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Crayfish invading Europe: the case study of *Procambarus clarkii*

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Abstract

The red swamp crayfish, *Procambarus clarkii*, native to northeastern Mexico and southcentral USA, is today the dominant macroinvertebrate in several European countries. While the first introduction of this species into Spain is well-documented, little is known about its pathways of invasion and the reason for its rapid spread in several European countries. Study of the biology of the species has revealed a number of properties that makes this crayfish a successful invader. *Procambarus clarkii* exhibits properties characteristic of an *r*-selected species, including early maturity at small body size, rapid growth rates, large numbers of offspring at a given parental size, and relatively short life spans. It is also plastic in its life cycle, able to disperse widely in the habitat and to tolerate environmental extremes. It displays generalist and opportunistic feeding habits, consuming macrophytes and preying on amphibians. *Procambarus clarkii* can also replace indigenous crayfish by a combination of mechanisms, including competitive exclusion and transmission of the fungus-like *Aphanomyces astaci*, responsible for the crayfish plague. Finally, this species shows a wide behavioral flexibility when coping with new types of predators. The results of these studies, combined with the increasing information available in the scientific literature on this and other crayfish species, will help us understand invasions in this taxon and make predictions about the identity of future crayfish invaders.

Keywords: *Biological invasions, freshwater, crayfish, Europe, Procambarus clarkii*

Introduction

The human-mediated introduction of species outside their native ranges has recently emerged as one of the “big five” issues of concern in conservation (Sala et al. 2000). Many of these introductions are indeed beneficial to humans (Ewel et al. 1999) or cause minimal environmental impacts (Williamson and Fitter 1996; Jerscke and Strayer 2005). Only a small, but significant proportion of nonindigenous species become invasive, meaning that they become numerically and ecologically prominent, spread from the point of introduction, and are often capable of dominating indigenous populations and communities (Kolar and Lodge 2001; Crooks 2002). The spread of cosmopolitan, invasive species,

combined with the extinction or range contraction of indigenous species, is also leading to a constant “homogenization” of the native biota, i.e. the reduction of regional differences among faunas and floras (McKinney and Lockwood 1999).

Recent analyses suggest that biodiversity in fresh waters declines at far greater rates than in the most affected terrestrial ecosystems (e.g. Ricciardi and Rasmussen 1999), and that biotic homogenization is accelerating in several freshwater systems (Rahel 2000). Among the other drivers of global biodiversity change (land use, atmospheric CO₂ concentration, nitrogen deposition and acid rain, and climate), the deliberate or accidental introduction of nonindigenous species was found to be relatively more important for aquatic than for terrestrial ecosystems (Sala et al. 2000). Indeed, diversity in lakes and in some streams is particularly vulnerable to biotic exchange, because, similarly to islands, their geographic isolation has led to local adaptation and sometimes to a low biodiversity (Sala et al. 2000). Freshwater systems are also highly susceptible to the colonization of invasive species as the result of both the strong affinity of humans for water (for commerce, transportation, recreation, or aesthetic reasons) and the dispersal ability of freshwater species (Lodge et al. 1998; Gherardi 2000; Beisel 2001). According to some realistic estimates (Taugbøl and Skurdal 1999), if the ongoing process of homogenization continues, almost all European watersheds will be dominated by a handful of cosmopolitan species among mammals, fish, mussels, crayfish, and plants in less than 100 years.

