstream spread along rivers was 16 km year^{-1} in 1973–1998 with a marked increase since 1995 to 49 km year^{-1} (1995–1998). Larval drift may have allowed the spread of *E. sinensis* between adjacent estuaries, like the Elbe and Weser (ca. 60 km). Where estuaries are further apart, the duration of the pelagic larval phase and the prevailing currents have to be

taken into consideration. Simulations of dispersal dynamics showed that winds can move coastal larval patches against this prevalent current in a south westerly direction (Ellien et al. 2000), which would have allowed the dispersal of *E. sinensis* from Germany to the Netherlands, then to Belgium and France. Potential for fast spread has also been shown for *C. maenas* with a maximum of 63 km year^{-1} in the eastern North American coast (Grosholz and Ruiz 1996), the Japanese shore crab *Hemigrapsus sanguineus* (De Haan) with 12 km year^{-1} in Eastern North America (McDermott 1991), and the barnacle *Elminius modestus* (Darwin) with 30 km year^{-1} along the northwest coast of Europe (Crisp 1958). Radiotelemetry was used to investigate the short-term movements of individual *P. clarkii* crayfish in diverse environmental contexts (Barbaresi et al. 2004; Gherardi and Barbaresi 2000), showing a complex pattern of locomotion, characterised by phases of high speed (nomadic movements) alternated with longer periods of slow or null speed (stationary phases). Particularly in some areas, such as rice fields in Spain, movement can be fast, even exceeding 3 km day^{-1} (Gherardi and Barbaresi 2000).

Environmental tolerance

Broad environmental tolerance is also likely to be a favourable trait when colonising new areas. During various stages of the colonisation process, colonists must be able to cope with a range of contrasting environmental conditions, which are often different from those encountered in native areas. Typical IAC are considered to be tolerant to wide ranges of water temperature, salinity, oxygen levels and anthropogenic disturbance (but see section on evolutionary factors). For example, *P. clarkii* can survive in anoxic and dry conditions in burrows and tolerates elevated turbidity, unlike most freshwater crayfish (Gherardi 2006). The massive invasion of amphipods into Central and Western Europe was possibly facilitated by the increasing ionic content of large European rivers caused by agricultural and industrial inputs (Jazdzewski and Konopacka 2000). *Gammarus tigrinus* (Sexton), an amphipod originating from the Atlantic seaboard of North America, was introduced into Britain early in the twentieth century, where it thrived in areas where the water was salty due to mining pollution as in the River Erewash in Derbyshire. Due to a decline in the coal mining industry in that area, the river became less saline, resulting in a dramatic decline in the species (Holdich and Pöckl 2007). In 1957, specimens from Wyken Slough near Coventry (West Midlands) were deliberately introduced into the rivers Weser and Werra in Germany where indigenous gammarids have disappeared due to pollution and survived such conditions (Bulnheim 1985). The DAISIE database classifies three of the most notorious invasive alien brachyurans *E. sinensis*, *C. maenas* and the swimming crab *Portunus pelagicus* (L.) as euryhaline, *E. sinsensis* being also eurytherme (DAISIE 2009). Salt tolerance was also shown in the isopod *Jaera istri* (Veuille), which has invaded many water bodies in Western Europe via the River Danube–Main–River Rhine Canal (Holdich and Pöckl 2007). A recent meta-analysis indicates however that elevated salinity tolerance is not a common feature among amphipod invaders in Europe (Piscart et al. 2011): only the North American *G. tigrinus* is more salt tolerant than their native counterparts, whereas the Eurasian *Gammarus roeseli* (Gervais), *Corophium curvispinum* (Sars) and *D. villosus* have similar salinity tolerances as native amphipod species.

Feeding behaviour

A wide feeding niche has long been thought to confer an advantage to invasive species, because this trait maximises the range of resources (dietary omnivory) and prey types (trophic omnivory) that are available to newly settled individuals (Sol and Lefebvre 2000; Romanuk et al. 2009; Baiser et al. 2010; Zhang et al. 2010). Typically, IAC conform to this theory and are predominantly omnivores: *Eriocheir sinensis* is capable of feeding on a wide range of plants, invertebrates, fish eggs and terrestrially derived detritus, but gastropods and bivalves are the dominant components of its diet (Dittel and Epifanio 2009). In the invaded areas, the freshwater river prawn *Atyaephyra desmaresti* (Millet) feeds on micro-organisms, algae, plants, detritus, live and dead animals (van der Velde et al. 2000). They are also often opportunistic and can efficiently exploit the most abundant food source available in the invaded area. This high degree of omnivory can lead to striking differences in diet between locations (Perkins et al. 1969), whether invaded or native, as described for example for *C. maenas*. The major prey items are bivalves in Massachusetts, New Hampshire and Nova Scotia; bivalves and gastropods for adults, and

gastropods and polychaetes for juveniles in South Wales; crustaceans, algae and bivalves for adults, and crustaceans and algae for juveniles in North Wales and Rhode Island; barnacles, bivalves and gastropods in Scotland; bivalves and gastropods in Danish waters, and decapods in the Danish Wadden Sea; gastropods, isopods and polychaetes in South Africa; and polychaetes and algae in France (Cohen et al. 1995). In a similar example, the diet of *P. clarkii* changes across sites and seasons in accordance with the diverse species dominating in each individual habitat (Gherardi and Barbaresi 2007).

