Understanding the impact of invasive crayfish

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INTRODUCTION

In a rather provocative article, Parker *et al.* (1999) claimed that, up to then, little scientific attention had been placed on developing either theoretical or operational generalizations about the impact of invasive species. Specifically, the authors lamented the lack of a general framework in which to discuss ''what impact is, or how we decide that the non-indigenous species exceeds that of another, or how we decide that the impact of a particular species is greater in one place than in another'' (Parker *et al.* 1999, p. 4). Today, this scenario seems to have changed for several freshwater non-indigenous species (NIS), e.g. the zebra mussel *Dreissena polymorpha* (Pallas) (e.g. Karatayev *et al.* 2002, Ricciardi 2003), but it has remained practically unaltered for other widely diffused bioinvaders that have, however, attracted much scientific attention in these latest years, such as freshwater crayfish.

Crayfish are the largest and amongst the longest lived invertebrate organisms in temperate freshwater environments, and often exist at high densities. Most species are keystone consumers (Nyström *et al.* 1996), feeding on benthic invertebrates, detritus, macrophytes, and algae in lotic and lentic waters (e.g. Whitledge and Rabeni 1997). They also constitute the main prey of several species, including otter (Slater and Rayner 1993), fish (e.g. Blake 1995), and birds (Rodríguez *et al.* 2005). Because of their capability to integrate into the food web at many levels and to persist on the substantial energy reserves of the detrital pool, crayfish are good candidates for invading aquatic systems (Moyle and Light 1996).

Crayfish native biodiversity is large but unequally distributed throughout the continents. Over 600 species have been described worldwide (Crandall 2002), the majority occurring in North and Central America (75% of the world's total). About 100 indigenous species live in the southern hemisphere, five in Europe, four in Asia, and none in continental Africa and in Antarctica (Hobbs 1988, Fitzpatrick 1995, Taylor *et al.* 1996, Taylor 2002). We know today that much of their present distribution is due to human intervention, even for the most celebrated ''indigenous'' species. For instance, as reported by Linnaeus (1746, p. 358) and confirmed by Pontoppidan (1775, p. 175), the noble crayfish *Astacus astacus* (Linnaeus) seems to have been imported into Sweden from Russia by John III (King of Sweden since 1568) and later into Finland (Westman 1973). Similarly, the white-clawed crayfish *Austropotamobius pallipes* (Lereboullet) might have been introduced into Ireland by monastic orders from France in the 12th century, as suggested by Reynolds (1997). Genetic evidence for this hypothesis has recently been obtained by Gouin *et al.* (2003).

In the last few decades, as a result of the exponential growth in the volume and complexity of the international trade, the world distribution of crayfish has dramatically changed (e.g. Pérez *et al.* 1997) mostly due to transcontinental or interstate translocations of a still relatively small proportion of crayfish species (hereafter referred to as NICS, i.e. non-indigenous crayfish species) – 20 according to Hobbs *et al.* (1989), but increasing all the time. Human-mediated translocations have been often accidental (in ballast, via canals, by escapes from holding facilities) but the introduction of some crayfish species was deliberate (for aquaculture and stocking, for food, as aquarium pets, as live bait, and for snail and weed control; see Lodge *et al.* 2000, Chapter 2). In Africa, the introduction of North American and Australian species from the 1970s onwards (Arrignon *et al.* 1990) was aimed to broaden the range of commercial fisheries in lakes and dams (Mikkola 1996) and to control freshwater snails that carry human schistosomiasis (Hofkin *et al.* 1991, Chapter 4). Indeed, most crayfish introductions were motivated by our desire to eat them (Holdich 1999a) that in its turn generates economic interests. Some species are in fact highly valued as food, and in countries like Scandinavia and Louisiana feasting on them has become a cultural icon. As a consequence, for instance in Europe, wild stocks are managed, leading to annual catches of more than 4,000 tons, and some species are cultivated with a total production of about 150 tons (Ackefors 1999).

Hence, crayfish introductions have certainly provided economic benefits to several countries, because of (1) restoring the productivity of indigenous stocks (e.g. in Sweden), (2) compensating for their lack (e.g. in Spain), or (3) developing extensive or semiintensive cultivation systems (e.g. in the People's Republic of China) (Ackefors 1999). However, once introduced for stocking and aquaculture and kept in outdoor ponds, crayfish of several species almost inevitably escape (Hobbs *et al.* 1989) and a proportion of them is able to establish self-sustaining populations in the colonized habitats. The invasion

process may continue: while some populations remain localized around the point of introduction, others spread widely, becoming invasive (Kolar and Lodge 2001). Compared to other aquatic species, the spread of this taxon is favored by the ability of some species to stay for relatively long periods out of water and to travel long distances, sometimes overland [e.g. *Procambarus clarkii* (Girard), Gherardi and Barbaresi 2000]. Contradicting the predictions made by the tens rule (Williamson 1996), the majority of the naturalized populations has the potential to become noxious. For instance, of the eight NICS imported into Britain since 1970 five have been found in the wild and four of these have become established, three being now officially classified as pests (Holdich 1999b). Today, the list of species that are causing concern in the introduced areas includes *Pacifastacus leniusculus* (Dana) in California (USA), Europe, and Japan, *Orconectes limosus* (Rafinesque) in Europe, *Orconectes rusticus* (Girard) in North America, *P. clarkii* in Africa, California, Europe, and Japan, *Astacus leptodactylus* Eschscholtz in some European countries, and *Cherax destructor* Clark in Africa and Australia (Holdich 1999a). Other species, like *Cherax quadricarinatus* (von Martens) in Ecuador, are expected to lead problems in the near future (Romero 1997).

Concerns relate to the modifications that NICS may induce in the structure of freshwater food webs (e.g. Lodge *et al.* 1998) and the economic damage they may inflict through, for instance, reduced recruitment of commercially valuable fish stocks (Nyström 1999). In the short term, they may decrease the biomass and species richness of macroinvertebrates, macrophytes, and periphyton (e.g. Lodge and Lorman 1987) and, in the long term, they may contribute to the decline of several invertebrate taxa, including indigenous crayfish species, amphibians, and fish (e.g. Guan and Wiles 1997, Chapter 29). Once added to a system, NICS have the potential to impose ''considerable environmental stress'' and, in most instances, they may induce ''irreparable shifts in species diversity'' (Hobbs *et al.* 1989, p. 309).

In this chapter, the literature focusing on the multiform ''environmental stress'' that NICS have been found to pose to the colonized areas around the world will be reviewed, as well as the ''shifts in species diversity'' that they have caused. In addition, information about their effects upon human economy and health will be discussed. By identifying several gaps in the existing literature, I will suggest the directions that research should take to extend and strengthen the current knowledge of the impact of NICS and to help prioritize interventions in freshwater systems.

THE LITERATURE ON THE IMPACT OF NICS

Since the 1980s, the effects exerted by NICS on the environment, indigenous species, national economies, and human health have been abundantly publicized (e.g. Holdich 1988, 1999a, Hobbs *et al.* 1989, Gherardi and Holdich
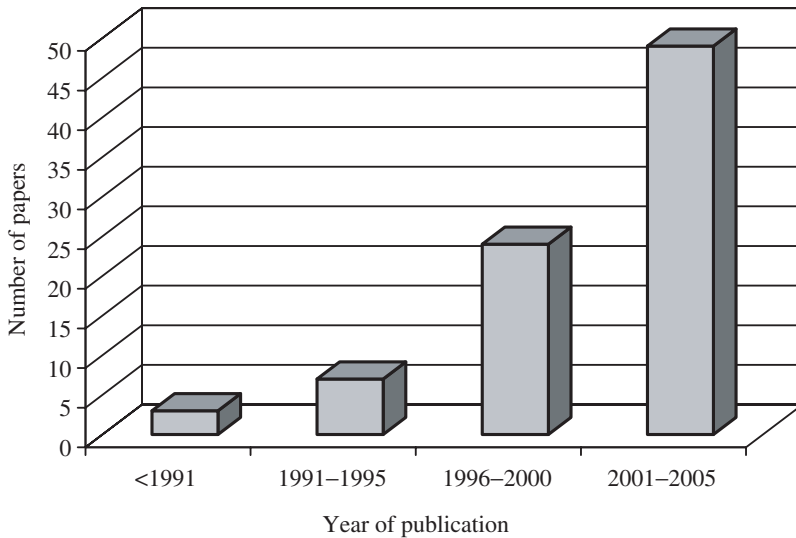
Fig. 1 The rise in the number of publications that described the impact of non-indigenous crayfish species (NICS). Papers (reaching a total of 103) were identified via keywords from Biosis (1967–February 2006), ASFA (1960–March 2006), and Zoological Record (1978–March 2006). Only papers reporting quantitative data published before 2006 (83) are included here.

1999, Lodge *et al.* 2000). The International Association of Astacology largely contributed in heightening awareness about the negative impact of NICS by adopting a resolution in 1987 (VII Symposium Lausanne, Switzerland), in which governments were recommended to ''find the means to stop the importation of living crayfish into their countries for any purpose…except for governmentally approved research, restockings or introductions''. This resolution was subsequently renewed (in: 1997, Florence, Italy; 1998, Amsterdam, Holland and Augsburg, Germany, and 2002, Querétaro, Mexico).

The consequent surge of interest in NICS encouraged more proactive research and led, since 1987, to a sharp increase, mostly in Europe, in the number of publications, that included 18 reviews (e.g. Holdich 1999a, Lodge *et al.* 2000, Nyström 2002, Westman 2002, Geiger *et al.* 2005), focused on describing the impact of some NICS (Fig. 1), particularly *P. clarkii* and *P. leniusculus* (Fig. 2). The studies that have attempted to quantify impacts have often done so using an experimental approach (reviewed in Chapter 30). However, short-term researches largely prevailed: only 12% of the 85 quantitative studies here analyzed monitored the effects of NICS on a system for more than 1 year. Some of these studies adopted classical *in situ* enclosure/exclosure experiments to analyze the effects of NICS on the abundance of several components of the
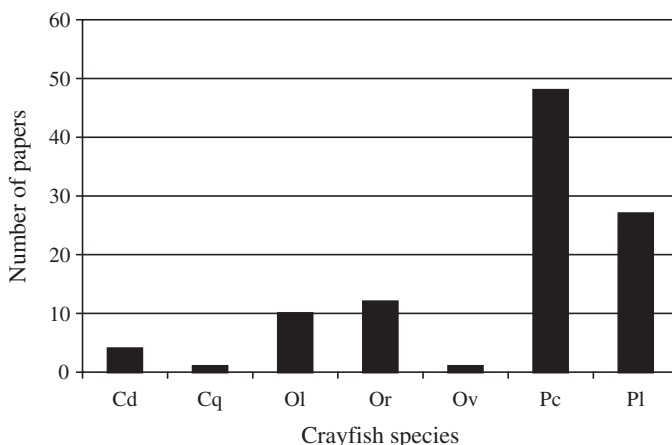
Fig. 2   The number of publications describing the impact of NICS (103, see Fig. 1) distributed among crayfish species. Cd = *Cherax destructor*; Cq = *C. quadricarinatus*; Ol = *Orconectes limosus*; Or = *O. rusticus*; Ov = *O. virilis*; Pc = *Procambarus clarkii*; Pl = *Pacifastacus leniusculus*.

resident community. Lodge *et al.* (1994) pioneered this experimental approach by revealing the control of *O. rusticus* on the trophic interactions existing in the littoral zone of some North American lakes.

   Several other studies applied a correlative approach by comparing NICS and indigenous crayfish species for growth rate, densities, vulnerability to predators, predatory ability, and behavioral dominance over food and shelter. On the one hand, the impact exerted on macrophytes and benthic invertebrate abundance has been elegantly compared between invasive and indigenous species through a combination of field and laboratory experiments (e.g. Olsen *et al.* 1991). On the other, to test the ability of several NICS to outcompete indigenous crayfish, experiments were mostly run in the laboratory (e.g. Söderbäck 1991, Holdich *et al.* 1995, Vorburger and Ribi 1999, Gherardi and Cioni 2004).

   Ideally, much knowledge of the effects of NICS on the community should derive from the comparison (1) of one site before and after their invasion and/or (2) of different sites, with and without an invader present, at the same time. Unfortunately, only a small minority of studies (e.g. Rodríguez *et al.* 2005, McCarthy *et al.* 2006) adopted this comparative approach, in large part because the interest in an invasive species most often arises after it has spread extensively and only when it has already had an impact. An obvious drawback of these studies is that results may be confounded by temporal or spatial trends in the environment such as pollution, harvesting, or climate change; they should therefore be accompanied by a thorough documentation of other contemporary modifications in the habitat.

Finally, there is a surprising lack in the literature on NICS of any quantitative estimate of the relative impact of a species between its native and invaded habitats. Indeed, this comparison would be critical to assess the varying success of an invasive species. Evolutionary history in fact plays a major role in this process and invasive species may display greater impacts in systems without co-evolved predators, parasites, and prey (see e.g. the ''enemy release'' hypothesis, Torchin *et al.* 2003). This is well illustrated by the impact of the North American *P. leniusculus* in the UK (Holdich *et al.* 2004).