Among these taxa, crayfish have received by far the least attention from biologists, policy makers, and the general public (Horwitz 1990; Lodge et al. 2000) despite their prominent role in freshwater ecosystems. Crayfish are the largest and relatively long-lived invertebrate organisms in temperate areas, and often exist at high densities. Most of them are keystone consumers (Nyström et al. 1996), feeding on benthic invertebrates, detritus, macrophytes, and algae in lotic and lentic waters (e.g. Lodge et al. 1994; Whitley and Rabeni 1997), and they constitute the main prey of several species, including otter (Slater and Rayner 1993), fish (e.g. Blake 1995), and birds (Rodríguez et al. 2005). Thus, additions of crayfish species may have significant consequences on the structure of freshwater food webs (Lodge et al. 1998; Covich et al. 1999). In the short term, introduced crayfish may reduce biomass and species richness of macroinvertebrates, macrophytes, and periphyton (e.g. Lodge and Lorman 1987; Feminella and Resh 1989; Charlebois and Lamberti 1996; Nyström and Strand 1996; Luttenton et al. 1998; Nyström et al. 2001; Nyström 2002; Cronin et al. 2002). They may also lead to direct economic outcomes, for instance, by decreasing recruitment of commercially fished species (Nyström 1999; Svärdson et al. 2001) or by reducing rice crops (Anastácio et al. 2005a, 2005b). In the long term, invasive crayfish may induce drastic habitat changes with the consequent decline of several invertebrate taxa, amphibians, and fish (e.g. Guan and Wiles 1997).

There is a long history of intentional or accidental introductions of crayfish. Hobbs et al. (1989) compiled a list of 20 crayfish species that have been introduced into new river basins, states, or continents throughout the world. Due to their high commercial value, the introduction and cultivation in Europe of nonindigenous species have increased during the last few decades (e.g. Pérez et al. 1997) and today most European countries have at least one nonindigenous crayfish (Gherardi and Holdich 1999). Once introduced for aquaculture and kept in outdoor ponds, crayfish almost inevitably escape (Hobbs et al. 1989), and a portion of them may establish self-sustaining populations in the colonized habitats. But the invasion process by crayfish may continue: while some populations remain localized around the point of introduction, others spread widely, becoming invasive (Kolar and Lodge 2001).

The purpose of this review article is threefold. First, the history of the introduction of a paradigmatic invasive crayfish, the red swamp crayfish *Procambarus clarkii* into

Europe is described. Second, the biological, ecological, and ethological properties that make this species an optimal invader is highlighted. Third, the potential that we have from this and other studies to predict the identity of future crayfish invaders is discussed.

The history of the introduction of *P. clarkii* into Europe

Procambarus clarkii occurs naturally in northeastern Mexico and in southcentral USA, extending westward to Texas, eastwards to Alabama, and northwards to Tennessee and Illinois (Hobbs 1972). This species has been extensively cultivated since the 1950s in the southern USA (Huner 2002), reaching the maximum production of 3000 kg ha⁻¹. Mostly due to its commercial value, it has been introduced into several states of the USA, its range now including east and west coasts and extending northward into the states of Idaho and Ohio (Huner 2002). Outside the continental USA, *P. clarkii* has been successfully introduced into Hawaii, western Mexico, Costa Rica, Dominican Republic, Belize, Brazil, Ecuador, Venezuela, Japan, mainland China, Taiwan, the Philippines, Uganda, Kenya, Zambia, Republic of South Africa, and Europe (Huner 2002). As a result of these translocations, today *P. clarkii* is the most cosmopolitan crayfish, being found in natural habitats in all continents except Australia and Antarctica (Huner 1977; Huner and Avault 1979).

The first introduction of the red swamp crayfish into Europe has been documented by several authors (e.g. Gutiérrez-Yurrita et al. 1999). It was encouraged by the results from stocking with the North American signal crayfish, *Pacifastacus leniusculus*, conducted in Sweden (Svårdson 1965) and Finland (Kirjavainen and Sipponen 2004). In June 1973, a batch of *P. clarkii* (100 kg) was imported from New Orleans, Louisiana (USA), into a farm in the Spanish province of Badajoz (Hasburgo-Lorena 1986), and a year later a second larger batch (400 kg) was released into an eel pond in the lower Guadalquivir (Puebla del Río, Seville), together with 100 kg of the white river crayfish *P. zonangulus* (Gutiérrez-Yurrita et al. 1999). While this latter species did not prosper, *P. clarkii* soon became naturalized: the absence of filters in the sites of release allowed crayfish to escape and to colonize ditches and canals nearby. Because of their elevated prices, crayfish expansion was accelerated by fishermen, who distributed individuals throughout the entire Guadalquivir marsh zone and the Doñana National Park. This was the first step of its subsequent expansion into the entire Iberian Peninsula, including the Azores, the Balearic, and the Canary Islands, and its contemporary translocation to several other European countries (Figure 1).