This ability to exploit a wide range of resources is contingent upon physical features that allow a degree of dietary generality, for example the versatile pincers of *C. maenas* and *P. clarkii*. However in some cases IAC's achieve a high degree of omnivory because they have specific physical adaptations to a range of food types. Several feeding modes have been described in *D. villosus* (Platvoet et al. 2009), including detritus feeding, grazing, particle feeding, coprophagy, predation on benthic and free swimming invertebrates, predation on fish eggs and larvae, as well as feeding on byssus threads of bivalves. Such propensity for omnivory was confirmed by the morphology of its mouthparts under scanning electron microscope analysis (Mayer et al. 2008). The stout mandibles with well-developed incisors enable the species to kill prey with robust integument. The setae on the maxillae and maxillipeds can be used, together with the gnathopods and the antennae, to filter suspended algae and other small particles from the water current and to collect detritus. No specific tool for scraping periphyton from the substratum is observed, however, and the molar surfaces of the mandibles are weakly structured, suggesting a limited efficiency in feeding on macrophytes. On the contrary, *G. roeseli*, displaced from many European water bodies by *D. villosus*, shows maxillulae armed with chisel-like setae and the maxillipeds bearing flattened setae, a possible specialisation for scraping off adherent food from the substratum. Besides, *G. roeseli*'s mandibles resemble rasps, which confirms its ability to grind firm plant material. Compared to *D. villosus*, the setation of the antennae and the gnathopods in *G. roeseli* is sparse and short, which indicates that filter feeding, one of the feeding modes of *D. villosus*, plays a minor role in the nutrition of *G. roeseli*. Thus trophic generalism, wide dietary niches and omnivory appear to be common traits in successfully established IAC.

Life history traits and reproductive mode

The initial successful colonization may be followed by the establishment of a self-sustaining population or a "minimum viable beachhead population" (MVBP), i.e. a reproducing population that is large enough to persist. Certain life history traits allow some Crustacea to form a MVBP more easily. The following life history traits have been cited as important in the invasion success of *D. villosus* in the Austrian Danube (Pöckl 2009), but are typical *r*-selected traits found in many IAC, i.e. long reproductive period and early sexual maturity (at three months, compared to four and five month in the indigenous *G. roeseli* and *Gammarus fossarum* (Koch), a short generation time and short duration of embryonic development with up to three generations and 14 cohorts being present at the same time, high growth rates resulting in large body size, high fecundity with large numbers of comparatively small eggs in the brood pouch (*D. villosus* females carry up to 350 eggs vs. the ca. 200 and 170 eggs carried by *G. fossarum* and *G. roeseli*, respectively) and optimal timing of neonate release.

Similarly, *P. clarkii* reaches maturity early at 10 g weight and is characterised by a quick individual growth rate (50 g in 3–5 months; Paglianti and Gherardi 2004) and relatively short life span (Lindqvist and Huner 1999). Its fecundity is relatively high: an average-sized female *P. clarkii* produces 400 pleopodal eggs, about four times those spawned by a similarly sized white-clawed crayfish *Austropotamobius pallipes* (Lereboullet) (Gherardi 2006). Relative high fecundity is a prerogative of other IAC: for example, a *P. pelagicus* female hatches up to one million eggs per spawning season (DAISIE 2009), whereas a similarly sized female of *Portunus gibbesii* (Stimpson), *Portunus spinicarpus* (Stimpson) and *Portunus spinimanus* Latreille hatches up to 200,000, 75,000 and 560,000 eggs, respectively (Reid and Corey 1991).

However, some typical K-selected traits might facilitate invasion success under certain conditions. Some IAC are long-lived, such as the red king crab *Paralithodes camtschaticus* (Tilesius) with a life span covering over 20 years (DAISIE 2009). Freshwater decapods lack planktonic larvae but brood the hatched juveniles under their abdomen until weaning.

Brooding time may be relatively long as in *P. clarkii* (Aquiloni and Gherardi 2008), which involves substantial expenditure of energy by mothers and costs in terms of losing time for growth and further reproduction, but enables offspring to thrive in harsh environmental conditions. Furthermore, substantial variation in life history among invasive alien populations or between native and invasive alien populations has been reported. *Eriocheir sinensis* requires 2–4 years to reach maturity in San Francisco Bay, 3–5 years in Elbe River (Germany) and 1–2 years in the native Yantze River (China) (Dittel and Epifanio 2009). The recorded size at maturity is most often around 38 mm carapace width, but it is smaller in San Francisco Bay (30 mm) and larger in the Odra Estuary (Poland) (45 mm) (Dittel and Epifanio 2009). Such variation may represent either an evolutionary response or an adaptive phenotypic plasticity but in any case it underlines the importance of life-history traits for invasion success.

Certain reproductive modes might also be advantageous for IAC. Organism which reproduce parthogenetically, such as the marble crayfish (Scholtz et al. 2003), or through self-fertilisation, such as *B. improvisus* (DAISIE 2009), are thought to have a colonisation advantage because a single individual can found a new population, Allee effects are reduced and population growth is faster compared to bisexually reproducing organisms. Of particular advantage for an invasive alien species might be a heterogonic reproductive cycle. This is typical of invasive alien Cladocera and in particular of Ponto-Caspian onychopods. Between late spring and early summer, onychopods hatch from resting eggs that survive the winter in bottom sediments. For the rest of the summer, they typically reproduce parthenogenetically and then switch to sexual reproduction in the fall to produce resting "winter" eggs (Rivier 1998). Such a combination of parthenogenetic and gamogenetic reproduction provides the colonisation advantage of asexuals with the adaptive potential of sexual reproduction. Storage of sperm packets in seminal receptacles is common in brachyuran crabs and might contribute to their invasion success. Similarly to unisexual reproduction, the possibility to store sperm also provides the opportunity for a single female to colonise a new habitat and reproduce successfully at low population densities. For example, sperm is stored in the spermatheca of females of *P. pelagicus* for a year or more (DAISIE 2009).