THE FIVE LEVELS OF ECOLOGICAL IMPACTS

According to Parker *et al.* (1999), the impact of an invader can be measured at five levels of biological complexity: (1) effects on individuals (life history, morphology, behavior); (2) population dynamic effects (abundance, population growth, etc.); (3) genetic effects (including hybridization); (4) community effects (species richness, diversity, trophic structure); and (5) effects on ecosystem processes (nutrient availability, primary productivity, etc). An overview of the literature on NICS clearly shows that some of these effects are documented much more than others (Fig. 3). The most understudied impacts were genetic changes that, on the contrary, should require much more attention by invasion biologists. They may in fact give rise to new invasive forms, induce decline of the
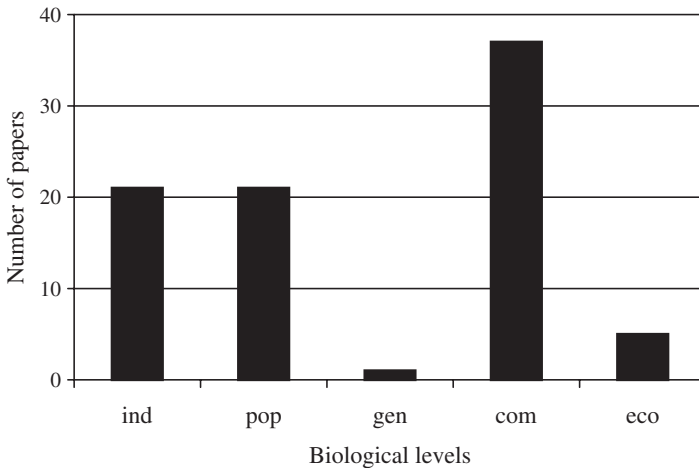

Fig. 3 The number of studies (85) reporting quantitative data on the impact of NICS at five different biological levels: individual (ind), population (pop), genetic (gen), community (com), and ecosystem function (eco). Single studies that reported impacts at more than one level were classified on the basis of the most prominent one.

indigenous species through e.g. introgressive hybridization, and eventually lead to long-term evolutionary shifts (Cox 2004).

The best examples of studies, classified at the biological level, which have quantified the impact of NICS, are reviewed below.

Effects on individuals and populations

The development of predator-prey or competitive interactions is expected to induce changes in the life history, morphology, and behavior of the interacting species. These changes are obviously adaptive as they should reduce the risks for the "weaker" species to be preyed upon or to be outcompeted by the "stronger" species (e.g. Lima 1998). When, on the contrary, no adaptation appears or the changes undergone do not suffice to develop a balance between the prey and the new predator or between competitors, the abundance, population dynamics, or distribution of the "weaker" species – usually the indigenous species – may be strongly affected. The most extreme effect at the population level is extinction, at the local or even at the global level.

Several studies have focused on an NICS acting as a predator upon a naïve species, either invertebrate or vertebrate. Most often they showed lethal or sublethal effects. For instance, *P. leniusculus* easily consumes *Lymnaea* snails and induces tail-cuts to *Rana temporaria* (Linnaeus) tadpoles (Nyström *et al.* 2001); *P. clarkii* (1) is able to prey upon the embryos and free swimming larvae of up to 13 amphibian species (Cruz and Rebelo 2005); (2) takes a significantly shorter time than the indigenous *A. pallipes* to capture *Triturus vulgaris* (Linnaeus) larvae and *Rana esculenta* Linnaeus tadpoles (Renai and Gherardi 2004); or (3) is not deterred by toxins contained in Californian newt [*Taricha torosa* (Rathke)] eggs (Gamradt and Kats 1996).

Obviously, lethal or sublethal effects exerted by NICS are mostly due to the relatively short coevolutionary history between them and the naïve prey that does not allow the latter to develop efficient antipredator behaviors, morphological structures, or chemical repellents. The absence of these mechanisms has been evoked to explain, for instance, the sharp decline of the California newt recorded in three streams in the Santa Monica Mountains of southern California after about 10 years from the introduction of *P. clarkii* (Gamradt and Kats 1996).

However, historical coexistence in the area of origin seems not to be the only prerequisite for the exhibition of efficient antipredator behaviors: notwithstanding their common history in the area of origin, naturalized mosquitofish [*Gambusia holbrooki* (Girard)], once exposed to visual and chemical stimuli of *P. clarkii* in a confined environment in Portugal, did not decrease their activity and did not avoid spaces with high predation risks (Leite *et al.* 2005). Mosquitofish were therefore subject to a strong predation pressure by the NICS as confirmed from the frequent occurrence of their remains in crayfish gut content (Gutiérrez-Yurrita *et al.* 1998, Correia 2003).

Often, prior experience with a predator species is not required by the prey to exhibit avoidance behaviors. These are on the contrary stimulated by chemical cues released by injured conspecifics (alarm odors). For instance, when exposed to alarm odors, the snail *Physa gyrina* (Say) significantly increases its use of spatial refugia by moving to the waterline, floating at the surface, or crawling out of the water (McCarthy and Dickey 2002). These behaviors were independent of the predator's identity and therefore were exhibited in the presence of both the known *Orconectes juvenilis* (Hagen) and the unknown *P. clarkii*.

In only one case was it found that the prey, although naïve, had quickly acquired the ability to recognize an NICS as a predator. An ecological study, conducted in Pennsylvania (USA), revealed that the snail *P. gyrina* moved under cover in the presence of pumpkinseed sunfish but moved to the water surface in the presence of *O. rusticus*; the combined effects of fish and crayfish were intermediate to their individual effects (Turner *et al*. 2000). On the one hand, these results can explain why periphyton standing crop in covered habitats was the lowest in the fish treatment when covered habitat use by snails was the highest, and the highest in the control and in the crayfish treatment when covered habitat use by snails was the lowest. On the other hand, they showed that the prey has learned some stimuli emitted by the NICS (possibly its odor) and behaves accordingly to avoid it. This is not the typical response shown by the snail to a generalized predator. On the contrary, the snail seems to be able to distinguish the specific identity of *O. rusticus* with respect to fish predators. Other behavioral responses to predatory NICS by potential prey, leading, for instance, to changes in their microhabitat selection, diurnal activity or foraging patterns, have never been studied.

As regards to competitive interactions, few studies have analyzed the effects induced on non-crayfish species by resource competition with NICS. In the laboratory setting, Carpenter (2005) conducted density manipulation experiments to analyze the competition between *O. virilis*, established in the Colorado River basin, and two endemic fish species, the Gila chub, *Gila intermedia* (Girard), and the flannelmouth sucker, *Catostomus latipinnis* (Baird and Girard). The results showed that growth of flannelmouth suckers, but not of Gila chub, was affected by crayfish more than by intraspecific competition, leading to the conclusion that each case of competitive interaction should be taken as a separate case. At a population level, the ability of crayfish to outcompete some fish species, for instance by expelling individuals from their shelters and therefore by making them more vulnerable to piscivorous fish, may have detrimental effects. In six riffles of the River Great Ouse (England), the numbers of *P. leniusculus* and of the two dominant benthic fish, bullhead [*Cottus gobio* (Linnaeus)] and stone loach [*Noemacheilus barbatulus* (Linnaeus)], were inversely correlated (Guan and Wiles 1997; other examples in Chapter 29).

The most commonly documented impact of NICS on competitive interactions is the agonistic dominance they show over indigenous crayfish species (Chapter 31), with the only known exception of *Astacopsis franklinii* (Gray), endemic to

Tasmania, which dominated equally sized specimens of the non-indigenous *C. destructor* (Elvey *et al.* 1996). When exposed in the laboratory to an NICS, indigenous crayfish changed their posture and behavior, quickly assuming the role of subordinates [e.g. *Procambarus acutus acutus* (Girard) *vs. P. clarkii*, Gherardi and Daniels 2004]. When, however, stable dominance hierarchies between NICS and indigenous crayfish species cannot be formed, as observed in the dyad *P. clarkii* and *A. pallipes* (Gherardi and Cioni 2004), the repetition of escalated fights may lead to injuries usually suffered by the weaker indigenous crayfish followed by its likely death. Indeed, NICS, e.g. *P. leniusculus*, may prey upon the indigenous *A. pallipes* and *A. leptodactylus*, and predation may have contributed to the gradual decline of *A. pallipes*, at least in England (Holdich and Domaniewski 1995).

Dominance hierarchies usually translate into a differential capability to compete for resources, such as shelters. It is known that shelters act as a ''principal resource bottleneck'' in crayfish populations (Hobbs 1991) serving to minimize predation risks and in some species to attract mates (Gherardi 2002). They are usually limited so that an inferior ability to compete for them may lead to a higher susceptibility to predation in subordinate species, being therefore the cause of their increased mortality (Gherardi and Cioni 2004). When tested in the laboratory, dominant NICS were most often found to competitively exclude subordinate indigenous crayfish from the offered shelter [in: *O. rusticus vs.* other *Orconectes* species, Hill and Lodge 1999; *P. leniusculus vs. A. astacus*, Söderbäck 1991; and *P. leniusculus vs. Cambaroides japonicus* (De Haan), Usio *et al.* 2001, Nakata and Goshima 2003] also when NICS showed a low preference for the shelter in a noncompetitive context [*P. clarkii vs. A. pallipes*, Gherardi and Cioni 2004, and *vs. P. acutus acutus*, Gherardi and Daniels 2004; but not *P. leniusculus vs. Austropotamobius torrentium* (Schrank), Vorburger and Ribi 1999]. Although conducted in an artificial setting, the results of these experimental studies are both informative and predictive, being a reflection of the documented range expansion of NICS. In fact, those crayfish species that were found to replace other crayfish species are also dominant in interspecific contests staged in the laboratory (e.g. Capelli 1982, Söderbäck 1991, Hill and Lodge 1994).

Predation and competition, both acting at the individual level and coupled with the potential for reproductive interference (i.e. females or males of a species may choose mates of the other species; Söderbäck 1994), enhance the effects of habitat loss, overexploitation, and pollution in inducing a dramatic decline of crayfish biodiversity. Of the 67 threatened species in North America, 5% were subject to interference by NICS, 62% to habitat degradation or habitat loss, and 33% to pollution (Wilcove *et al.* 1998). NICS have already contributed to the global extinction of other crayfish species: *Pacifastacus nigrescens* (Stimpson), once common in the creeks of the San Francisco Bay area in northern California, is now extinct due to the combined pressures of urbanization, overexploitation, and introductions of NICS (Bouchard 1977). In the same area, a similar process is ongoing. Shasta crayfish [*Pacifastacus fortis* (Faxon)],

designated endangered in 1988, is now limited to small, isolated populations, having been displaced at several locations in its native watershed by habitat loss and interactions with *P. leniusculus* (Light *et al.* 1995). Subject to similar threats from NICS, the European indigenous species *A. astacus*, *A. pallipes*, and *A. torrentium* have been designated as vulnerable by Groombridge (1993) and as protected in Appendix III of the Bern Convention. The European Habitats Directive (Directive 92/43/EEC) considers them as species whose exploitation and harvesting should be subject to control. *Austropotamobius pallipes* and *A. torrentium* are also listed in Appendix V, as species that require the setting up of special areas of conservation for their protection (Souty-Grosset *et al.* 2006).

Population effects on indigenous species may also be caused by indirect mechanisms, for instance through the transmission of pathogens and diseases. There is an extensive literature showing that North American crayfish species carry a subclinical infection of the oomycete *Aphanomyces astaci* Schikora, the aetiological agent of the crayfish plague (e.g. Alderman and Polglase 1988, Diéguez-Uribeondo and Söderhäll 1993). This disease does not require its host in order to spread, as the spores can become attached to damp surfaces and be transported in this manner. So, crayfish plague has spread and is still spreading via the hundreds of thousands of crayfish trappers and their gear. A large number of European crayfish populations has been decimated by the plague since 1860, leading to reduced production of *A. astacus* and *A. leptodactylus* by up to 90% particularly in Scandinavia, Germany, Spain, and Turkey. For example, in Sweden 90 tons were exported in 1908 (from a total catch of 200 tons), but export dropped to 30 tons by 1910 (Holdich 1999a). In Finland exports declined from 16 million *A. astacus* in 1890 to less than 2 million in 1910 (Westman 1991). When the plague spread to Turkey in the 1980s, the annual catch of *A. leptodactylus* plunged from 7,000 to 2,000 tons (Köksal 1988). It declined even further in the early 1990s, reaching 200 tons in 1991, which virtually eliminated exports from Turkey to western Europe. However, since then there has been a steady increase in stocks (Harlioğlu 2004). The impact of the crayfish plague is still high in Europe; to mitigate this, it has even been suggested that plague-resistant strains of native species should be created through genetic engineering (Westman 2002), which, in their turn, might pose additional threats to the original biodiversity.

The large emphasis that researchers have given to *A. astaci* has created, as Edgerton *et al.* (2004) lamented, a kind of ''inertia'' in astacology, ''which has curtailed researchers, state fish-disease diagnosticians, and resource managers from fully assessing and considering the existence of other serious pathogens of crayfish and the ensuing consequences for the native species'' (p. 1473). Indeed, notwithstanding that the range of crayfish diseases is repeatedly assumed to be much wider than previously thought (e.g. Vogt 1999), especially in North America, little attention has been given to commensals or parasites other than *A. astaci*. It seems unlikely that these pathogens are

species-specific; so, introduced crayfish might bring a host of organisms that may profoundly affect indigenous species. To make the picture worse, some commensals or parasites of crayfish may affect other animals, humans included (helminth parasites of vertebrates; Hobbs *et al.* 1989; bacterial fish diseases, enteric redmouth, Dunlin *et al.* 1976; infectious pancreatic necrosis, Halder and Ahne 1988). As a consequence, there is an urgent need for researchers to address the issue of crayfish diseases from a broader perspective than has been done up to now.