Strong economic and social reasons apparently led to the first introduction of *P. clarkii* into Europe. On the one hand, populations of the indigenous species (the noble crayfish, *Astacus astacus*, and the white-clawed crayfish, *Austropotamobius pallipes*) had been greatly reduced in number and distribution due to the so-called crayfish plague. We know today that outbreaks of the plague were caused by different genotypes of the fungus-like *Aphanomyces astaci* (Vogt 1999). The first genotype entered Italy in the 1860s, possibly via infected crayfish being released in ballast waters from a North American ship (Unestam 1973), and the others were repeatedly introduced and spread throughout Europe together with the importation of their natural North American crayfish host species, *Orconectes limosus*, *P. leniusculus*, and *P. clarkii*. On the other hand, there was great demand in the European market for crayfish which were considered a traditional (and healthy) dish in many countries, such as Sweden (Ackefors 1999). So, the first introductions into Spain were helped and even solicited by local institutions striving to ameliorate the low economic

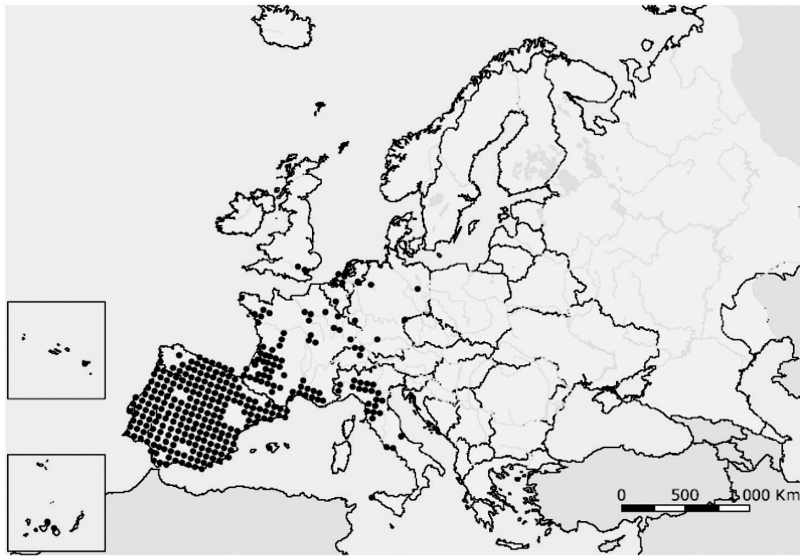


Figure 1. Distribution of *P. clarkii* in Europe denoted by black dots (from Souty-Grosset et al. 2006, under permission).

conditions in those areas. All the legal procedures were followed and respected; there was even the consensus of American experts who previously visited Spain to identify zones appropriate for crayfish introductions (Hasburgo-Lorena 1986). Given that the indigenous *A. pallipes* had never been present in, nor was suited to the areas of introduction, and little was known about the North American crayfish potential to transfer the plague, there was confidence, scientifically supported, that *P. clarkii* would be innocuous to the native stocks of the European crayfish. On the contrary, the North American species, resistant to the plague, could provide large economical benefits to the local populations. Unfortunately, there was no concern in those times about the adverse environmental impact of this potentially invasive species (Geiger et al. 2005). The habit of selling it alive as a food item and as an aquarium pet surely accelerated the successful invasion of this species into natural waters (Henttonen and Huner 1999).

While the first introduction of *P. clarkii* into Spain is well-documented and the rationale is known, there is still much mystery around the rapid spread of *P. clarkii* from the Iberian Peninsula to other European countries. It is, on the contrary, of great practical importance to determine the locality of origin of nonindigenous populations and their route of invasion (Cox 2004). From this knowledge, we can obtain useful information about the vectors and the number of introductions. We can also attempt to halt or slow down the invasion process if it is ongoing.