Processes facilitating establishment and spread

Environmental heterogeneity

Although many invaders have a broad environmental tolerance, the fitness and competitive ability of any species vary to a certain degree along an environmental gradient. Consequently certain combinations of environmental conditions will be less favourable for IAC than others and the establishment success of the invader and its impacts will vary across a spatially heterogeneous landscape. For example, a large spatial variation in invasion success of the spiny water flea *Bythotrephes longimanus* (Leydig) is likely due to the environmental variation among native habitats (Brown 2009). In freshwater habitats physico-chemical parameters are key determinants of species distribution and favour the spread of IAC. Kestrup and Ricciardi (2009) experimentally demonstrated that the competitive ability of the invasive alien amphipod *E. ischnus* decreases in relation to its native counterpart with decreasing water conductivity. There is also evidence that invasive alien amphipods in Europe have an advantage over natives only at sites with high, rather than low, water conductivity. In Grabowski et al.'s (2009) study, water conductivity is determined by anthropogenic pollution. It could thus be argued that euryhalinity in these invaders provides advantages in disturbed habitats only. Computer simulations on cladocerans have shown that the competitive advantage of an invader has to be large in order to displace native species (Dgebuadze and Feniova 2009).

Host-parasite interactions

Host-parasite interactions are regarded to be important determinants of alien species' proliferation. Indeed, the enemy release hypothesis (ERH) predicts that reduced pressure from specialist enemies in newly invaded habitats can provide a competitive advantage for the invader (reviewed in Colautti et al. 2004; Roy et al. 2011). However, evidence of ERH's role during Crustacea invasion is lacking (Roy et al. 2011). While increased growth rates of the green crab *C. maenas* were recorded in its invasive range in the absence of a castrating parasite (Torchin et al. 2001), other IAC, such as the amphipod *Crangonyx pseudogracilis* (Bousfield), show no sign of reduced parasite burden

(Slothouber Galbreath et al. 2010). In contrast, recent evidence suggests that parasites facilitate invasions by increasing the predatory impact of some IAC (Dunn 2009). Parasitized individuals of the invasive predatory amphipod *Gammarus pulex* (L.) showed an increased feeding rate, whereas the negative impact of the same parasite on fitness traits of the invader such as growth and reproduction appears to be low (Dick et al. 2010).

Evolutionary factors

Environmental conditions encountered in the invaded habitat often differ from those in the native range. IAC must therefore respond to changed selection pressure in order to maintain their fitness. Although, as discussed above, eurytolerance and high phenotypic plasticity are commonly regarded as typical traits of invasive alien species, it is widely acknowledged that evolutionary factors play a major role during their establishment process (Lee 2002). The considerable lag-phase often observed between initial introduction and further spread indicates that evolutionary processes maximise the fitness of a species during establishment (Sakai et al. 2001). For example, *E. sinensis* became established in the UK in 1973, but the population remained at a very low level until the early 1990s when it began to grow rapidly, especially in the Thames River estuary (Herborg et al. 2005). Furthermore, there is evidence for at least two separate introductions of *E. sinensis* into the UK in 1935 and 1949, both of which failed (Herborg et al. 2005), which denotes that these two populations were not able to adapt fast enough to the new environment. Similarly, long lag-phases characterise the invasions of both *Orconectes virilis* (Hagen) in the Netherlands (Souty-Grosset et al. 2006) and *H. anomala* in England (Holdich et al. 2006). Direct evidence of evolutionary responses during invasions is difficult to obtain, because quantitative genetic experiments are required to disentangle genetic and environmental effects on the observed phenotypic difference. One of the few examples is the evolution of salinity tolerance during several independent invasions of fresh waters by the calanoid copepod *Eurytemora affinis* (Poppe). Native source populations are unable to fully acclimate to freshwater conditions (Lee 1999), suggesting that tolerance for low salinities has evolved recently. Transplant experiments also showed that alien freshwater populations of *E. affinis* undergo a clear reduction in tolerance of high salinities compared to native populations (Lee et al. 2003).

A key issue, which has recently received much attention but remains poorly understood, is the role of genetic diversity in determining the outcome of introductions of alien species. Introductions of species are often based on the release of a low number of founding propagules containing only a fraction of the genetic variation of the source populations (Lee 2002). Such reduced genetic diversity theoretically limits a species' ability to establish and compete with native populations, which led researchers to invoke the existence of a "genetic paradox" (Lee 2002). Indeed, many IAC show reduced genetic diversity. For example, invasive alien populations of *E. sinensis* show significantly lower levels of variation at microsatellite loci than their native counterparts (Herborg et al. 2007c; Sui et al. 2009). Other examples of colonization bottlenecks include the predatory cladoceran *C. pengoi* (Cristescu et al. 2001), the amphipod *E. ischnus* (Cristescu et al. 2004) and the water flea *B. longimanus*. In the latter case, there is evidence that high levels of gene flow from native populations and between invasive alien populations have offset the effect of the colonisation bottleneck. The effects of such bottlenecks may be counteracted by admixture among genetically divergent source populations (Lawson Handley et al. 2011; Roman and Darling 2007). For example, multiple introductions have resulted in high genetic diversity of invasive alien populations of *G. tigrinus* in Europe (Kelly et al. 2006). Theoretically, admixture not only dilutes the founder effects but can also create novel genotypes which might facilitate the colonization of new habitats. Roman (2006) showed that the range expansion of *C. maenas* from the east coast of North America into Nova Scotia was associated with the introduction of a new distinct phylogenetic lineage and subsequent admixture. Nevertheless, it is currently unknown whether such admixture is merely a side-effect of the invasion process or a facilitator of the establishment process. It has also been proposed that evolutionary processes lead not only to adaption to specific new environments but also to the evolution of the invasive potential. This could occur through a number of mechanisms, such as selection for adaptive phenotypic plasticity (Ghalambor et al. 2007), maintenance of high genetic variation through balancing selection at ecologically important