Genetic effects

Invaders may exert indirect genetic impacts on indigenous species, resulting in altered patterns of natural selection or gene flow within indigenous populations. They may change selection regimes or, in a subtler way, disrupt gene flow due, for instance, to their fragmenting populations of indigenous species and lead them to risky bottlenecks. Hybridization between an invader and an indigenous species is a direct effect that may have three possible consequences: (1) the creation of a new invasive genotype; (2) the production of sterile hybrids with the resulting waste of gametes and resource competition with indigenous species; and (3) the production of a hybrid swarm and widespread introgression, leading to a virtual extinction of indigenous taxa through ''genetic pollution'' (Parker *et al.* 1999).

There has been little mention in the literature of the occurrence of hybridization between indigenous and invading crayfish, e.g. *A. astacus* and *A. leptodactylus* (Cukerzis 1968), although in that case both belonged to the same family and were of European origin. Unique genetic documentation has been provided by Perry *et al.* (2001, 2002) for hybridization between indigenous and invading *Orconectes* species. Using diagnostic nuclear and mitochondrial DNA markers along with morphological data, these authors compared crayfish from allopatric and sympatric populations of the invasive *O. rusticus* and of the indigenous *Orconectes propinquus* (Girard) and *O. virilis* (Hagen) in Wisconsin (USA). Hybridization occurred between *O. rusticus* and *O. propinquus* in sympatric sites, whereas *O. virilis* hybridized with neither of these species. A detailed study of the dynamics of hybridization conducted in Trout Lake showed that over 6% of the crayfish were F_1 hybrids, 4% were F_2 individuals (hybrid × hybrid origin), and 13% were backcrosses (product of hybrid × parental matings). The majority of F_1 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 F_1 hybrids backcrossing to *O. propinquus*, whereas 13% represent backcrosses to *O. rusticus*. The F_1 hybrids, therefore, appeared to mate disproportionately with pure *O. rusticus* that led to much greater genetic introgression of nuclear DNA from *O. propinquus* to *O. rusticus* than in the reverse direction. A consequence of this is the gradual elimination of *O. propinquus* genes from the population.

These results add to the wide morphological evidence of putative hybrids among crayfish species (Perry *et al.* 2002). The implication of Perry *et al.*'s (2002) study is clear that hybridization and introgression pose a substantial threat to the conservation of crayfish biodiversity and that further research is required to test the potential for hybridization among resident and invasive species. These studies have the potential to predict species at risk of losing their genetic identity.

Effects on communities

While NICS clearly cause direct impacts on prey or on competitors and alter their abundance and distribution, they may also indirectly change interactions within communities that sometimes result in trophic cascades.

A large variety of articles has shown that, because of their omnivorous nature, introduced crayfish can profoundly modify the trophic structure of freshwater communities at several levels, often acting as keystone species (*sensu* Paine 1966). They also display a wide plasticity in their feeding behavior, switching from detritivore/scavenger to herbivore/carnivore habits in response to food availability (Hobbs *et al.* 1989). For instance, the large niche breadth and trophic diversity shown in the gut contents of a naturalized *P. clarkii* population in Portugal denoted that a wide variety of aquatic macroinvertebrates is consumed by this species and that the specific composition of the prey changes according to its seasonal availability (Correia 2002).

Several experimental studies, most often conducted in the littoral zone of lentic systems (an exception in Stenroth and Nyström 2003), have detailed the direct and indirect trophic effects that NICS have on the food web structure. On the contrary, little is known about the influence directly or indirectly exerted by NICS on e.g. the pelagic compartments of the invaded systems. Figure 4 is an attempt to summarize the trophic links that NICS may produce in littoral zones of ponds and lakes (see also Nyström 1999, 2002). All these effects are most often density dependent (e.g. Charlebois and Lamberti 1996) even if relatively low densities of the potentially invasive *O. virilis* (Chambers *et al.* 1990), and of the invasive *O. rusticus* (e.g. Lodge *et al.* 1994) and *P. clarkii* (Gherardi and Acquistapace 2007) can dramatically reduce biomass and species richness of submersed macrophytes and the abundance of invertebrate prey. The impact on food web structure may also be influenced by the digestion rate of the crayfish species (e.g. Bernardo and Ilhéu 1994), the species composition of the community (Nyström 2002), and the presence of a second introduced predator (Nyström *et al.* 2001), all conditions that make any generalizations provisional.

Young and adult NICS are represented in Fig. 4 as different components of the food web, as supported by the literature (Nyström 1999). In fact, although adult crayfish, at least in the laboratory, can efficiently prey upon juvenile or small fish, amphibian eggs and tadpoles, and macroinvertebrates (e.g. Gherardi *et al.*
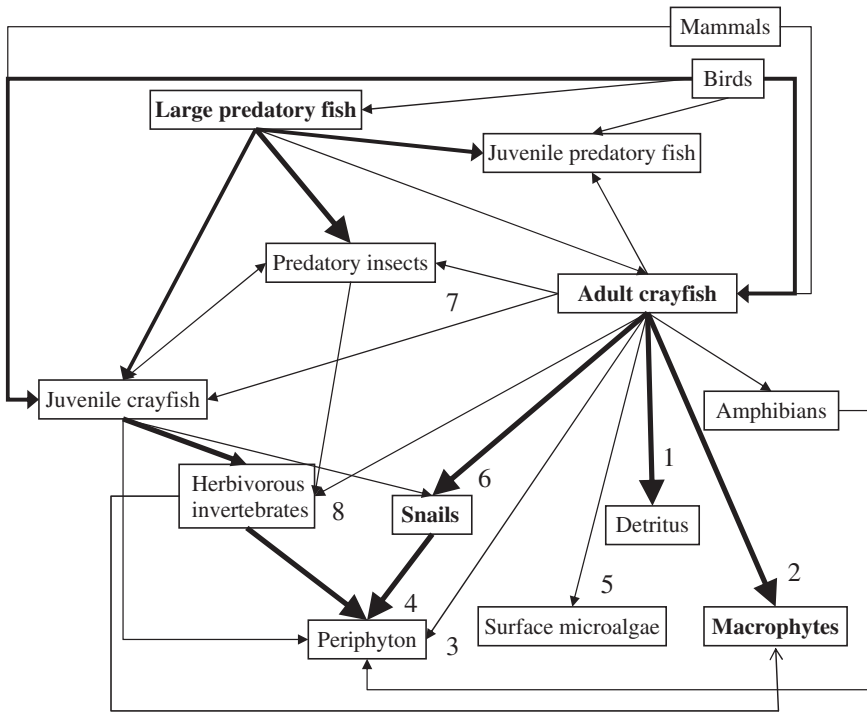
Fig. 4   Food web links (those numbered are discussed in the text) in a littoral zone of a lake or pond. Arrow thickness denotes the hypothesized strength of the interactions. The most important interactors in the food web are in bold.

2001, Renai and Gherardi 2004) including juvenile crayfish, the guts of many species contain a large proportion of organic detritus and plants, especially macrophytes, whereas juveniles feed predominantly upon macroinvertebrates (Momot *et al.* 1978, Momot 1995). For instance, in a Swedish stream, 46% of the adult *P. leniusculus* were found to have consumed invertebrates as opposed to 87% of the juveniles (Nyström 1999). In a laboratory study, adult *P. clarkii* even exhibited feeding preference for plant food over animal food when the energetic cost of active predation was high (Ilhéu and Bernardo 1993a, 1995). When kept together, juveniles may be easily cannibalized by adults. However, the cannibalistic behavior of crayfish has not been confirmed in field studies (Momot 1995), although it is expected to be most severe upon molting individuals in the wild (Reynolds and O'Keeffe 2005). The presence of crayfish remains in crayfish stomachs in enclosures was assumed to derive from the crayfish consumption of their exuviae (Stenroth and Nyström 2003). Additionally, both large predatory invertebrates and fish can reduce the abundance of juvenile crayfish (Nyström 1999). Subsequently, young crayfish have less influence on

the food web structure than adult crayfish due to the strong negative effects exerted on them by vertebrate and invertebrate predators.

Typically, adult NICS affect the biomass of organic detritus (link 1, Fig. 4) and of macrophytes (link 2, Fig. 4). In their turn, changes in detritus and macrophyte biomass have multiple non-trophic effects on the community, because of their role of either protective cover or substrate and breeding sites for a multitude of organisms. Detritus is considered to be a highly nutritive food for crayfish for its ''microbial conditioning'' or ''chemical-defense leaching'' (Newman 1991) and for their easier handling by crayfish (Cronin *et al.* 2002). It may be preferred to green plants in laboratory experiments (Ilhéu and Bernardo 1995) and has been often found in gut contents of *P. clarkii* (Ilhéu and Bernardo 1993b, Gutiérrez-Yurrita *et al.* 1998) and *P. leniusculus* (Stenroth and Nyström 2003).

The intense grazing on aquatic macrophytes by *O. rusticus*, *P. leniusculus*, and *P. clarkii* (e.g. Lodge *et al.* 1994, Nyström *et al.* 1996, Gherardi and Acquistapace 2007), coupled with their non-consumptive plant clipping and uprooting (Lodge *et al.* 1994, Nyström and Strand 1996, Smart *et al.* 2002, Gherardi and Acquistapace 2007) and their preference for seedlings rather than for older plants (Nyström and Strand 1996), may induce a significant decline in macrophyte abundance. In enclosure/exclosure experiments, *O. rusticus* abundance of 19 g m^{-2} reduced total macrophyte biomass of 64%, while abundance >140 g m^{-2} eliminated all macrophytes in 12 weeks (Lodge and Lorman 1987). More than 80% of macrophyte biomass was lost about 20 years after *P. clarkii*'s introduction in the Doñana National Park (Spain) (Gutiérrez-Yurrita *et al.* 1998). The destruction of much more plant tissue than the crayfish can eat (Lodge 1991) may induce a positive effect to the system, because fragmentation could produce nutritious coarse particulate organic matter (CPOM) (Vannote *et al.* 1980). However, macrophyte destruction in nutrient-rich conditions, particularly in eutrophic shallow lakes, is generally followed by a switch from a clear to a turbid state dominated by surface microalgae, like *Microcystis*, growth (Rodríguez *et al.* 2003). In its turn, this may lead to a decrease in primary production of macrophytes and periphyton due to the reduced light penetration.

By feeding selectively (Lodge and Lorman 1987, Nyström *et al.* 1996), crayfish may reduce the biodiversity of macrophytes and even control aquatic weeds (Warner and Green 1995). Cronin *et al.* (2002) studied feeding preferences of *P. clarkii* among 14 species of freshwater macrophytes (including macroscopic algae) and measured this species' response to manipulation of the combined plant traits of morphology, toughness, and surface features, and their response to chemistry. The preference of crayfish was related to plant phenolics, protein, nitrogen, fiber, lignin, cellulose, ash, and carbon. Like most generalist herbivores or omnivores (reviewed in Cirujano *et al.* 2004, Anastácio *et al.* 2005a), *P. clarkii* seems to base its feeding decisions on multiple plant traits, such as morphology, structure, chemical defenses, and nutritive value. Often, it feeds upon plants whose finely branched or filamentous morphologies

make them easier to handle and to consume, and not because of their nutritional value. Similarly, *O. rusticus* consumes single-stemmed species more than rosulate or highly branched forms (Lodge and Lorman 1987). NICS usually avoid plants, which are chemically defended by multiple compounds, notwithstanding their high concentrations of protein, nitrogen, and dry mass (Bolser *et al.* 1998). The preference for some macrophyte species (e.g. *Chara hispida* Linnaeus *vs. Ceratophyllum submersum* Linnaeus) can even influence *P. clarkii*'s distribution and abundance, as found in a Spanish wetland (Cirujano *et al.* 2004).

However, no single macrophyte trait appears to be a good predictor of its palatability and factors other than plant tissue quality and morphology, such as cover or protection from predators afforded by the plant (e.g. Damman 1987), the consumer's state or hunger (e.g. Cronin and Hay 1996), and the consumer's prior feeding experiences (e.g. Dorn *et al.* 2001), may also be important in determining feeding decisions. Differences in the impact of crayfish on macrophyte growth were also found to be related to crayfish sex and activity, and to the abundance of alternative foods (Chambers *et al.* 1990).