The advent of molecular genetic techniques is now providing the opportunity for a more detailed description of invasion events. Molecular genetic analysis today provides a very powerful set of tools for characterizing populations of nonindigenous species and for relating them to the populations of their native and invaded ranges (Cox 2004). These techniques have been successfully used to pinpoint the source areas and the routes of dispersal followed by a number of freshwater alien crustaceans (e.g. the cladoceran *Cercopagis pengoi*; Cristescu et al. 2001). It is more difficult to describe the dynamics of human-mediated introductions of invasive species because they often follow unsuspected pathways. Theoretical models of

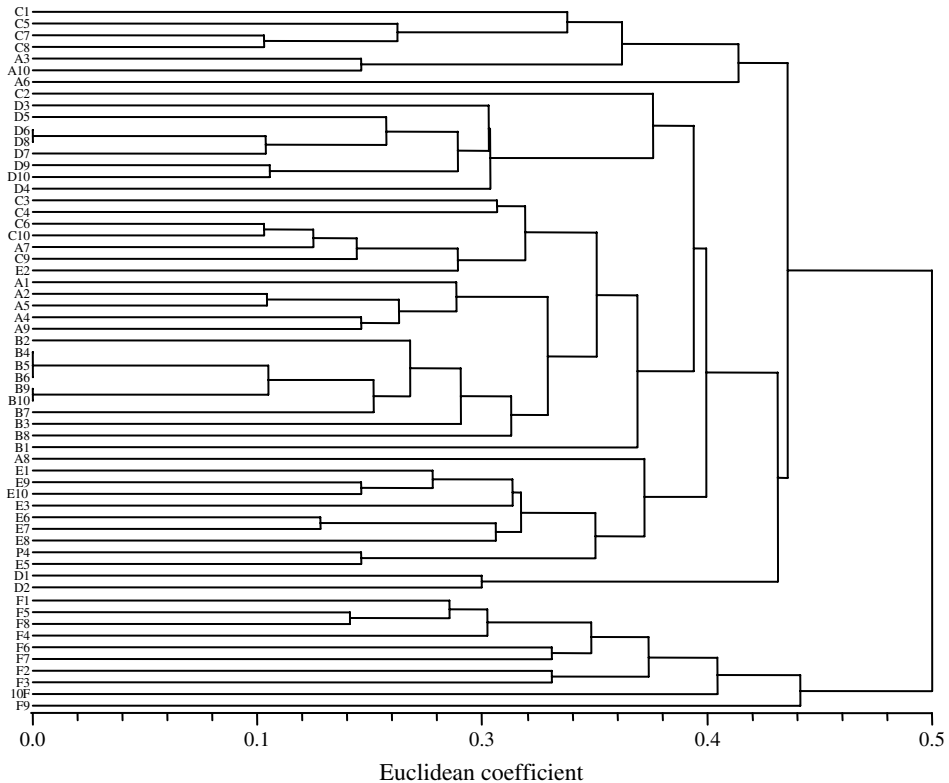


Figure 2. UPGMA dendrogram based on the Euclidean distance between the 60 sampled crayfish. Letters refer to populations and numbers to specimens. A, B, and C are populations from the Tuscan Region (Italy), specifically A refers to the Massaciuccoli Lake population, B to the Fucecchio wetland population, and C to the population inhabiting irrigation ditches in the neighbourhood of Florence; D is a population from Malalbergo in the Emilia-Romagna Region, Italy, and E from Évora, Alentejo (Portugal). F indicates a sample from the native Louisiana (New Orleans, USA), used as the control.

genetic organization and population structure following a founder effect depict two different outcomes: the first model predicts that subpopulations will show strong genetic structuring and clinal genetic variation, while the second model involves extinction and recolonization, which enhance gene flow among subpopulations and reduce interpopulation differentiation (Alvarez-Buylla and Garay 1994).