loci and positive selection for traits which are associated with colonisation and establishment potentials. However, there is circumstantial evidence for the evolution of invasiveness. Some IAC populations have a higher potential to invade new habitats than their native counterparts. This so-called "bridgehead effect", documented for the global invasion of the harlequin ladybird (Lombaert et al. 2010), seems to occur in at least one IAC. Molecular data indicate that the Central European *E. sinensis* population was the source for the invasion of the River Tagus in Portugal and of the Laurentian Great Lakes and San Francisco Bay in North America (Hänfling et al. 2002; Tepolt et al. 2007). In the latter case, a direct colonisation from China might have been more parsimonious (Cohen and Carlton 1997). Genetic variation of invasive alien populations can also be increased through hybridisation with native species leading to introgression of locally adapted genes. Whilst hybridisation is common in other taxonomic groups, such as fish (Hänfling 2007) and plants (Ellstrand and Schierenbeck 2000), and possibly contributes to the invasion success, there are few cases demonstrating that IAC hybridise with their native counterparts. Particularly in several decapods, the complexity of mating behaviour and the specificity of sex pheromones might act as an efficient mechanism for prezygotic isolation, thus making hybridisation less likely. The only documented case is the hybridisation between the invasive alien *O. rusticus* and the native *Orconectes propinquus* (Girard) in Wisconsin (USA) (Perry et al. 2002). The majority of F1 hybrids (95%) were the result of *O. rusticus* females mating with *O. propinquus* males: only 1% of the total crayfish population was the product of F1 hybrids backcrossing to *O. propinquus*, whereas 13% represent backcrosses to *O. rusticus*. The F1 hybrids, therefore, appeared to mate disproportionately with pure *O. rusticus*. This led to much greater genetic introgression of nuclear DNA from *O. propinquus* to *O. rusticus* than in the reverse direction, which could have potentially facilitated rapid adaptation of *O. rusticus* to local environmental conditions.

Impacts

IAC often inflict severe negative impacts on native ecosystems either through direct interaction with the native community via altering trophic interactions, interference competition and disease transmission or indirectly through habitat modification (Snyder and Evans 2006). The results are changes in native species composition and some instances of extirpation of local native populations. For example, the amphipod *G. pulex* is replacing the endangered native *Gammarus duebeni celticus* Stock and Pinkster in both Ireland (Dick et al. 2002) and Brittany (Piscart et al. 2009). *Cercopagis pengoi* is causing changes in the zooplankton communities of both the Baltic Sea and Lake Ontario: in the Baltic, the species affects the population size of the previously abundant cladoceran *B. coregoni maritima* (Ojaveer et al. 2000), whereas in Lake Ontario it suppresses some native zooplankton species, including rotifers and juveniles of *B. longirostris* (Laxson et al. 2003).

Trophic interactions

The impacts of IAC on native communities are often reflected in the changes induced in the food web structure and trophic hierarchy, which in turn affect the flows of energy, matter and nutrients through the ecosystem. The trophic role of IAC is complex, since they are often omnivorous and can therefore feed on every trophic level of the invaded food web (van der Velde et al. 2009). Additionally, IAC often become prey of native species. They can have profound effects on populations of native prey, particularly when they are poorly adapted to avoid the new predator. In the Laurentian Great Lakes, invasion by *B. longimanus* has had a very strong impact on Cladocera and Copepoda, though predation and dampening of vertical migration, native species being vulnerable due to their vertical distribution in the water column, escape responses and morphology (Barbiero and Tuchman 2004; Pangle et al. 2007; Strecker et al. 2006). The effects on the food web structure may propagate through different levels but can be counterintuitive. The invasion of Dutch reservoirs by *H. anomala* dramatically affected grazing Ostracoda and Rotifera but did not result in cascading effects on algal density, because *H. anomala* also consumes algae (Ketelaars et al. 1999).

IAC sometimes provide native predators with a new and abundant food type. In France and Germany, invasive alien crayfish and, to a greater extent, amphipods now dominate the diet of riverine fish

such as perch (*Perca fluviatilis* L.), eel [*Anguilla anguilla* (L.)], pike (*Esox lucius* L.) and ruffe [*Gymnocephalus cernuus* (L.)] (Kelleher et al. 2000; Neveu 2001). Similarly, *P. clarkii* has become a food source for mammals and birds in Mediterranean wetlands (Geiger et al. 2005) and *C. maenas* has become one of the main prey of larger crabs in the North-eastern coast of the USA (Griffen et al. 2008). However, the wider implications of these trophic interactions cannot be predicted. For example, *C. maenas* is preyed upon by seagulls, but the large increase in *C. maenas* population size did not translate into an analogous increase in seagull populations (Grosholz et al. 2000). Similarly, though otters [*Lutra lutra* (L.)] feed heavily on *P. clarkii*, no increase in the density of otter populations has ever been observed (Beja 1996).

Intra-guild predation (IGP), here defined as predation events between potential competitors, is commonly observed between Crustacea and other species. Unbalanced mutual predation between pairs of species or between cohorts of the same species determines which species dominate the guild and best exploit resources (Polis et al. 1989). For example, mutual predation between the Japanese native crayfish *Cambaroides japonicus* De Haan and *P. leniusculus* is strongly asymmetric, having contributed to the displacement of *C. japonicus* (Nakata and Goshima 2006). In other cases, guild structure is far more complex. A well described example is the amphipod assemblage of the River Rhine where a number of alien and native species co-occurs. This assemblage has been increasingly dominated by *D. villosus* but also includes *C. curvispinum*, *E. ischnus*, *G. duebeni*, *G. pulex*, *G. roeseli*, *G. tigrinus*, etc. Mutual predation within this guild is common, but invariably favours the larger *D. villosus* (Dick 2008; Dick and Platvoet 2000; Kinzler et al. 2009). *Gammarus tigrinus* has impacted populations of *G. duebeni* in part through asymmetric IGP, but both are now impacted by *D. villosus* (Dick and Platvoet 2000). IGP is also believed to be the mechanism by which *D. villosus* has displaced *G. pulex* and the Mediterranean invader *Echinogammarus berilloni* (Catta). Furthermore, incidence of cannibalism is lower in *D. villosus* than in its Ponto-Caspian congeners *Dikerogammarus haemobaphes* (Eichwald) and *Dikerogammarus bispinosus* Martynov, which failed to become established (Kinzler and Maier 2003).