NICS may affect periphytic algae (link 3, Fig. 4) in a number of ways that may result in positive (+) or negative (−) effects by: (1) consuming and dislodging periphyton during feeding, movement, or burrowing (−), (2) reducing the abundance of algivorous invertebrates (or vertebrates), which can indirectly increase algal abundance (+) (Luttenton *et al.* 1998); (3) fertilizing periphyton with their faeces (+) (Charlebois and Lamberti 1996); and (4) consuming or destroying macrophytes on which some algae grow (−) (Lodge *et al.* 1994). Therefore, periphyton responses to the crayfish impact are expected to vary in function of the effect that prevails in the system. Due to the morphology of their feeding apparatus, *O. rusticus* and *P. leniusculus* are not as efficient grazers on microalgae as snails are (Lodge *et al.* 1994, Luttenton *et al.* 1998, Nyström *et al.* 1999, Nyström *et al.* 2001) and their consumption is not so intense as to outweigh the positive indirect effect of the crayfish-induced reduction in snail densities (the crayfish–snail–periphyton link is strong). Other potential periphyton grazers, e.g. amphibian tadpoles (Nyström 1999) and herbivorous insects, may be preyed on by crayfish but probably their consumption is not so extensive to produce an indirect positive effect on microalgal abundance (the crayfish–amphibian–periphyton and the crayfish–insect grazers–periphyton links are weak; Lodge *et al.* 1994, Nyström *et al.* 1999). As a result, because snails are both the prey group primarily affected by crayfish and the functionally most important grazer group among the many other grazing taxa, crayfish may indirectly generate an increased abundance of microalgae by relaxing them from the grazing pressure of snails (link 4, Fig. 4), thus inducing – although being omnivorous – a trophic cascade in the food webs of the littoral zones of lakes or ponds. However, in the habitats characterized by abundant filamentous algae, the intense grazing from crayfish seems not to be sufficient to compensate for the reduced grazing from snails (Nyström *et al.* 1996).

A correlation between the density of *P. clarkii* and the abundance and composition of surface (but not pelagic) microalgae (link 5, Fig. 4) has been recently found in an *in situ* experiment conducted in a Mediterranean wetland (Gherardi and Lazzara 2006). Six areas (10×7 m) were delimited along a channel in the ''Padule di Fucecchio'' (Italy) to host crayfish populations at either low (1 m^{-2}) or high (14 m^{-2}) density. The analysis of chlorophylls *a*, *b*, and *c*, and phaeopigments showed that biomass of surface microalgae, mostly composed of Cyanobacteria, was strongly affected by the presence of dense populations of *P. clarkii*. The potential of their direct consumption by *P. clarkii* was confirmed by behavioral studies that showed crayfish on macrophytes feeding on the floating film.

In both lentic and lotic systems, crayfish can have direct and indirect negative effects on the biomass and species richness of macroinvertebrates (links 6, 7, and 8, Fig. 4) as the result of several mechanisms (Charlebois and Lamberti 1996), i.e.: (1) consumption; (2) increased drift through prey escape and incidental dislodgment by their foraging; and (3) possible inhibition of invertebrate colonization. Each of these mechanisms could have different consequences (e.g. direct mortality *vs.* displacement to downstream areas) for the local macroinvertebrate assemblage. When crayfish become abundant in lentic systems, species composition of invertebrates may change towards less vulnerable prey species.

Gastropoda are the taxon most affected by NICS (link 6, Fig. 4) and are sometimes eliminated. In Trout Lake, Wisconsin, snails declined from >10,000 to <5 individuals m^{-2} after 19 years of colonization by *O. rusticus* (Wilson *et al.* 2004). Also bivalves may be affected by NICS; for instance, predation by *O. rusticus* may have a significant impact on the colonization rate of zebra mussels (Perry *et al.* 1997, 2000).

NICS are selective in their choice of snails, thin-shelled snails being preferred to thick-shelled species because they are easier to handle (Nyström and Pérez 1998). Hence, in systems invaded by NICS, snail species composition may be altered from the thin-shelled *Lymnaea* spp. to the thick-shelled *Bithynia* spp. (Nyström *et al.* 2001). Large snails are also less profitable, because handling time of shells increases exponentially: adult *P. leniusculus* took less than a minute to feed upon small *Lymnaea stagnalis* (Linnaeus) but spent more than 27 minutes handling and consuming large snails. However, in complex habitats such as macrophyte beds crayfish may be less indiscriminate in their selection (Nyström and Pérez 1998). Also crayfish naïveté to a mollusk, although never definitively proved, may influence consumption. In a laboratory experiment Correia *et al.* (2005) showed that *P. clarkii* is able to capture the exotic snail *Physa acuta* (Draparnaud), but never preyed upon the Asian clam *Corbicula fluminea* (Muller). Possibly, prior experience coupled with the availability of alternative prey may be decisive as to whether the predator will proceed with or abort an attack.

The direct impact of NICS on non-snail macroinvertebrates (links 7 and 8, Fig. 4) largely depends on the life style and behavior of any single species.

In lentic waters, crayfish predation is weak on species that: (1) move quickly enough to escape tactile-feeding crayfish (e.g. isopods, amphipods, some Diptera, Heteroptera, and Coleoptera); (2) circumvent crayfish recognition ability by living in cases (e.g. Trichoptera); or (3) avoid contact by living in the sediment (e.g. some Diptera) (Lodge *et al.* 1994, Nyström *et al.* 1996). In streams, crayfish may have less predictable effects on invertebrate communities than in lentic waters (Stenroth and Nyström 2003) even if, also in these systems, slow-moving species are expected to decline (i.e. leeches, dragonflies, caddisflies, isopods, and mollusks) whereas more mobile prey or prey living in sediments seem to be less affected (i.e. chironomids and stoneflies).

The indirect impact of NICS on zoobenthic communities is particularly complex. Through consumption and destruction of macrophytes, crayfish can alter littoral habitats, leading to declines in macrophyte-associated taxa (Nyström *et al.* 1996). Crayfish may also influence detrital substrates through bioturbidation and feeding: the reduction in detritus has potential consequences for zoobenthic communities, particularly collector-gatherers (e.g. some Ephemeroptera, Trichoptera, and Diptera). Finally, crayfish predation upon, or competition with other zoobenthic predators such as Odonata larvae could reduce their occurrence, subsequently leading to an increase in the abundance of their prey (McCarthy *et al.* 2006).

Recently, the effects of *O. rusticus* – and of other NICS – on benthic invertebrate densities were examined by McCarthy *et al.* (2006) by applying a fixed-effect model meta-analysis on pre-existing data. A comparison was made among cage experiments conducted in 14 studies that excluded crayfish as the control and maintained a given density of crayfish as the treatment. The negative effect of crayfish on the total invertebrate abundance appeared to be driven by the significant decline of a few taxonomic orders, specifically Gastropoda and Diptera (Fig. 5). However, the abundance of Amphipoda, Coleoptera, Ephemeroptera, Oligochaeta, and Trichoptera was also reduced in crayfish treatments, although results for these taxa were not significant. Comparisons across orders showed that the greatest negative impact was exerted on Gastropoda (followed by Diptera, Amphipoda, and Ephemeroptera).

Finally, NICS can be prey items for fish, birds, and mammals, constituting a new resource for higher trophic levels in several areas of their introduction. In the Lower Guadalquivir Basin (Spain), before the introduction of *P. clarkii*, eels mostly preyed upon fish species (mosquitofish and carp). After crayfish introduction, only 17% of their stomachs (*vs.* 50% before crayfish introduction) contained other fish species, whereas the dominant prey item was *P. clarkii* reaching 67% of occurrence (Montes *et al.* 1993). As they readily feed upon *P. clarkii*, eels were proposed as selective biological control organisms (Mueller and Frutiger 2001). Still in southern Spain, *P. clarkii* is also an important part of the diet of at least six bird species, in particular white storks, night herons, and little egrets, whose diet is composed of up to 80% of crayfish (Rodríguez *et al.* 2005). Though no quantitative study has been yet made,
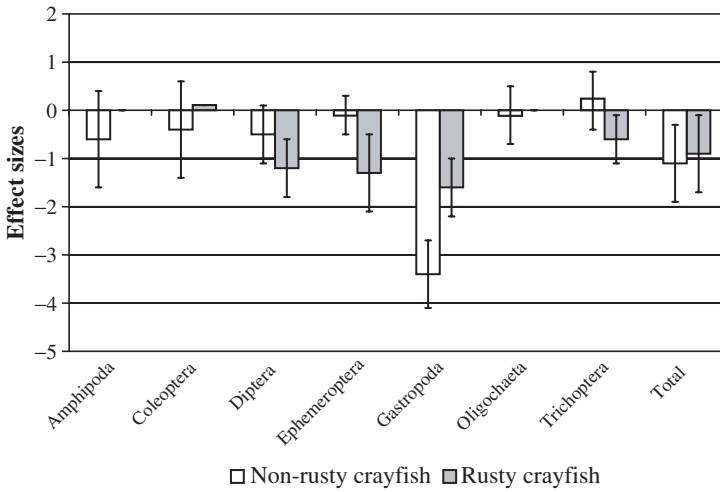
Fig. 5   Results from a fixed-effect model meta-analysis applied by McCarthy *et al.* (2006) on data obtained from 14 enclosure/exclosure experiments from the published literature. The effect size is the difference between the effects of crayfish on zoobenthic abundance in normal versus elevated densities, measured in units of standard deviation. Effect sizes (±95% Confidence Interval) are shown for total invertebrate and individual order densities. Negative values indicate a negative effect of crayfish on invertebrate density.

the appearance of *P. clarkii* has been considered responsible for the increase in a number of avian species, like some Ardaeidae, together with cormorants, in some European areas, such as in Massaciuccoli Lake (Tuscany) (Barbaresi and Gherardi 2000). In Doñana National Park it has also become the most common prey category of the otter, *Lutra lutra* (Linnaeus) (Delibes and Adrian 1987).

Notwithstanding the large amount of available data, much information derives from short-term studies and therefore the long-lasting strength of each link can only be hypothesized. A few long-term studies have attempted to analyze – all the other factors being equal – changes in species richness after the introduction of NICS. The study of Rodríguez *et al.* (2005) reviewed the existing information on the communities before the appearance of *P. clarkii* in Chozas Lake (Spain) and compared it with the data collected after its invasion. For macroinvertebrates, data from proximal non-invaded wetlands were also used in the analysis. The results (Table 1) were clear in showing the decline in submerged vegetation and the decrease of macroinvertebrate populations, both leading to a dramatic depletion of food resources, shelters, and breeding sites for fish, amphibians, and birds.

In a northern temperate lake in Wisconsin, USA (Sparkling Lake), McCarthy *et al.* (2006) conducted a 24-year time series analysis of *O. rusticus* and zoobenthos abundances. As a confirmation of a companion study (see above),

Table 1   Changes in the vegetation cover and faunal abundance as occurred in Chozas Lake (Spain) after the introduction of an NICS (*Procambarus clarkii*). (Modified after Rodríguez *et al.* 2005)

	Before	After	Loss (%)
Vegetation cover (%)	95	<3	99
Macroinvertebrates (genera, number)	31	9	71
Waterfowl (species, number)	50	26	52
Amphibians (species, number)	6	1	83

this crayfish species was found to exert a significant, although variable, impact on zoobenthic communities, its abundance being negatively correlated with the abundance of total zoobenthos and of Diptera, Ephemeroptera, Odonata, and Trichoptera. However, the authors proved that the invertebrate taxa had much resilience in the long term. Nearly all invertebrate taxa were negatively affected by the crayfish within a 1-year lag, but no taxa exhibited sustained declines over the course of the *O. rusticus* invasion. Several factors may explain this pattern. Large-bodied invertebrate taxa, such as snails and crayfish, have slower generation times and are not as productive as smaller taxa, and are thus less able to respond numerically following population reductions of crayfish. In addition, aquatic insect larvae have a winged adult stage and, as a consequence, great dispersal ability – thus facilitating quick recovery. Whatever the explanation might be, McCarthy *et al.*'s (2006) results are illustrative in underlining the importance of a long-term monitoring of the invaded community to capture the complex picture of the impact of NICS.

Effects on ecosystems

As compared with the individual, population, and community levels, documented changes to ecosystem processes have been rarely reported in the literature on NICS. This probably reflects a lack of measurements of ecosystem processes rather than a lack of impact on these processes. The abundantly documented community effects are on the contrary expected to determine significant changes in energy flux and nutrient cycling in the invaded systems.