In a recent study, Barbaresi et al. (2003) used the Random Amplified Polymorphic DNA analysis (RAPD) technique to study five European crayfish populations (three in central Italy, one in northern Italy, and one in southern Portugal), and to compare their genetic structure with a sample from the native Louisiana. The results showed that the genetic diversity in the populations that have recently colonized the different analyzed localities is higher than expected. A simple colonization model would have led to low genetic diversity due to the founder effect, together with a high-population differentiation. On the contrary, the Unweighted Pair Group Method with Arithmetic mean (UPGMA) dendrogram (Figure 2) showed that each population is heterogeneous for its genetic structure, although a certain grouping pattern can be identified. In central Italy, the population of site A (Massaciuccoli Lake) appears to be the most heterogeneous,

supporting the hypothesis that this locality might be the source of the populations in central Italy (Barbaresi and Gherardi 2000). However, site B (Fucecchio wetland) shows a much higher variation than that expected on the basis of a simple derivation from site A, hinting at multiple introductions from different areas. These results, although preliminary, reveal that several populations in Europe are the result of sequential introductions of crayfish from different source areas. This might explain the high genetic diversity observed and also the genetic differentiation among populations (resulting from the casual bias of introductions). While Spain is certainly an important source of red swamp crayfish stocking material, it is becoming clear from other genetic studies (Barbaresi 2003) that commerce in live crayfish from other more distant areas including the Far East, the USA, and Kenya has been also responsible for some of the successful introductions of *P. clarkii* into Italy and other European countries, and that often the motivation for its translocation are different from restocking and cultivation (e.g. the use of live crayfish as food or pets).

***Procambarus clarkii* as a successful invader**

Ecologists often share a pessimistic attitude towards any effort to predict invasions. Predictions, it has been claimed, are the “Holy Grail of invasion biology” (Enserink 1999), whereas the occurrence and timing of most invasions are “as unpredictable as earthquakes” (Williamson 1999). Other authors (e.g. Kolar and Lodge 2001), on the contrary, do acknowledge the role of quantitative studies in delineating the identity of might-be invaders.

Indeed, there is much awareness today that several biological, ecological, and ethological properties predispose a species to become invasive. On the one hand, the knowledge of the biology of a species, even if partial, would tell us a great deal about how life history traits evolve and how biotic communities are assembled. On the other hand, it might reveal the most effective means to prevent or manage future invasions (Mack et al. 2000).

Our experience with *P. clarkii* in Italy, where it first appeared in 1977 (Gherardi et al. 1999), clearly revealed its invasive potential. It exhibits characteristics of an *r*-selected species, including early maturity at small body size (10 g, Paglianti and Gherardi 2004), rapid growth rates (50 g in 3–5 months, Paglianti and Gherardi 2004), large numbers of offspring at a given parental size (a female of an average size producing 400 pleopodal eggs, about four times those produced by a similarly sized *A. pallipes*; L. Aquiloni, unpublished data), and relatively short life spans (Lindqvist and Huner 1999).

It is also characterized by an enhanced plasticity of life cycle (Gutiérrez-Yurrita and Montes 1999; Gutiérrez-Yurrita et al. 1999; Gherardi et al. 1999, 2000) that allows the species to invade a diversity of environments. Its invasive potential is therefore high, and is further enhanced by its dispersal capability. Short- and long-term movements of individual crayfish and their activity were investigated in diverse environmental contexts by radio-telemetry (Gherardi and Barbaresi 2000; Barbaresi et al. 2004b; Aquiloni et al. 2005). The use of this technique allowed us to study individuals continuously and without disturbance, which helps compensate for the disadvantages of small sample sizes imposed by the high cost of the system (Robinson et al. 2000). From radio-telemetric studies, the pattern of movement of *P. clarkii* has been shown to be complex, being composed of phases of high speed of locomotion (nomadic movements) alternated with longer periods of slow or null speed (stationary phases). Particularly in some areas, such as the rice fields, movement can be fast, even exceeding 3 km per day (Gherardi and Barbaresi 2000), and the use of the habitat can be massive.