Co-existence between native and alien species within a guild occurs by niche partitioning, particularly when it is made possible by high habitat complexity. For example, in Dutch lakes, *D. villosus* is found on rocks in shallow waters and *C. curvispinum* in soft sediments in deeper waters, whereas *G. tigrinus* dominates in mats of zebra mussels (Noordhuis et al. 2009). In the River Rhine, *D. villosus* and *G. tigrinus* occupy the same benthic stony habitats, but *E. ischnus* occupies the water column, macrophyte beds and the shoreline. Thus, *D. villosus* and *E. ischnus* can co-occur, but *G. tigrinus* has been gradually displaced by *D. villosus* (Kley and Maier 2005; van Riel et al. 2009). On the West coast of North America, there is very little overlap in the distribution of *C. maenas*, which dominates the more saline, cooler lower estuary, and the larger red rock crab, *Cancer productus* J.W. Randall, which dominates the less saline, warmer upper estuary (Hunt and Yamad 2003).

The ontogeny of single IAC has a strong bearing on predator–prey relations, including IGP. For example, *D. villosus* preys on juveniles of the invasive alien crayfish *O. limosus*, but adult crayfish prey on *D. villosus*. *Dikerogammarus villosus* has more abundant populations than crayfish, so predation on juvenile crayfish will have big impact, whereas large crayfish are likely to have little impact on *D. villosus* populations (Bůrič et al. 2009). Diet may also change altogether with ontogeny: *P. clarkii* and *P. leniusculus* display a shift from predation to herbivory and detritivory (Correia 2003; Usio et al. 2009).

Competition

A second important impact that IAC inflict at the community level is competition with native species for food and shelter. A new species invading a community may occupy an ecological niche which overlaps with some native species, particularly those that are functionally and/or morphologically similar, i.e. belong to the same guild. The resulting competition is likely to have a negative impact on the abundance of native species, but the magnitude of impact is context-dependent. Laboratory studies showed that juveniles of *E. sinensis* in the River Thames can successfully exclude similarly-sized crabs of the native *C. maenas* from shelter (Gilbey et al. 2008). On the other hand, invasive alien *C. maenas* in the East coast of North

America is a superior competitor for food to juvenile *Callinectes sapidus* J.M. Rathbun, an ecologically and commercially important native species (MacDonald et al. 2007). When competing for food with *Hemigrapsus oregonensis* (Dana), native to the North American west coast, *C. maenas* was dominant, whereas it was subordinate to the alien *H. sanguineus* (Jensen et al. 2002). However, both species of *Hemigrapsus* consistently dominate in contests for shelter. Given the importance of intertidal cover for small crabs, such competitive interactions will likely affect patterns of habitat use by *C. maenas* on the east coast and may have important implications for the ultimate distribution and impact of this species in the north-eastern Pacific.

One of the most important interactions between alien and native species is the competition to avoid a shared predator, or 'apparent competition' (Holt and Lawton 1994). Indirect effects mediated by relative vulnerability to shared predators (whether morphological or behavioural) play a crucial role in shaping the trophic pathways in the invaded assemblage and are a determinant of successful invasions. For example, in the Gulf of Maine, the coexistence with the predator crab *C. maenas* makes the gastropod *Littorina littorea* (L.) able to outcompete the native *Littorina saxtalis* (Olivi), which is more susceptible to predation than the former species (Eastwood et al. 2007). In another system, the invasive alien porcellanid crab *Petrolisthes armatus* (Gibbes) is the preferred prey of the native mud crab, which relieves predation on native bivalve species (Hollebone and Hay 2008). In the River Rhine, *D. villosus* is preyed by fish and crayfish less often than native amphipods because it displays a lower activity level and a greater affinity for coarse stony substrata (Hesselschwerdt et al. 2009; Kinzler and Maier 2006). Similar lower vulnerability to fish observed in other invasive alien amphipods has contributed to the displacement of native species across western Europe and North America (Kaldonski et al. 2008; Pennuto and Keppler 2008).

Vectors of disease

IAC can facilitate the introduction and spread of new parasites or pathogens among invaded communities. The lack of co-evolution between alien pathogens and native hosts predicts that either hosts or parasites may have a fitness advantage. Although the introduction of novel parasites through alien Crustacea has been seldom detected, it can have devastating consequences when the virulence of the parasite is not matched by a co-adapted host immune defence. The most studied example is the crayfish plague in Europe (Snyder and Evans 2006). A genetically distinct strain of the oomycetes pathogen *Aphanomyces astaci* Schikora was introduced to Italian freshwater systems around 1860, possibly through ballast water of a ship coming from North America (Alderman et al. 1984). Further spread throughout Europe was facilitated by the subsequent introduction of alien North American crayfish (*O. limosus*, *P. leniusculus* and *P. clarkii*), which show a low susceptibility to the crayfish plague and can therefore act as a healthy carrier for the disease. European crayfish, such as *A. astacus* and *A. pallipes*, are in contrast highly susceptible to *A. astaci*, which led to the rapid decline or extirpation of native crayfish populations (Lilley et al. 1997). The impact of crayfish plague on European crayfish populations was reinforced by the repeated introduction of alien North American crayfish species following the decline of native crayfish stocks (Lodge et al. 2000).