Essentially, the introduction of NICS may alter the pathways of the energy flux in two ways, i.e. through augmenting connectance by feeding at several trophic levels and through increasing the availability of autochthonous carbon as a food source for higher trophic levels (Stenroth and Nyström 2003). This was clearly proved by Geiger *et al.* (2005) in temporary freshwater marshes in Spain. Before the introduction of *P. clarkii* (Fig. 6a), macrophytes and the associated periphyton were the dominant primary producers. Only a small portion of the energy was transmitted from them to herbivores, whereas most of
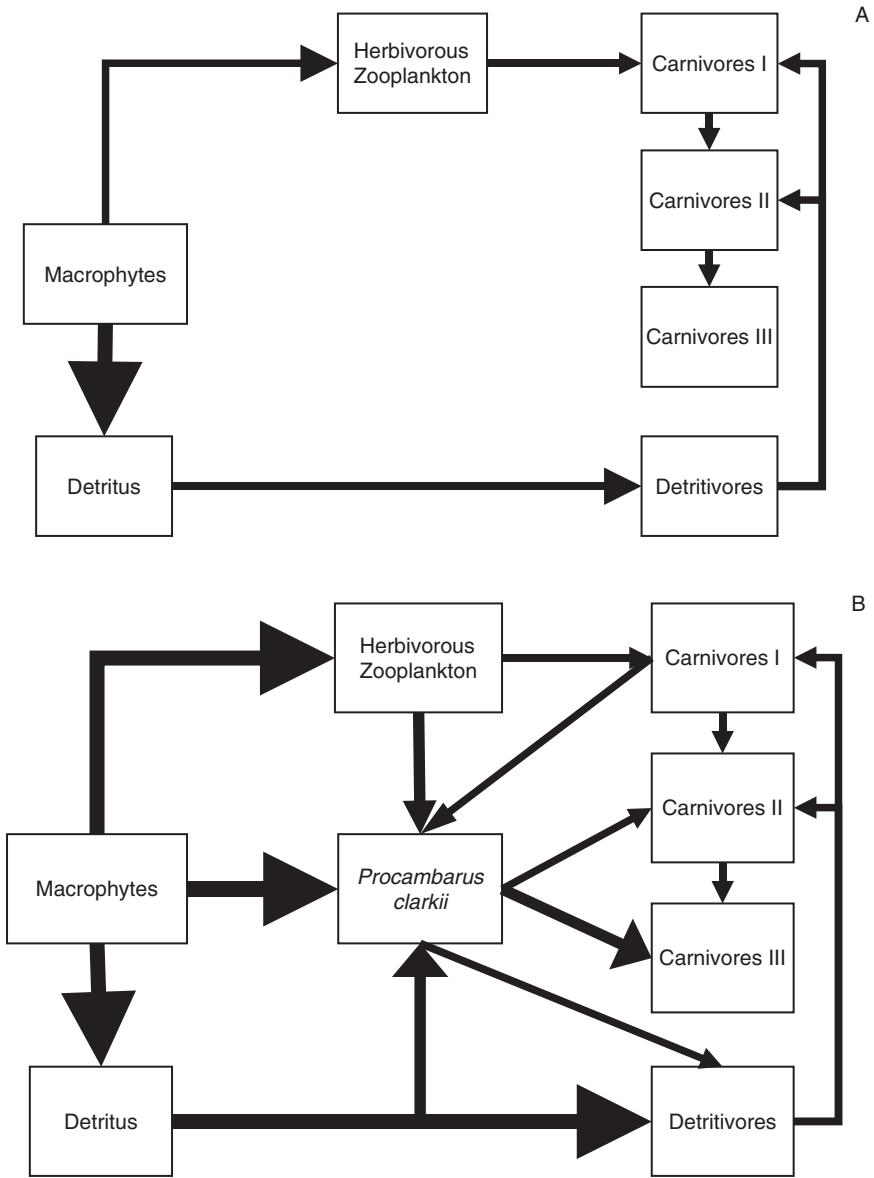
Fig. 6   Hypothesized energy flows in a marshland system before (A) and after (B) the introduction of an NICS (*Procambarus clarkii*). (Modified after Geiger *et al.* 2005)

it was lost to the detritus pool, which accumulated large amounts of organic matter. Detritivores, mainly macroinvertebrates (oligochaetes, chironomids) and meiofauna (nematodes, ostracods), used only a small fraction of the
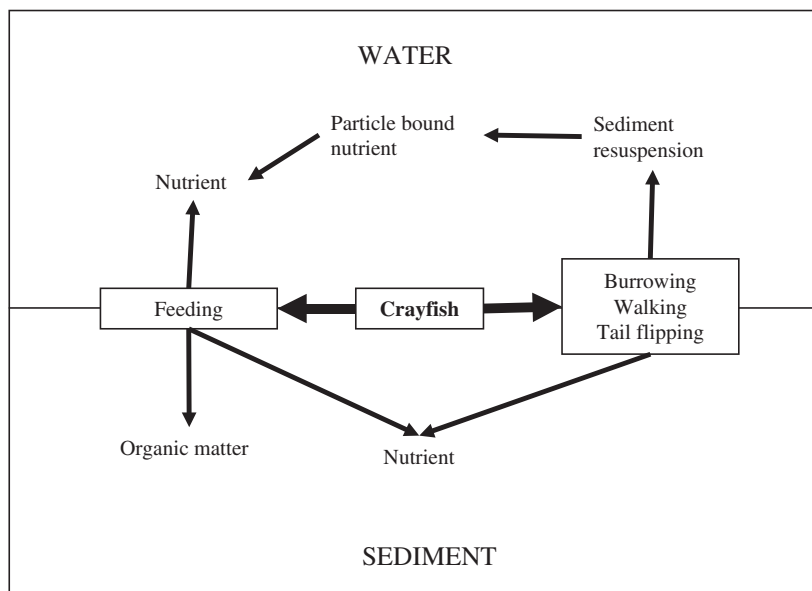
Fig. 7 Effects of the benthic activity of an NICS (*Procambarus clarkii*) on physical and chemical characteristics of water and sediments in a floodplain wetland in Spain. (Modified after Angeler *et al.* 2001)

deposited material. This system was characterized by a high diversity of herbivores and consisted of a minimum of four levels of consumers. Due to the large number of trophic levels and losses of energy to the detritus pool, the energy transferred to top predators such as birds and mammals was comparatively low. After the introduction of crayfish (Fig. 6B), much of the detritus was consumed by *P. clarkii* and the energy gained was directly transferred to the top predator level (fish, birds, and mammals). This resulted in a decreased importance of macrophytes, herbivores, and primary carnivores but offered a larger availability of energy for vertebrate predators.

The role that NICS may play through their benthic activity on physical and chemical characteristics of water and sediments was investigated by Angeler *et al.* (2001) in a floodplain wetland in Spain. *Procambarus clarkii* was hypothesized to affect the ecosystem processes by: (1) recycling sediment bound nutrients and (2) resuspending sediments associated with crayfish foraging, burrowing, and locomotory activity (walking, tail flipping) (Fig. 7). Compared to the control, the enclosures with crayfish showed a significant increase in both dissolved inorganic nutrients (soluble reactive phosphorus and ammonia) and total suspended solids as a result of crayfish bioturbation. At the same time, crayfish reduced the content of organic matter in the sediment and slightly

increased total phosphorus and nitrogen content in sediments as the effect of its benthic activity.

Crayfish-mediated bioturbation has the general effect of impoverishing water quality by increasing total suspended solids and hence turbidity and by reducing light penetration and plant productivity (Anastácio and Marques 1997, Rodríguez *et al.* 2003). Crayfish may also alter sediment characteristics as a result of oxygen supply due to their activity. Bioturbation is often associated with crayfish constructing burrows, as commonly observed in *P. clarkii*, *P. leniusculus*, and *C. destructor* (e.g. Sommer and Goldman 1983, Gutiérrez-Yurrita and Montes 1999). However, crayfish, like *O. limosus*, can also move bottom sediments due to the friction between the extremities of its pereopods and the bottom during walking, the force exerted above the bottom by the uropods and the telson of escaping crayfish, and the pressure of the uropods and claws into the substrate to slow its movement while walking in fast currents (Maude and Williams 1983). In experimental flumes, Statzner *et al.* (2000, 2003) showed that *O. limosus* at a fixed biomass ($174 \ \mathrm{g \ m^{-2}}$) significantly affected sand and gravel erosion. Its effect of bioturbator varied in function of the presence of refugia and aggression: sediment erosion averaged 2.8 and 1.4 kg dry weight $\mathrm{m^{-2} \ d^{-1}}$ when crayfish hierarchies were established and refugia were available. Once the refugia were removed, these rates increased to 4.0 and 3.2 kg dry weight $\mathrm{m^{-2} \ d^{-1}}$. Additionally, bioturbation by crayfish was found to change bedform roughness, physical particle consolidation, proportion of sand in gravel interstices, sand cover by gravel, and the cover of filamentous algae. Such changes, in turn, may affect the abundance and structure of the entire benthic community, e.g. by modifying their substrate or by reducing algae and biofilm available for grazers. Also, sand reduction among gravel might alter the egg survival of gravel-breeding fish, like salmonids.

WHY DO NICS CAUSE MORE PROBLEMS THAN INDIGENOUS CRAYFISH?

In areas without any indigenous ecological equivalent, the changes caused by the introduction of NICS may be complex and usually affect all levels of ecological organization. Impacts range from subtle behavioral modifications of resident species to altered energy and nutrient fluxes in the ecosystem. Impacts at the community level can be strong when the introduced crayfish experience little predation or competition from native predators and have prey that lack efficient defense adaptations to them (Nyström *et al.* 2001). The modes of resource acquisition by NICS and their capacity to develop new trophic relationships, coupled with their action as bioturbator, may lead to dramatic direct and indirect effects on the ecosystem.

When NICS replace an indigenous ecological equivalent, their resource-acquisition mode should not be novel to the colonized community and therefore

the resulting impact is expected to be weak. But the overall effect of NICS can be strong if, once introduced, they are capable of building high densities and/or of reaching large size. Indeed, several introduced crayfish often reach much higher densities than indigenous crayfish, e.g. *P. leniusculus vs. A. pallipes* (Guan and Wiles 1996). Densities of *O. limosus* ranged between 0.4 and 77 m^{-2} in a reservoir in Poland, of *O. rusticus* between 0.18 and 21 m^{-2} in North American streams, and of *P. leniusculus* between 3.7 and 21.7 m^{-2} in an English river (reviewed in Nyström 1999). On the contrary, densities of the indigenous species have been estimated to reach a maximum of 14.3 m^{-2} for *A. astacus* (in a Swedish lake), 3 m^{-2} for *A. pallipes* (in France), 3.6 m^{-2} for *C. japonicus* (in Japan), 0.83 m^{-2} for *P. fortis* (in USA), and 3.3 m^{-2} for *Paranephrops planifrons* White (in New Zealand) (references in Nyström 1999). The drastic decline of biota recorded by Wilson *et al.* (2004) in Trout Lake, Wisconsin (USA), when *O. rusticus* catches reached a threshold of nine crayfish trap^{-1}, suggests that its high abundance is the primary reason for its large impact, even in lakes with pre-existing crayfish populations.

Several biological traits contribute to the achievement by crayfish of high densities/large size. Relatively to indigenous crayfish, some NICS are characterized by higher fecundity, faster growth rates, and better physiological tolerances to changing environmental conditions (Lindqvist and Huner 1999, Chapter 12). They also might be better at coping with changes induced by human activities that cause pollution and habitat destruction. For instance, *P. clarkii* is a good colonizer of disturbed aquatic habitats and can survive in anoxic conditions in burrows (Gherardi 2006). Also, higher survival rate, hence leading to higher densities and/or larger sizes, is expected when a species is introduced without a full complement of specific parasites, pathogens, and enemies. And large sizes, in their turn, make crayfish both resistant to gape-size limited predators (such as many fish) and agonistically superior in resource fights. As a consequence, because of their large numbers, coupled with their wide trophic plasticity, NICS exert a greater direct (through consumption) or indirect (through competition) effect on the other biota, particularly on crayfish species, benthic fish, mollusks, and macrophytes (Nyström *et al.* 1996). This is also true for those species that apparently have not caused much environmental degradation, such as *A. leptodactylus* in England whose high numbers are producing considerable problems for anglers (Holdich 1999b). Obviously, large size usually translates into an overall higher energy and nutrient demand, but NICS may also be more efficient energy converters and may display higher metabolic rate when compared with similarly sized crayfish species.

As a consequence, a combination of larger size and greater weight-specific consumption of macrophytes and snails may explain the greater ecological impact suffered by those North American lakes where *O. rusticus* had replaced its congeners (Olsen *et al.* 1991) (Table 2), whereas the more efficient grazing by *P. leniusculus* than *A. astacus* seems to be the cause of the dramatic decrease

Table 2   Summary of test results after Olsen *et al.* (1991) for mechanisms governing the greater impact of *Orconectes rusticus* (Or) relative to *O. propinquus* (Op) and *O. virilis* (Ov) on a benthic community structure.

Mechanisms	Replace Op	Replace Ov
1. Individual size	Or > Op	Or < Ov
2. Population density	Or < Op	Or < Ov
3. Population biomass	Or < Op	Or < Ov
4. Weight-specific consumption, C, and sublethal damage, D, of snails	C: Or > Op D: Or = Op	C: Or > Ov D: Or > Ov
5. Weight-specific selection for single-stemmed macrophytes	Or = Op	Or = Ov
6. Weight-specific consumption, C, and destruction, D, of macrophytes	C: Or > Op D: Or = Op	C: Or = Ov D: Or = Ov

of macrophytes biomass (including the extinction of several rare *Chara* species), as recorded by Nyström and Strand (1996) in Sweden.

EFFECTS ON HUMAN ECONOMY AND HEALTH

From an anthropocentric perspective, a useful approach to measure impacts is to assess the damage caused by NICS by calculating the economic cost they induce to human societies, also in terms of the social and ethical problems associated with their potential harm to human health. A review of the existing literature in the matter shows that much of the discussion has been purely anecdotal. A negative consequence is the often encountered difficulty in justifying to decision makers the need of containing the spread of NICS and of mitigating the risks they pose.

The introduction of NICS has been often assumed to have contributed in a positive way to human economy by: (1) restoring some traditions proper to the cultural heritage of a country, e.g. crayfishing in Sweden and Finland (Kirjavainen and Sipponen 2004); (2) producing some economic benefits for many families in poorly developed areas, e.g. in Andalusia, Spain (Geiger *et al.* 2005); (3) leading to a diversification of agriculture to include astaciculture, e.g. by crayfish farmers in Britain and in Spain (Holdich 1999a); and (4) increasing trade between countries inside Europe as well as between European and extra-European countries (Ackefors 1999).