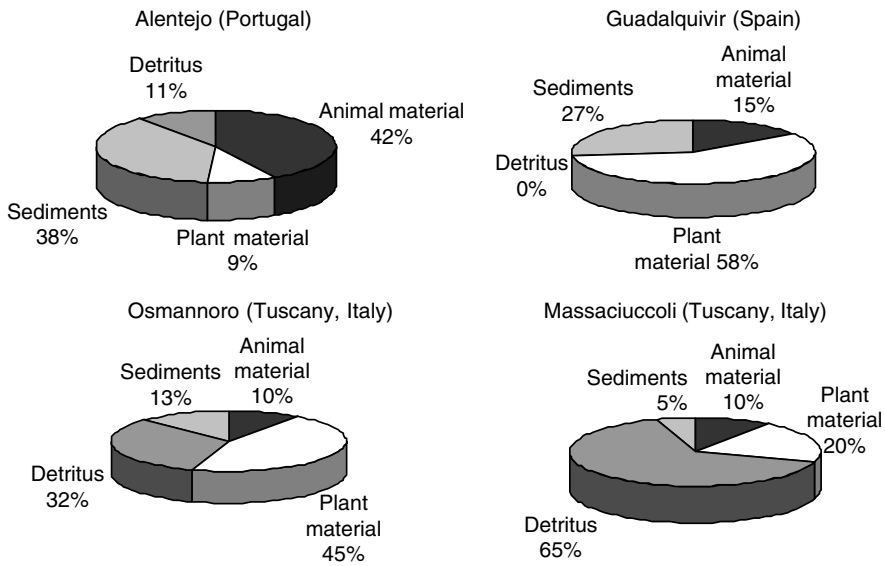


Figure 3. Food items (in %) contained in the gut of 20 *P. clarkii* collected from different sites in Europe. Food was classified into the categories of sediments, detritus, plant material, and animal material.

Procamparus clarkii is highly environment tolerant and adaptable to extreme environments such as temporary streams in southern Portugal (Gherardi et al. 2002c) and polluted habitats (Gherardi et al. 2000). Heavy metals accumulate in its hepatopancreas and exoskeleton at concentrations that exceed those found in other decapods native to Italy (*A. pallipes* and the river crab *Potamon fluviatile*; Gherardi et al. 2002a). The ability of this crayfish to withstand environmental extremes is related to its burrowing activity (Huner and Barr 1984). Barbaresi et al. (2004a) recently showed its “consumerist” use of the banks: the time of burrow occupation is short and crayfish are not faithful to the same burrow (even if they appear capable of homing in the laboratory; Barbaresi and Gherardi 2006). At the end of their foraging excursions they excavate new burrows. On one hand, the intense burrowing activity increases water turbidity with the inhibition of primary production (Rodríguez et al. 2003). On the other, the extreme perforation of banks induces their rapid collapse, often producing damage to agricultural fields (Correia and Ferreira 1995; Huner 2002).

Crayfish in general, and invasive crayfish in particular, display generalist and opportunistic feeding habits (Gutiérrez-Yurrita et al. 1998). Gut content analyses showed that *P. clarkii* feeds on the diverse items present in a given invaded habitat in proportion to their availability and that its diet can change with habitats (Figure 3; F. Gherardi, unpublished data). The negative effect of this species on macrophytes and invertebrates was clearly demonstrated in a 3-wk field study conducted in a shallow oligotrophic lake in Tuscany (Lago della Doccia, Pistoia) (Acquistapace et al. 2006). Twelve cages (bottom area: 0.45 m²) were placed along a 30-m reach exposed to full sunlight from dawn to noon in a randomized block design. Equal biomass of mosquitofish fry (*Gambusia affinis*), snails (*Physa* sp.), and three aquatic macrophytes (*Nymphaoides peltata*, *Potamogeton* sp., and *Utricularia australis*) were introduced into the cages. After a week, adult male crayfish were added to the cages in densities (crayfish × m⁻²) of 0 (as a control), 5, and 10. The results showed that even low densities