Habitat modification

Invasive alien decapods may also alter the physical habitat of the recipient ecosystems. For example, the burrowing activities of some decapods can cause physical damage to irrigation structures and banks of rivers and lakes, which can lead to large scale environmental degradation. Burrows of *E. sinsenis* are often tightly packed and interconnected and have caused widespread damage to riverbanks and dikes in both Europe and North America (Dittel and Epifanio 2009). The resulting destruction has not only caused large economic costs but also ecological damage through increased sediment erosion. Some alien decapods can also modify the biotic habitat, because they consume aquatic macrophytes and their seedlings, thus reducing the area covered by plants. This impacts epiphytic algae and invertebrates by depriving them of attachment space and shelter (Nyström 1999). IAC also modify the dynamics of fine sediments, which has positive and negative indirect effects on other biota. For example, the filter-feeding *C. curvispinum* can swamp large areas of the stony

substrata in the River Rhine with mud (van Riel et al. 2006). Similarly, invasive alien crayfish species, due to their intense activity, disturb the benthos and resuspend fine sediments (Gherardi 2007). Increased water turbidity excludes other species of invertebrates in lentic habitats (Usio et al. 2009), whereas in lotic habitats, where suspended sediment is washed away, production by benthic algae may be higher due to the increased irradiance (Stenroth and Nyström 2003).

Ecosystem functioning and services

At the ecosystem level, IAC may remove, create or modify links between ecosystem components, often causing a shift in key functions of ecosystems, such as energy flux and nutrients cycle. In turn, these effects translate into changes in ecosystem services, i.e. biodiversity, fisheries yield and water quality. For example, the opossum shrimp *Mysis diluviana* (Audzijonyte and Väinölä) caused a dramatic impact at all trophic levels, including top carnivores. This species was intentionally introduced into Flathead Lake (North America) as a prey for kokanee salmon *Oncorhynchus nerka* (Walbaum in Artedi) (Spencer et al. 1991) but, contrary to any expectation, the species outcompeted the preferential prey of kokanee, the cladocerans *Daphnia longiremis* G.O. Sars and *Leptodora kindtii* (Focke). This was suggested not only to have induced a precipitous crash in the abundance of the kokanee population but also had the potential to impact predators of salmon, including some flagship species such as grizzly bear, *Ursus arctos horribilis* Ord. and bald eagle, *Haliaeetus leucocephalus* (L.).

Prevention and control

The cost of preventing invasions by alien Crustacea is trivial if compared to any measure taken after their establishment (Vander Zanden et al. 2010). IAC can be hard to detect and disperse rapidly, making any attempt of their eradication or control extremely difficult and expensive. In Scotland, for example, the cost of an ongoing eradication campaign against the crayfish *P. leniusculus* amounts to £250,000 every five months (S. Peay 2010, "personal communication"). In theory, intentional introductions are easier to prevent. In practice, however, the large economic

interest in IAC often hampers the implementation of preventative measures against their introduction or expansion. For example, no decision has been made yet in Norway on how to prevent *P. camtschaticus* from further migrating south- and westwards after that the species has become a valuable fishing resource (DAISIE 2009). Similarly, the Kuruma prawn, *Marsupenaeus japonicus* (Bate) and the blue swimming crab, *P. pelagicus* (L.), that both entered the Mediterranean through the Suez Canal, have become highly prized species for the Levantine fisheries, which makes their expansion even desirable (DAISIE 2009).

Legislation against the introduction of IAC is in force in some countries. For example, in the UK the crayfish *A. astacus*, *Astacus leptodactylus* Eschscholtz, and *P. leniusculus* have been designated as pests under the Wildlife and Countryside Act making it largely illegal to keep exotic crayfish. Similarly, in Japan all species of *Astacus* and *Cherax, O. rusticus* and *P. leniusculus* have been classified as IAS under the Invasive Alien Species Act: their importation and husbandry are banned except for scientific purposes. On the contrary, only *Eriocheir* spp. (and their viable eggs) among Crustacea have been included in the USA list of Injurious Wildlife Species. Contrary to the USA, the European Union adopts a "white" list approach: according to the recent Council Regulation No 708/07 "concerning use of alien and locally absent species in aquaculture" (European Parliament 2007, 2008a), species, with some exceptions (i.e. the species listed in Annex IV), can be imported for aquaculture purposes only after having been appropriately screened thorough a risk assessment analysis. The current Annex IV (European Parliament 2008b) does not include any crustacean species except the giant river prawn *Macrobrachium rosenbergii* (De Man) for French overseas departments.

The need to prevent the harmful effects of introduced species without unduly impeding trade has produced among scientists a large interest in developing science-based criteria for risk assessment. Most attention has been directed to organism-based protocols: each taxon has its own set of characteristics that defines and limits options for risk assessment. These include the size, reproductive biology and life cycle of an organism, as well as its detectability, association with specific transport vectors, usefulness to humans, and potential to cause negative impacts. Currently,

screening procedures with good accuracy rates (even >80%) are available for diverse taxa. For example, toolkits for the identification of the invasiveness of marine and freshwater invertebrates have been produced by the UK Centre for Environment, Fisheries and Aquaculture Science (CEFAS). The Freshwater Invertebrate Invasiveness Scoring Kit (FI-ISK) has been recently adapted by Tricarico et al. (2010) as a screening tool for identifying potentially invasive alien crayfish: using receiver operating characteristic (ROC) curves, FI-ISK was shown to distinguish accurately (and with statistical confidence) between potentially invasive and non-invasive alien species of crayfish.