There are, however, several examples showing that often the introduction of commercially valuable crayfish has also led to negative results in the market-place. Despite the original aim of crayfish farmers in Britain to produce crayfish for export to the Scandinavian market where they fetch a high price (Holdich 1993), most of the exports are now being made with crayfish harvested from

natural waters and not from farming (Holdich 1999b). Similarly, in Africa, very few of the several projects that led to crayfish importations since the 1960s can be regarded as successful (de Moor 2002). For instance, in Lake Naivasha, Kenya, only about 40 metric tons of *P. clarkii* are now caught annually exclusively for local consumption (mainly tourism), after their first harvests in 1975 of several hundred tons per year (Smart *et al.* 2002). Crayfish were reported to spoil valuable fish (tilapia and largemouth bass) caught in gillnets (up to 30% of the catch) and to damage fish nets (de Moor 2002). They are also responsible for the decline of the rooted vegetation and therefore of the increase of phytoplankton, decrease of water transparency, and reduction of fish, including commercial species, in the littoral zone (de Moor 2002).

In several countries, introduced crayfish have today much lower commercial values than indigenous species, as exemplified by the Scandinavian market where consumers are willing to pay substantially higher prices for the indigenous *A. astacus* than for the naturalized *P. leniusculus* (Holdich 1999a). Crayfishing, in its turn, may produce extensive environmental impacts and associated costs, as the result of the continuous roaming of fishermen, causing a physical alteration of the habitat and the capture of non-target organisms (e.g. turtles) in the crayfish traps (Geiger *et al.* 2005).

There are several examples of damage to other human activities. *Procambarus clarkii* is a recognized pest in rice cultures in various parts of the world. Although in Louisiana (USA) double cropping crayfish and rice are practiced with success (Chien and Avault 1980), the species produces economic costs in rice fields in Portugal (Correia 1993). As an example, economic losses per ha of Euro 43.40 of the 2004 rice production (a 6.3% decrease in profits) was reported in the ''Baixo Mondego'' area exclusively due to crayfish (Anastácio *et al.* 2005a). Damage to rice production primarily consists of crayfish consuming seedlings, but negative effects derive from the increased turbidity and decreased dissolved oxygen content due to the crayfish bioturbation (Anastácio *et al.* 2005a, b, c).

Burrowing by several NICS (e.g. *P. clarkii*, *P. leniusculus*, and *C. destructor*) can be a problem in areas other than agricultural, e.g. lawns, golf courses, levees, dams, dykes, and in rivers and lakes (e.g. Anastácio and Marques 1997). A few authors have lamented the damage caused by *C. destructor* burrowing to dam walls and irrigation canals (de Moor 2002). More often cited is the effect of *P. clarkii* to ''honeycomb'' banks, with their consequent structural damage (Huner 1977) that seriously affects areas with extensive canal irrigation systems and water control structures (Adão and Marques 1993). Although not recorded as a burrowing species in its native North American habitat (Holdich 1999a), *P. leniusculus* causes considerable damage to river banks by burrowing in the UK (Sibley 2000).

Indeed, if a monetary value were to be assigned to species extinctions and losses in biodiversity, ecosystem services, and aesthetics, the total economic damage of introduced crayfish might be enormous. Neither do we have records

of the financial costs of control and remediation, except an estimate of US$4.5 million for the restitution of *P. fortis* in California (USA) (US Fish and Wildlife Service) and the £100,000 spent trying, unsuccessfully, to eradicate *P. leniusculus* from rivers in Scotland (Collins 2006).

Up to today, little attention has been paid to the potential harm that NICS pose to human health. NICS, such as *P. clarkii*, often live in areas contaminated by sewage and toxic industrial residues and may have high heavy metal concentrations in their tissues (Geiger *et al.* 2005); they were found to bioaccumulate metals such as nickel, lead, and zinc in their tissues and organs at a significantly higher rate than the indigenous species (Gherardi *et al.* 2002). Their potential to transfer contaminants to their consumers, including man, is obviously high. Measurements of accumulation of heavy metals in waterfowl and other wetland birds living and feeding in a toxic spill area of Spain showed that heavy metals like arsenic have entered the food chain and were detected in some bird species, such as white storks, spoonbills and grey herons, all predators of crayfish (Geiger *et al.* 2005).

The finding that *P. clarkii* may consume Cyanobacteria is of increasing concern for human health (Gherardi and Lazzara 2006). Several Cyanobacteria release a wide range of toxins and BMAA (β-*N*-methylamino-ʟ-alanine) that may produce lethal animal and human intoxications (e.g. Carmichael 1988, Cox *et al.* 2005). Among the few organisms so far investigated, *P. leniusculus* and *P. clarkii* were found to accumulate such toxins in their tissues (Lirås *et al.* 1998, Vasconcelos *et al.* 2001), being therefore able to transfer them to more sensitive organisms, man included.

The other side of the coin is the ability of *P. clarkii* to control, through predation and competition, populations of the pulmonate snails *Biomphalaria* and *Bulinus* known to host *Schistosoma mansoni* and *S. haematobium*, the agents of human schistosomiasis (Chapter 4). Schistosomiasis is one of the most widespread diseases in Africa: in Kenya alone, it is known to affect 3.5 million individuals with 12 million more at risk of infection. As suggested by Mkoji *et al.* (1999), due to the quick spread of this crayfish in African waterbodies, the epidemiology of schistosomiasis is expected to be significantly altered with time although the possibilities remain that African snails will soon evolve measures to avoid crayfish predation before their extinction or that the parasite will change its host.

WHAT COMES NEXT?

Despite the considerable attention that NICS have received since 1987, a review of the many papers published in the last few years has revealed the absence in the literature of a general framework about their impact. Nonetheless, a global view is required to help us coordinate and improve both control and research efforts for the existing NICS and hopefully predict the impact of future introductions.

First, this review lamented the general lack of simultaneous measurements of the impact of NICS at multiple ecological levels. This is unfortunate, because information about responses at several levels of organization is required to fully understand the range of the impact observed (Simon and Townsend 2003). Also, little effort has been made to study the impact of NICS at the genetic level. We cannot even guess therefore what their role might be in determining the future evolutionary pathway that the invaded system will follow after the introduction of NICS. Neither do we have quantitative estimates about direct or indirect monetary (and social) costs induced by NICS to the human economy and health. And only a few paradigmatic invasive species, namely *P. leniusculus*, *P. clarkii*, and *O. rusticus*, have been extensively studied, whereas information is scanty or even absent about other species, like *C. destructor*.

Short-term laboratory and field studies have revealed a myriad of direct and indirect effects of crayfish on some compartments of the invaded ecosystem (most often the littoral zone). Their results were certainly able to provide mechanistic insights into the interactions between crayfish and the other organisms in the community and to quantify the immediate impact of NICS. However, these sometimes complex interactions have been only seldom investigated at larger levels. Few comparative field studies (e.g. Charlebois and Lamberti 1996) and even fewer long-term studies (Wilson *et al.* 2004, McCarthy *et al.* 2006) have been conducted to examine the dynamic relationships among organisms, including the prolonged effects of crayfish invaders on native communities over multiple generations.

Indeed, coupling the results of small- and large-scale studies may help capture a more realistic picture of the impact of NICS. As held by McCarthy *et al.* (2006), each method is not without its own biases. Along with characterizing only short-term ecological responses, small-level studies may suffer from experimental artifacts. In contrast, long-term studies certainly provide important insights into the long-term threats of an NICS and the potential adaptability of the native taxa to it, but their results may also be confounded by environmental factors that cannot be controlled (Parker *et al.* 1999). Because the disadvantage of one approach is the advantage of another, coupling multiple levels of analyses certainly provides a method in which interactions at one level can be successfully translated to another.

Finally, we need much more intensive work on the whole-system impact of crayfish invasion; specifically, we need to learn more about the natural variability among systems and the extent to which the impact of an NICS depends on the community or ecosystem where it is measured. So, on what level can we generalize across systems? And how often does the impact of a crayfish invader depend on the presence of other NIS? Not before having answered to these and to the other questions above will we be able to generalize, and even predict, which species is more likely to have the greatest impact in aquatic systems (Parker *et al.* 1999).

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REFERENCES

Ackefors, H. 1999. The positive effects of established crayfish. Pages 49–61 in F. Gherardi and D. M. Holdich, editors. Crayfish in Europe as alien species: How to make the best of a bad situation? A. A. Balkema, Rotterdam, The Netherlands.

Adão, H. and J. C. Marques. 1993. Population biology of the red swamp crayfish *Procambarus clarkii* (Girard, 1852) in southern Portugal. Crustaceana **65**, 336–345.

Alderman, D. J. and J. L. Polglase. 1988. Pathogens, parasites and commensals. Pages 167–212 in D. M. Holdich and R. S. Lowery, editors. Freshwater crayfish: biology, management and exploitation. Croom Helm (Chapman & Hall), London, UK.

Anastácio, P. M., A. M. Correia, and J. P. Menino. 2005a. Processes and patterns of plant destruction by crayfish: effects of crayfish size and developmental stages of rice. Archiv für Hydrobiologie **162**, 37–51.

Anastácio, P. M., A. M. Correia, J. P. Menino, and L. Martins da Silva. 2005b. Are rice seedlings affected by changes in water quality caused by crayfish? Annales de Limnologie – International Journal of Limnology **41**, 1–6.

Anastácio, P. M. and J. C. Marques. 1997. Crayfish, *Procambarus clarkii*, effects on initial stages of rice growth in the lower Mondego River valley (Portugal). Freshwater Crayfish **11**, 608–617.

Anastácio, P. M., V. S. Parente, and A. M. Correia. 2005c. Crayfish effects on seeds and seedlings: identification and quantification of damage. Freshwater Biology **50**, 697–704.

Angeler, D. G., S. Sánchez-Carrillo, G. García, and M. Alvarez-Cobelas. 2001. The influence of *Procambarus clarkii* (Cambaridae, Decapoda) on water quality and sediment characteristics in a Spanish floodplain wetland. Hydrobiologia **464**, 9–98.

Arrignon, J. C. V., J. V. Huner, and P. J. Laurent. 1990. L'écrevisse rouge des marais. Maisonneuve et Larose, Paris, France, 87 pp.

Barbaresi, S., F. Gherardi. 2000. The invasion of the alien crayfish *Procambarus clarkii* in Europe, with particular reference to Italy. Biological Invasions **2**, 259–264.

Bernardo, J. M. and M. Ilhéu. 1994. Red swamp crayfish (*Procambarus clarkii*): contribution to material cycling. Verhandlungen Internationale Vereinigung Limnologie **25**, 2447–2449.

Blake, M. A. 1995. The vulnerability of juvenile signal crayfish to perch and eel predation. Freshwater Biology **33**, 233–244.

Bolser, R. C., M. E. Hay, N. Lindquist, W. Fenical, and D. Wilson. 1998. Chemical defenses of freshwater macrophytes against crayfish herbivory. Journal of Chemical Ecology **24**, 1639–1657.

Bouchard, R. W. 1977. Distribution, systematics status, and ecological notes on five poorly known species of crayfishes in western North America (Decapoda: Astacidae and Cambaridae). Freshwater Crayfish **3**, 409–423.

Capelli, G.M. 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). Limnology and Oceanography **27**, 741–745.

Carmichael, W. W. 1988. Toxins of freshwater algae. Pages 121–147 in A. T. Tu, editor. Handbook of natural toxins, Vol. 3, Marine toxins and venoms. Marcel Dekker, New York, NY.

Carpenter, J. 2005. Competition for food between an introduced crayfish and two fishes endemic to the Colorado River basin. Environmental Biology of Fishes **72,** 335–342.

Chambers, P. A., J. M. Hanson, J. M. Burke, and E.E. Prepas. 1990. The impact of the crayfish *Orconectes virilis* on aquatic macrophytes. Freshwater Biology **24**, 81–91.

Charlebois, P. M. and G. L. Lamberti. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on peryphyton and macroinvertebrates. Journal of the North American Benthological Society **15**, 551–563.

Chien, Y. H. and J. W. Avault Jr. 1980. Production of crayfish in rice fields. Progress in Fish Cultivation **42**, 67–71.

Cirujano, S., J. A. Camargo, and C. Gómez-Cordovés. 2004. Feeding preferences of the red swamp crayfish *Procambarus clarkii* (Girard) on living macrophytes in a Spanish wetland. Journal of Freshwater Ecology **19**, 219–226.

Collins, V. 2006. £100,000 battle against alien crayfish ends in defeat. Crayfish News - International Association of Astacology Newsletter **28**, 10–11.

Correia, A. M. 1993. Situation de l'acclimatation de l'écrevisse rouge des marais *Procambarus clarkii* au Portugal. L'Astaciculteur de France **35**, 2–9.

Correia, A. M. 2002. Niche breadth and trophic diversity: feeding behaviour of the red swamp crayfish (*Procambarus clarkii*) towards environmental availability of aquatic macroinvertebrates in a rice field (Portugal). Acta Oecologica **23**, 421–429.

Correia, A. M. 2003. Food choice by the introduced crayfish *Procambarus clarkii*. Annales Zoologici Fennici **40**, 517–528.