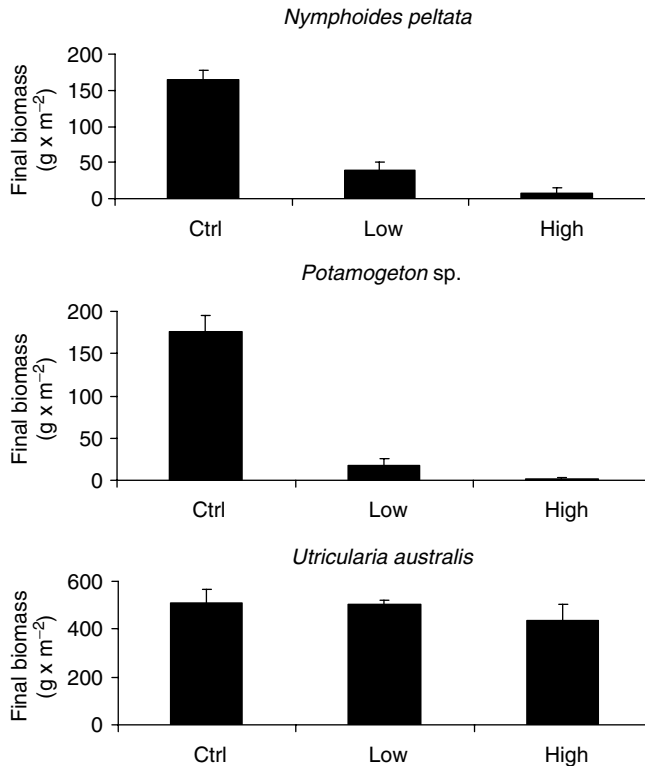


Figure 4. Average final biomass (and SE) of three macrophytes weighed at the end of a 3-wk field study conducted in an oligotrophic lake in Tuscany (Lago della Doccia, Italy) using cages (bottom area: 0.45 m²) that contained no crayfish (ctrl, $n = 3$) and crayfish at the density of 5 (low, $n = 3$) and 10 (high, $n = 3$).

of *P. clarkii* can greatly affect the abundance of some species of submerged macrophytes (*N. peltata* and *Potamogeton sp.*) (Figure 4) and of snails. On the contrary, crayfish had no effect on *U. australis*, possibly because this plant contains some chemicals that make it unpalatable to the crayfish (e.g. Bolser et al. 1998; Nyström 1999). Additionally, the reduction of the macrophyte biomass may not only be due to the direct consumption by crayfish: *P. clarkii* also destroys macrophytes by nonconsumptive cutting of the stems (Nyström and Strand 1996). The crayfish action on macrophytes may lead to the increased water turbidity due to the plankton blooms and resuspended particles, and their selective feeding on plants and animals may be a cause of the progressive reduction of biodiversity in freshwater systems (see also Rodríguez et al. 2003, 2005).

Along with habitat destruction, pollution, and other environmental stressors, the predatory ability of *P. clarkii* may pose an additional threat for species of conservation concern, such as amphibians. In fact, under laboratory conditions *P. clarkii* was shown to consume amphibian larvae more efficiently than the indigenous *A. pallipes* (Gherardi et al. 2001; Renai and Gherardi 2004). Apparently, the deterrent contained in several amphibians is not effective on *P. clarkii*. Similarly, in California, Gamradt and Kats (1996) found that the introduced *P. clarkii* were able to consume *Taricha torosa* larvae, notwithstanding that they contain a tetrodotoxin poison that serves as an effective defence against indigenous crayfish predators. Also, in northern Europe, eggs of the common toad,