Accidental introductions of Crustacea are more difficult to control through legislation but might be slowed down by international/regional regulations which target potential dispersal vectors in combination with developing technology. In 2004, 30 countries ratified the International Convention for the Control and Management of Ships' Ballast Water and Sediments (http://www.imo.org) in an attempt to reduce the translocation of aquatic species through shipping transport. Since 1993, the oceanic ballast water exchange (BWE) has become mandatory for all vessels entering the Laurentian Great Lakes with ballast on board. Although the efficacy of BWE had been questioned since the rate of species introductions did not show any decrease after 1993, Ellis and MacIsaac (2009) have recently proven that the treatment in itself is effective. The authors showed that short exposure to highly saline water dramatically reduced survival of all eight species investigated. Thus, limitations to the practice of BWE are due to different reasons than the salinity tolerance of potential invaders: first, a vessel does not have to conduct an oceanic exchange if this is deemed to be unsafe; second, BWE typically does not result in a complete replacement of all ballast water and sludge; and, third, the regulations do not apply to vessels entering the lakes with no ballast on board, which typically carry tons of sludge, home to many alien organisms. A number of technological alternatives to BWE currently exist, such as heating and filtration, but the cost-efficiency of each of them varies widely across vessels (Rigby and Taylor 2001) as does the efficacy of these methods against some organisms, including crustacean species. An example is the Ponto-Caspian amphipod *C. curvispinum*, a species

which warrants concern as a potential future invader of the Laurentian Great Lakes (Ricciardi and MacIsaac 2000). Currently, *C. curvispinum* is widely distributed in Europe and occurs at high densities at Baltic Sea ports from where it can "jump" to the Laurentian Great Lakes. If heating techniques are used to kill these organisms once entered the ships' ballast, a temperature of 40.8 °C is required for a 90% efficacy which is difficult to achieve in cold waters (Horan and Lupi 2005). Filtration has also shown limited efficacy in eradicating *C. curvispinum* from ballast water (Horan and Lupi 2005). Technology, including electric barriers in freshwater systems, air-bubble curtains or environmental barriers such as salinity locks, might in principle reduce the movement of biota through canals. However, these methods may also impede the movement of native species and cannot work with species adhering to hull surfaces. There are only anecdotal reports about their potential efficacy against IAC, as in the case of electrical screens installed on the rivers' bottom in Germany in the 1930s to 1940s to prevent migration by *E. sinensis* (Gollasch 2006).

A number of approaches to managing the risks of introductions associated with human activities such as aquarium trade and commerce of live specimens have been proposed but never applied. These include controlling the conditions and location of sale for potentially harmful species, the use of tariffs to internalize invasion costs to the industries that benefit from trade in alien species, and the substitution of alien species by native species in aquaculture and pet industry (Ewel et al. 1999).

In the past, most effort has been focused on preventing introductions of alien species. Given however that even with the best effort prevention of new introductions will sometimes fail, efforts should also be directed to preventing establishment and spread. To this end, early detection programs using knowledge of local people should be used, and immediate reporting to local biosafety authorities could alert managers to the establishment of a new IAC species (Gherardi 2011b). For example, in the UK public engagement in monitoring invasive species is promoted through the GB-Non-Native Species secretariat website (https://secure.fera.defra.gov.uk/nonnativespecies/home/index.cfm). For small aquatic crustaceans, such as amphipods, detection can be optimized using risk-based sampling designs combined with high-sampling intensity in areas

deemed most vulnerable to invasions, rather than less intensive sampling at more sites. More user-friendly identification guides are important tools (Souty-Grosset et al. 2006) and new high-tech diagnostic tools need to be developed for detecting crustacean larvae and small organisms, such as DNA barcoding.

If a newly introduced species has been detected, early successful eradication programs or the prevention of further spread might be possible. Much effort should be paid in predicting the intensity and direction of spread of Crustacea and thus the areas that are more at risk of invasion (Kolar and Lodge 2002; MacIsaac et al. 2004). The progress made toward developing risk maps is the result of advances in remote sensing, modelling methods, and computing. For example, Herborg et al. (2007a) developed environmental niche models using genetic algorithm for rule set prediction (GARP) to forecast the potential distribution of *E. sinensis* in North America. These models predict the lower Laurentian Great Lakes, most of the eastern seaboard, the Gulf of Mexico and southern extent of the Mississippi River watershed and the Pacific northwest as suitable environments for mitten crabs. Similar models were used to predict the potential European distribution of mitten crabs based on the distribution of the species in its native Asia (Herborg et al. 2007b). The result is that the Mediterranean coast of Europe is highly vulnerable to future invasion by *E. sinensis* and thus requires strong legislative and educational efforts to limit that risk.

Early detection should be followed by a rapid response, i.e. a quick and well coordinated eradication program. Eradication consists in eliminating the entire invading population from a defined area by a time-limited campaign. Eradication needs to be achieved by a fixed date, because an eradication campaign without a specified end point is *de facto* continuing control, i.e. harvesting or killing a fraction of a population on a sustained basis (Bomford and O'Brien 1995). However, successful eradication attempts of IAC are to date rare. For the majority of the already established populations, the only feasible option is to adopt a control policy using some mitigation tools that might maintain their density at a very low level and thus reduce their negative impacts. Mechanical control of fouling invasive alien organisms such as *B. improvisus* can be effective by applying high temperatures (over

36°C for more than 30 h in *B. improvisus*) and oxygen deficiency to ship hulls, as well as by the use of antifouling paints and chlorine treatment of water intake pipelines during the most intensive settling period (DAISIE 2009). Removal of mobile IAC following the "catch as many as you can" strategy has had some effect on populations only when conducted for an extended period of time, which means considerable cost and manpower. The control of North American crayfish species in Europe has been often attempted by the use of traps of various design and with different baits or electro-fishing in fresh waters, but the success was limited (Gherardi et al. 2011; Holdich et al. 1999). The use of sex pheromones as bait might be effective (Stebbing et al. 2004; Aquiloni and Gherardi 2010), although any attempt to identify the molecular structure of sex pheromones in crustacean species has had little or no success.