Correia, A. M., N. Bandeira, and P. M. Anastácio. 2005. Predator-prey interactions of *Procambarus clarkii* with aquatic macroinvertebrates in single and multiple prey systems. Acta Oecologica **28**, 337–343.

Cox, G. W. 2004. Alien species and evolution. Island Press, Washington, DC.

Cox, P. A., S. A. Banack, S. J. Murch, U. Rasmussen, G. Tien, R. R. Bidigare, J. S. Metcalf, L. F. Morrison, G. A. Codd, and B. Bergman. 2005. Diverse taxa of Cyanobacteria produce β-N-methylamino-L-alanine, a neurotoxic amino acid. Proceedings of the National Academy of Sciences USA. **102**, 5074–5078.

Crandall, K. A. 2002. Crayfish as model organisms. Freshwater Crayfish **13**, 3–10.

Cronin, G. and M. E. Hay. 1996. Seaweed-herbivore interactions depend on recent history of both the plant and animal. Ecology **77**, 1531–1543.

Cronin, G., D. M. Lodge, M. E. Hay, M. Miller, A. M. Hill, T. Horvath, R. C. Bolser, N. Lindquist, and M. Wahl. 2002. Crayfish feeding preferences for fresh water macrophytes: The influence of plant structure and chemistry. Journal of Crustacean Biology **22**, 708–718.

Cruz, M. J. and R. Rebelo. 2005. Vulnerability of Southwest Iberian amphibians to an introduced crayfish, *Procambarus clarkii*. Amphibia-Reptilia **26**, 293–303.

Cukerzis, J. 1968. Interspecific relations between *Astacus astacus* L. and *A. leptodactylus* Esch. Ekologia Polska Ser. A **16**, 629–636.

Damman, H. 1987. Leaf quality and enemy avoidance by the larvae of a pyralid moth. Ecology **68**, 88–97.

Delibes, M. and I. Adrián. 1987. Effects of crayfish introduction on otter *Lutra lutra* in the Doñana National Park, SW Spain. Biological Conservation **42**, 153–159.

Diéguez-Uribeondo, J. and K. Söderhäll. 1993. *Procambarus clarkii* Girard as a vector for the crayfish plague fungus, *Aphanomyces astaci* Schikora. Aquaculture and Fisheries Management **24**, 761–765.

Dorn, N. J., G. Cronin, and D. M. Lodge. 2001. Feeding preferences and performance of an aquatic lepidopteran on macrophytes: plant hosts as food and habitat. Oecologia **128**, 406–415.

Dunlin, M., T. Huddleston, R. E. Larson, and G. W. Klontz. 1976. Enteric redmouth disease. University of Idaho Forest, Wildlife and Range Experiment Statistic Bulletin **8**, 1–15.

Edgerton, B. F., P. Henttonen, J. Jussila, A. Mannonen, P. Paasonen, T. Taugbøl, L. Edsman, and C. Souty-Grosset. 2004. Understanding the causes of disease in European freshwater crayfish. Conservation Biology **18**, 1466–1474.

Elvey, W., A. M. M. Richardson, and L. Bermuta. 1996. Interactions between the introduced yabby, *Cherax destructor*, and the endemic crayfish, *Astacopsis franklinii*, in Tasmanian streams. Freshwater Crayfish **11**, 349–363.

Fitzpatrick Jr, J. F. 1995. The Eurasian Far-eastern crawfishes: a preliminary review. Freshwater Crayfish **8**, 1–11.

Gamradt, S. C. and L. B. Kats. 1996. Effect of introduced crayfish and mosquito fish on California newts (*Taricha torosa*). Conservation Biology **10**, 1155–1162.

Geiger, W., P. Alcorlo, A. Baltanás, and C. Montes. 2005. Impact of an introduced Crustacean on the trophic webs of Mediterranean wetlands. Biological Invasions **7**, 49–73.

Gherardi, F. 2002. Behaviour. Pages 258–290 in D. M. Holdich, editor. Biology of freshwater crayfish. Blackwell, Oxford, UK.

Gherardi, F. 2006. The red swamp crayfish (*Procambarus clarkii*) in Europe: a lesson for biodiversity conservation. Marine and Freshwater Behaviour and Physiology **39**, 175–191.

Gherardi, F. and P. Acquistapace. 2007. Invasive crayfish in Europe: the impact of *Procambarus clarkii* on the littoral community of a Mediterranean lake. Freshwater Biology, **52**, 1249–1259.

Gherardi, F. and S. Barbaresi. 2000. Invasive crayfish: activity patterns of *Procambarus clarkii* in the rice fields of the Lower Guadalquivir (Spain). Archiv für Hydrobiologie **150**, 153–168.

Gherardi, F., S. Barbaresi, O. Vaselli, and A. Bencini. 2002. A comparison of trace metal accumulation in indigenous and alien freshwater macro-decapods. Marine and Freshwater Behaviour and Physiology **35**, 179–188.

Gherardi, F. and A. Cioni. 2004. Agonism and interference competition in freshwater decapods. Behaviour **141**, 1297–1324.

Gherardi, F. and W. H. Daniels. 2004. Agonism and shelter competition between invasive and indigenous crayfish species. Canadian Journal of Zoology **82**, 1923–1932.

Gherardi, F. and D. M. Holdich, editors. 1999. Crayfish in Europe as alien species: How to make the best of a bad situation? A. A. Balkema, Rotterdam, The Netherlands.

Gherardi, F. and L. Lazzara. 2006. Effects of the density of an invasive crayfish (*Procambarus clarkii*) on pelagic and surface microalgae in a Mediterranean wetland. Archiv für Hydrobiologie **165**, 401–414.

Gherardi, F., B. Renai, and C. Corti. 2001. Crayfish predation on tadpoles: a comparison between a native (*Austropotamobius pallipes*) and an alien species (*Procambarus clarkii*. Bulletin Français de la Pêche et de la Pisciculture **361**, 659–668.

Gouin, N., F. Grandjean, S. Pain, C. Souty-Grosset, and J. Reynolds. 2003. Origin and colonization history of the white-clawed crayfish, *Austropotamobius pallipes*, in Ireland. Heredity **9**, 70–77.

Groombridge, B. 1993. 1994 IUCN Red list of threatened animals. World Conservation Monitoring Centre, Cambridge, UK.

Guan, R.-Z. and P.R. Wiles. 1996. Growth, density and biomass of crayfish, *Pacifastacus leniusculus*, in a British lowland river. Aquatic Living Resource **9**, 265–272.

Guan, R.-Z. and P.R. Wiles. 1997. Ecological impact of introduced crayfish on benthic fishes in a British lowland river. Conservation Biology **11**, 641–647.

Gutiérrez-Yurrita, P. J. and C. Montes. 1999. Bioenergetics and phenology of reproduction of the introduced red swamp crayfish, *Procambarus clarkii*, in Doñana National Park, Spain, and implications for species management. Freshwater Biology **42**, 561–574.

Gutiérrez-Yurrita P. J., G. Sancho, M. Á. Bravo, Á. Baltanás, and C. Montes. 1998. Diet of the red swamp crayfish *Procambarus clarkii* in natural ecosystems of the Doñana National Park temporary fresh-water marsh (Spain). Journal of Crustacean Biology **18**, 120–127.

Halder, M. and W. Ahne. 1988. Freshwater crayfish *Astacus astacus* – a vector for infectious pancreatic necrosis virus (IPVN). Diseases of Aquatic Organisms **4**, 205–209.

Harlioğlu, M. M. 2004. The present situation of freshwater crayfish, *Astacus leptodactylus* (Eschscholtz, 1823) in Turkey. Aquaculture **230**, 181–187.

Hill, A. M. and D. M. Lodge. 1994. Diel changes in resource demand: competition and predation in species replacement among crayfishes. Ecology **75**, 2118–2126.

Hill, A. M. and D. M. Lodge. 1999. Replacement of resident crayfishes by an exotic crayfish: the roles of competition and predation. Ecological Applications **9**, 678–690.

Hobbs Jr, H. H. 1988. Crayfish distribution, adaptive radiation and evolution. Pages 52–82 in D. M. Holdich and R. S. Lowery, editors. Freshwater crayfish: biology, management and exploitation. Croom Helm, London, UK.

Hobbs, H. H. III. 1991. Adaptations and convergence in North American crayfishes. Freshwater Crayfish **2**, 541–549.

Hobbs, H. H. III, J. P. Jass, and J. V. Huner. 1989. A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). Crustaceana **56**, 299–316.

Hofkin, B. V., G. M. Mkoji, D. K. Koech, and E. S. Loker. 1991. Control of schistosome-transmitting snails in Kenya by the North American crayfish *Procambarus clarkii*. Journal of Tropical Medicine and Hygiene **45**, 339–344.

Holdich, D. M. 1988. The dangers of introducing alien animals with particular reference to crayfish. Freshwater Crayfish **7**, XV–XXX.

Holdich, D. M. 1993. A global review of astaciculture – freshwater crayfish farming. Aquatic Living Resources **6**, 307–317.

Holdich, D. M. 1999a. The negative effects of established crayfish introductions. Pages 31–61 in F. Gherardi and D. M. Holdich, editors. Crayfish in Europe as alien species: How to make the best of a bad situation? A. A. Balkema, Rotterdam, The Netherlands.

Holdich, D. M. 1999b. The introduction of alien crayfish species into Britain for commercial exploitation – An own goal? Pages 85–97 in J. C. Von Vaupel Klein and F. R. Schram, editors. The biodiversity crisis and Crustacea. A. A. Balkema, Rotterdam, The Netherlands.

Holdich, D. M. and J. C. J. Domaniewski. 1995. Studies on a mixed population of the crayfish *Austropotamobius pallipes* and *Pacifastacus leniusculus* in England. Freshwater Crayfish **10**, 37–45.

Holdich, D. M., J. P. Reader, W. D. Rogers, and M. Harlioglu. 1995. Interactions between three species of crayfish (*Austropotamobius pallipes*, *Astacus leptodactylus* and *Pacifastacus leniusculus*). Freshwater Crayfish **10**, 46–56.

Holdich, D. M., P. J. Sibley, and S. Peay. 2004. The white-clawed crayfish – a decade on. British Wildlife **15**, 153–164.

Huner, J. V. 1977. Introductions of *Procambarus clarkii* (Girard) – an update. Freshwater Crayfish **3**, 93–202.

Ilhéu, M. and J. M. Bernardo. 1993a. Experimental evaluation of food preference of redswamp crayfish, *Procambarus clarkii*: vegetal versus animal. Freshwater Crayfish **9**, 359–364.

Ilhéu, M. and J. M. Bernardo. 1993b. Aspects of trophic ecology of red swamp crayfish (*Procambarus clarkii* Girard) in Alentejo, South of Portugal. Pages 417–423 in Proceedings VI Spanish Meeting on Limnology, Granada, Spain.

Ilhéu, M. and J. M. Bernardo. 1995. Trophic ecology of red swamp crayfish *Procambarus clarkii* (Girard) – preference and digestability of plant foods. Freshwater Crayfish **10**, 132–139.

Karatayev, A. Y., L. E. Burlakova, and D. K. Padilla. 2002. Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. Pages 433–446 in E. Leppäkoski, S. Gollasch, and S. Olenin, editors. Invasive aquatic species of Europe. Distribution, impacts and management. Kluwer, Dordrecht, The Netherlands.

Kirjavainen, J. and M. Sipponen. 2004. Environmental benefit of different crayfish management strategies in Finland. Fisheries Management and Ecology **11**, 213–218.

Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution **16**, 199–204.

Köksal, G. 1988. *Astacus leptodactylus* in Europe. Pages 365–400 in D. M. Holdich and R. S. Lowery, editors. Freshwater crayfish: biology, management and exploitation. Croom Helm, London, UK.

Leite, E. P., P. M. Anastácio, M. Ferreira, L. Vicente, and A. M. Correia. 2005. Do Eastern mosquitofish exhibit anti-predator behavior towards red swamp crayfish? Zoological Studies **44**, 513–518.

Light, T., D. C. Erman, C. Myrick, and J. Clarke. 1995. Decline of the Shasta crayfish (*Pacifastacus fortis* Faxon) of Northeastern California. Conservation Biology **9**, 1567–1577.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. What are the ecological effects of anti-predator decision-making? BioScience **48**, 25–33.

Lindqvist, O. V. and J. V. Huner. 1999. Life history characteristics of crayfish: what makes some of them good colonizers? Pages 23–30 in F. Gherardi and D. M. Holdich, editors. Crayfish in Europe as alien species: How to make the best of a bad situation? A. A. Balkema, Rotterdam, The Netherlands.

Linnaeus, C. 1746. Fauna Suecica. Stockholm, Sweden, 411 pp.

Lirås, V., M. Lindberg, P. Nyström, H. Annadotter, L. A. Lawton, and B. Graf. 1998. Can ingested cyanobacteria be harmful to the signal crayfish (*Pacifastacus leniusculus*)? Freshwater Biology **39**, 233–242.

Lodge, D. M. 1991. Herbivory on freshwater macrophytes. Aquatic Botany **41**, 195–224.

Lodge, D. M. and J. G. Lorman. 1987. Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. Canadian Journal of Fisheries and Aquatic Sciences **44**, 591–597.

Lodge, D. M., M. W. Kershner, J. E. Aloi, and A. P. Covich. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology **75**, 1265–1281.

Lodge, D. M., R. A. Stein, K. M. Brown, A. P. Covich, C. Brönmark, J. E. Garvey, and S. P. Klosiewski 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Australian Journal of Ecology **23**, 53–67.

Lodge, D. M., C. A. Taylor, D. M. Holdich, and J. Skurdal 2000. Non-indigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. Fisheries **25**, 7–20.

Luttenton, M. R., M. J. Horgan, and D. M. Lodge. 1998. Effects of three *Orconectes* crayfish on epilithic microalgae: a laboratory experiment. Crustaceana **71**, 845–855.

Maude, S. H. and D. D. Williams. 1983. Behavior of crayfish in water currents: Hydrodynamics of eight species with reference to their distribution patterns in southern Ontario. Canadian Journal of Fisheries and Aquatic Sciences **40**, 68–77.

McCarthy, J. M., C. L. Hein, J. D. Olden, and M. J. Vander Zanden. 2006. Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. Freshwater Biology **51**, 224–235.

McCarthy, T. M., and B. F. Dickey. 2002. Chemically mediated effects of injured prey on behavior of both prey and predators. Behaviour **139**, 585–602.

Mikkola, H. 1996. Alien freshwater crustacean and indigenous mollusk species with aquaculture potential in eastern and southern Africa. South African Journal of Aquatic Sciences **22**, 90–99.

Mkoji, G. M., B. V. Hofkin, A. M. Kuris, A. Stewart-Oaten, B. N. Mungai, J. H. Kihara, F. Mungai, J. Yundu, J. Mbui, J. R. Rashid, C. H. Kariuki, J. H. Ouma, D. K. Koech, and E. S. Loker. 1999. Impact of the crayfish *Procambarus clarkii* on *Schistosoma haematobium* transmission in Kenya. American Journal of Tropical Medicine and Hygiene **61**, 751–759.

Momot, W. T. 1995. Redefining the role of crayfish in aquatic ecosystems. Reviews in Fisheries Science **3**, 33–63.

Momot, W. T., H. Gowing, and P. D. Jones. 1978. The dynamics of crayfish and their role in ecosystems. American Midland Naturalist **99**, 10–35.

Montes, C., M. A. Bravo-Utrera, A. Baltanás, C. Duarte, and P. J. Gutiérrez-Yurrita. 1993. Bases ecológicas para la gestión del Cangrejo Rojo de las Marismas en el Parque Nacional de Doñana. ICONA, Ministerio de Agricultura y Pesca, Madrid, Spain.

Moor, I., de 2002. Potential impacts of alien freshwater crayfish in South Africa. African Journal of Aquatic Sciences **27**, 125–139.

Moyle, P. B. and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation **78**, 149–161.

Mueller, R. and A. Frutiger. 2001. Effects of intensive trapping and fish predation on an (unwanted) population of *Procambarus clarkii*. Abstracts of Annual Meeting of the North American Benthological Society, LaCrosse, WI, 3–8, June 2001.

Nakata, K. and S. Goshima. 2003. Competition for shelter of preferred sizes between the native crayfish species *Cambaroides japonicus* and he alien crayfish species *Pacifastacus leniusculus* in Japan in relation to prior residence, sex difference, and body size. Journal of Crustacean Biology **23**, 897–907.

Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. Journal of the North American Benthological Society **10**, 89–114.

Nyström, P. 1999. Ecological impact of introduced and native crayfish on freshwater communities: European perspectives. Pages 63–84 in F. Gherardi and D. M. Holdich, editors. Crayfish in Europe as alien species: How to make the best of a bad situation? A. A. Balkema, Rotterdam, The Netherlands.

Nyström, P. 2002. Ecology. Pages 192–235 in D. M. Holdich, editor. Biology of freshwater crayfish. Blackwell, Oxford, UK.

Nyström, P., C. Brönmark, and W. Granéli. 1996. Patterns in benthic food webs: a role for omnivorous crayfish? Freshwater Biology **36**, 631–646.

Nyström, P. and J. R. Pérez. 1998. Crayfish predation on the common pond snail (*Lymnaea stagnalis*): the effect of habitat complexity and snail size on foraging efficiency. Hydrobiologia **368**, 201–208.

Nyström, P. and J. A. Strand. 1996. Grazing by a native and an exotic crayfish on acquatic macrophytes. Freshwater Biology **36**, 673–682.

Nyström, P., O. Svensson, B. Lardner, C. Brönmark, and W. Granéli. 2001. The influence of multiple introduced predators on a littoral pond community. Ecology **82**, 1023–1039.

Olsen, T. M., D. M. Lodge, G. M. Capelli, and R. J. Houlihan. 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. Canadian Journal of Fisheries and Aquatic Sciences **48**, 1853–1861.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**, 65–75.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions **1**, 3–19.

Pérez, J. R., J. M. Carral, J. D. Celada, M. Sáez-Royuela, C. Munoz, and A. Sierra. 1997. Current status of astaciculture production and commercial situation of crayfish in Europe. Aquaculture Europe **22**, 6–13.

Perry, W. L., J. E. Feder, and D. M. Lodge. 2001. Implications of hybridization between introduced and resident *Orconectes* crayfish. Conservation Biology **15**, 1656–1666.

Perry, W. L., D. M. Lodge, and J. E. Feder 2002. Importance of hybridization between indigenous and nonindigenous freshwater species: an overlooked threat to North American biodiversity. Systematic Biology **51**, 255–275.

Perry, W. L., D. M. Lodge, and G. A. Lamberti. 1997. Impact of crayfish predation on exotic zebra mussels and native invertebrates in a lake-outlet stream. Canadian Journal of Fisheries and Aquatic Sciences **54**, 120–125.

Perry, W. L., D. M. Lodge, and G. A. Lamberti. 2000. Crayfish (*Orconectes rusticus*) impacts on zebra mussel (*Dreissena polymorpha*) recruitment, other macroinvertebrates and algal biomass in a lake-outlet stream. American Midland Naturalist **144**, 308–316.

Pontoppidan, E. 1775. The natural history of Norway. Linde, London, UK.

Renai, B. and F. Gherardi. 2004. Predatory efficiency of crayfish: comparison between indigenous and non-indigenous species. Biological Invasions **6**, 89–99.

Reynolds, J. D. 1997. The present status of freshwater crayfish in Ireland. Bulletin Française de la Pêche et de la Pisciculture **347**, 693–700.

Reynolds, J. D. and C. O'Keeffe. 2005. Dietary patterns in steam- and lake-dwelling populations of *Austropotamobius pallipes*. Bulletin Française de la Pêche et de la Pisciculture **376–377**, 715–730.

Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. Freshwater Biology **48**, 972–981.

Rodríguez, C. L., E. Bécares, and M. Fernández-Aláez. 2003. Shift from clear to turbid phase in Lake Chozas (NW Spain) due to the introduction of American red swamp crayfish (*Procambarus clarkii*). Hydrobiologia **506–509**, 421–426.

Rodríguez, C. L., E. Bécares, M. Fernández-Aláez, and C. Fernández-Aláez. 2005. Loss of diversity and degradation of wetlands as a result of introducing exotic crayfish. Biological Invasions **7**, 75–85.

Romero, X. M. 1997. Redclaw crayfish aquaculture in Ecuador: the new boom. NAGA, The ICLARM Quarterly **20**, 18–21.

Sibley, P. 2000. Signal crayfish management in the River Wreake catchment. Pages 95–108 in D. Rogers and J. Brickland, editors. Crayfish Conference Leeds. Environment Agency, Leeds, UK.

Simon, K. S. and C. R. Townsend. 2003. Impacts of freshwater invaders at different levels of ecological organization, with emphasis on salmonids and ecosystem consequences. Freshwater Biology **48**, 982–994.

Slater, F. M. and G. Rayner. 1993. *Austropotamobius pallipes* in otter diet in the mid-Wye catchment of central Wales. Freshwater Crayfish **9**, 365–367.

Smart, A. C., D. M. Harper, F. Malaisse, S. Schmitz, S. Coley, and A.-C. Gourder de Beauregard. 2002. Feeding of the exotic Louisiana red swamp crayfish, *Procambarus clarkii* (Crustacea, Decapoda), in an African tropical lake: Lake Naivasha, Kenya. Hydrobiologia **488**, 129–142.

Söderbäck, B. 1991. Interspecific dominance and aggressive interaction in the freshwater crayfishes *Astacus astacus* (L.) and *Pacifastacus leniusculus* (Dana). Canadian Journal of Zoology **69**, 1321–1325.

Söderbäck, B. 1994. Reproductive interference between two co-occurring crayfish species, *Astacus astacus* L. and *Pacifastacus leniusculus* Dana. Nordic Journal of Freshwater Research **69**, 137–143.

Sommer, T. R. and C. R. Goldman. 1983. The crayfish *Procambarus clarkii* from California ricefields: ecology, problems and potential harvest. Freshwater Crayfish **5**, 418–428.

Souty-Grosset, C., D. M. Holdich, P. Y. Noël, J. D. Reynolds, and P. Haffner, editors. 2006. Atlas of Crayfish in Europe. Muséum national d'Histoire naturelle, Paris, France (Patrimoines naturels, 64), 188 pp.

Statzner, B., E. Fièvet, J.-Y. Champagne, R. Morel, and E. Herouin. 2000. Crayfish as geomorphic agents and ecosystem engineers: biological behavior affects sand and gravel erosion in experimental streams. Limnology and Oceanography **45**, 1030–1040.

Statzner, B., O. Peltret, and S. Tomanova. 2003. Crayfish as geomorphic agents and ecosystem engineers: effect of a biomass gradient on baseflow and flood-induced transport of gravel and sand in experimental streams. Freshwater Biology **48**, 147–163.

Stenroth, P. and P. Nyström. 2003. Exotic crayfish in a brown water stream: effects on juvenile trout, invertebrates and algae. Freshwater Biology **48**, 466–475.

Taylor, C. 2002. Taxonomy and conservation of native crayfish stocks. Pages 236–257 in D. M. Holdich, editor. Biology of freshwater crayfish. Blackwell Science, Oxford, UK.

Taylor, C. A., M. L. Warren Jr., J. F. Fitzpatrick Jr, H. H. Hobbs III, R. F. Jezerinac, W. L. Pflieger, and H. W. Robinson. 1996. Conservation status of crayfishes of the United States and Canada. Fisheries **21**, 25–38.

Torchin, M. E., K. D. Lafferty, A. P. Dobson, V. J. McKenzie, and A. M. Kuris. 2003. Introduced species and their missing parasites. Nature **421**, 628–630.

Turner, A. M., R. J. Bernot, and C. M. Boes. 2000. Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snail. Oikos **88**, 145–158.

Usio, N., M. Konishi, and S. Nakano. 2001. Species displacement between an introduced and a 'vulnerable' crayfish: the role of aggressive interactions and shelter competition. Biological Invasions **3**, 179–185.

Vannote, R. L., G. W. Minshal, K. W. Cummins, J. R. Sedell, and C. E. Cushing 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**, 130–137.

Vasconcelos, V., S. Oliveira, and F. O. Teles. 2001. Impact of a toxic and a non-toxic strain of *Microcystis aeruginosa* on the crayfish *Procambarus clarkii*. Toxicon **39**, 1461–1470.

Vogt, G. 1999. Diseases of European freshwater crayfish, with particular emphasis on interspecific transmission of pathogens. Pages 87–103 in F. Gherardi and D. M. Holdich, editors. Crayfish in Europe as alien species. How to make the best of a bad situation? A. A. Balkema, Rotterdam, The Netherlands.

Vorburger, C. and G. Ribi. 1999. Aggression and competition for shelter between a native and an introduced crayfish in Europe. Freshwater Biology **42**, 111–119.

Warner, G. F. and E. I. Green. 1995. Choice and consumption of aquatic weeds by signal crayfish (*Pacifastacus leniusculus*). Freshwater Crayfish **8**, 360–363.

Westman, K. 1973. The population of the crayfish *Astacus astacus* in Finland and the introduction of the American crayfish *Pacifastacus leniusculus* Dana. Freshwater Crayfish **1**, 41–55.

Westman, K. 1991. The crayfish fishery in Finland – its past, present and future. Finnish Fisheries Research **12**, 187–216.

Westman, K. 2002. Alien crayfish in Europe: negative and positive impacts and inter-actions with native crayfish. Pages 76–100 in E. Leppäkoski, S. Gollasch and S. Olenin, editors. Invasive aquatic species of Europe. Distribution, impacts and management. Kluwer, Dordrecht, The Netherlands.

Whiteledge, G. W. and C. F. Rabeni. 1997. Energy sources and ecological role of cray-fishes in an Ozark stream: insights from stable isotopes and gut analysis. Canadian Journal of Fisheries and Aquatic Sciences **54**, 2555–2563.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Philips, and E. Losos 1998. Quantifying threats to imperiled species in the United States. BioScience **48**, 607–615.

Williamson, M. 1996. Biological invasions Chapman & Hall, London, UK.

Wilson, K. A., J. J. Magnuson, D. M. Lodge, A. M. Hill, T. K. Kratz, W. L. Perry, and T. V. Willis. 2004. A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake. Canadian Journal of Fisheries and Aquatic Sciences **61**, 2255–2266.