The preferred habitat might also be used to catch and remove IAC. The Australasian isopod *Sphaeroma quoyanum* H. Milne Edwards, invasive in North America, has a clear preference for decayed wood. A potential control method could thus involve out-planting the preferred substrate and removing it once it has been colonised (Davidson et al. 2008).

Harvesting edible crustaceans for consumption and sale can be a productive alternative strategy under the philosophy of "making the best of a bad situation" (Gherardi et al. 2011). Where *P. leniusculus* are present within the restricted region in the U.K., angling clubs can apply to remove them for purposes of fisheries management and can reduce the cost of doing this by allowing commercial trappers to take the crayfish for sale (Peay 2009). Similarly, Clark et al. (2009) suggest commercial harvesting of the *E. sinensis* in the River Thames Estuary and export to China where the species is considered a culinary delicacy. However, the assignment of a commercial value to invasive alien species almost inevitably results in further, often intentional introductions of the species (Edsman 2004). Additionally, some IAC, such as *P. clarkii*, are known to damage the health of their consumers, including humans, because of their capacity to accumulate heavy metals and toxins in tissues and organs (Gherardi 2007; Gherardi et al. 2011). Drainage of ponds, diversion of rivers, and construction of barriers (either physical or electrical) may be also used in the case of confined crustacean

populations, but very little is known about the efficacy of these methods. The erection of a barrier in the River Buåa at the border between Sweden and Norway was unsuccessful in preventing migration of *P. leniusculus* to the Norwegian part of the river (Johnsen et al. 2008).

Biocides, such as organophosphates, organochlorines, pyrethroids, rotenone and surfactants, are potentially highly efficient for species eradications but often lack specificity so that native invertebrates may be eliminated along with the target crustacean species. Furthermore, bioaccumulation and biomagnification in the food chain are likely. Natural biocides such as derivatives of pyrethrum have relatively few side-effects on non-target species. The biocide Pyblast was chosen for the attempted eradication of *P. leniusculus* in the North Esk catchment in Aberdeenshire, Scotland (Peay et al. 2006). No crayfish were found in the following summer but some individuals were caught at the pre-treated site. Thus, monitoring is necessary before declaring the complete success of the treatment.

Other solutions lay in autocidal control methods consisting of interfering with the reproduction of IAC populations in order to reduce their breeding success (Gherardi et al. 2011). The potential use of the sterile male release technique (SMRT) for the management of invasive alien crayfish has been recently tested in the laboratory (Aquiloni et al. 2009) and in the field (L. Aquiloni et al., unpublished data), leading to promising results: the high meiotic rate in male gonads makes them particularly radiosensitive, so irradiation can kill cells or inhibit their growth, eventually causing the partial or total sterility of the treated subjects (Aquiloni et al. 2009).

Traditional biological control methods include the use of predators, disease-causing organisms (e.g. in the case of invasive alien crayfish, engineered strains of *A. astaci*, the etiological agent of the crayfish plague; see above), and use of microbes that produce toxins, such as strains of the bacterium *Bacillus thuringiensis* Berliner. The introduction of predaceous fish species has provided some positive results in the control of populations of *P. clarkii* in Italy (Aquiloni et al. 2010). Eels, burbot, perch and pike are well known predators of crayfish though they are usually gape-size limited, preying only on small individuals. However, in some instances the presence of fish predators has a negative, but sublethal, effect

because it induces a change in the behaviour of crayfish by reducing their feeding activity and increasing the time spent in shelter (Aquiloni et al. 2010). A potential control agent of *C. maenas* is the parasitic barnacle *Sacculina carcini* Thompson. This species, however, can settle on, infect, and kill a number of native crab species (Goddard et al. 2005) and thus the application of this method necessitates a thorough cost-benefit analysis.

Despite the mixed results of each single control method listed above, there is an increasing consensus that it is the strategic combination of different methods that can lead to some success against IAC. For example, in Sparkling Lake (Wisconsin, USA) *O. rusticus* was mechanically removed from 2001 to 2005 and the harvest of fish species known to prey on crayfish was restricted. As a result, crayfish catch rates declined by 95%, from 11 crayfish per trap per day in 2002 to 0.5% crayfish in 2005, and the native community showed a slow but steady recovery (Hein et al. 2007).

Last but not least, an essential prerequisite of any attempt to prevent the introduction of IAC and to mitigate their damage is the thorough understanding of their threats by the general public, decision-makers and the other stakeholders (Gherardi 2011b). Educating the public and the relevant stakeholders on their negative impacts and on the importance of early detection and rapid response would help build a solid support for the management of IAC (Vander Zanden et al. 2010).

Concluding remarks

The recurring role of Crustacea in aquatic invasions suggests that much future research should focus on this taxon. There appears to be a good understanding regarding the main dispersal vectors of IAC, but more effort should be taken to translate this knowledge into efficient strategies to reduce pathways for their dispersal. Most research effort has been previously directed towards identifying traits that can be used to assess the invasive potential of an alien crustacean species. However, the role of environmental factors and the possible effects of climate change on moulding future scenarios are still poorly understood, whereas a deeper knowledge of these issues will help find appropriate measures to prevent new

introductions of IAC and mitigate the damage inflicted by the already introduced species. Advances in food web ecology and community stability will allow a greater understanding of the wider impacts of species invasions, for example on ecosystem services. Finally, future research is also expected to clarify the complex links existing between species traits and environmental heterogeneity from an evolutionary perspective (Facon et al. 2006).

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