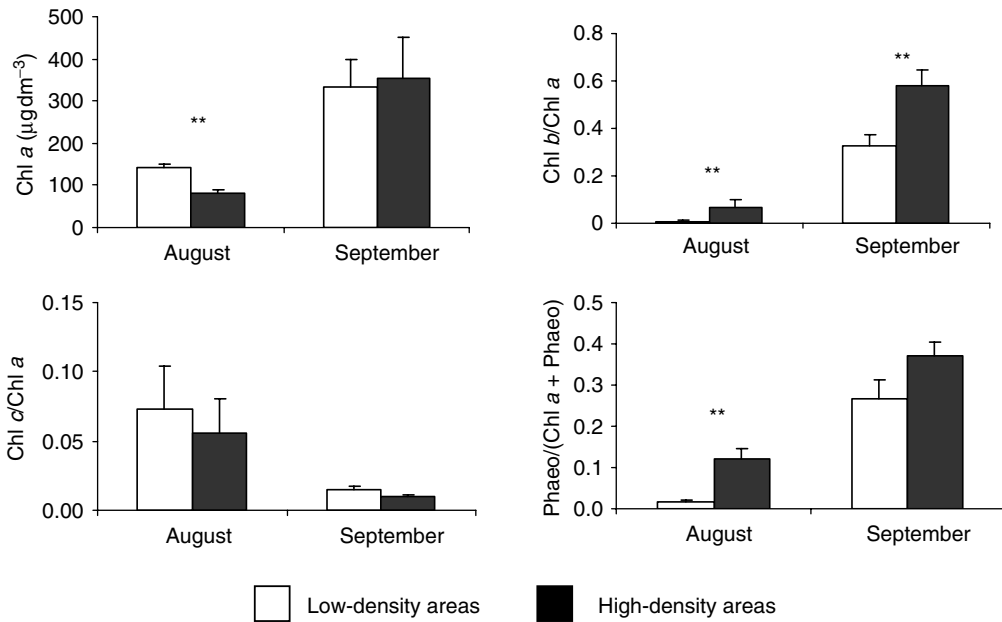


Figure 5. Comparisons between experimental areas and between sampling periods (August and September) in the concentration of chlorophylls (Chl) *a* (a), *b* (b), *c* (c), and phaeopigments (Phaeo) (d) (mean + SE) from a total of eight samples of phytoplankton. Experiments were conducted in six 10 × 7 m areas along a channel in the wetland “Padule di Fucecchio” (Italy). Each of the six areas was randomly chosen to host crayfish populations at either low (1 crayfish m⁻²) or high densities (14 crayfish m⁻²). During August (the period of its more intense foraging activity), the biomass of surface microalgae was strongly affected by the presence of dense populations of the crayfish, chlorophyll *a* and phaeopigments (the products of chlorophyll degradation), showing a significantly lower and higher concentration, respectively, in areas hosting a high, rather than a low, crayfish density. Two asterisks denote a significant difference of at least $P < 0.001$ after nested ANOVA.

Bufo bufo, are unpalatable to newts and predatory insects but are readily consumed by the invasive crayfish *P. leniusculus* (Axelsson et al. 1997). Crayfish populations may also affect the value of a pond as a breeding site for several amphibians, which are dependent on macrophytes as a substrate for eggs and usually breed in habitats with abundant aquatic vegetation (Nyström 1999).

Although laboratory experiments revealed that *P. clarkii* may consume trout fry (Gherardi et al. 2001), the impact that this species has on fish populations in nature remains to be investigated. *Procambarus clarkii*, for instance, may increase the vulnerability of some fish species to predators by evicting them from shelters (Guan and Wiles 1997).

A recent study (Gherardi and Lazzara 2006) unexpectedly proved that the abundance and composition of surface microalgae (Cyanobacteria and euglenoids) are most likely affected by direct top-down effects of crayfish consuming the organically-enriched film at the water surface (Figure 5). This phenomenon might be of importance in littoral zones of lentic water bodies and/or in shallow lakes, and ponds with emergent vegetation, whereas it is probably insignificant in deep and lotic waters. Crayfish are able to accumulate in their tissues the toxins and possibly BMAA (β -*N*-methylamino-L-alanine) produced by cyanobacteria and to transfer them to their predators, humans included, inducing lethal

intoxications (e.g. Carmichael 1988; Cox et al. 2005). Future attention should therefore be paid to examining the mechanisms of crayfish consumption of phytoneuston.

Examples from Sweden, Britain, and Italy have shown that nonindigenous crayfish can replace the indigenous crayfish species by a combination of several interacting mechanisms, including competitive exclusion, differential susceptibility to predation, and reproductive interference (Holdich and Domaniewski 1995; Söderbäck 1995; Gherardi and Cioni 2004). These mechanisms add to the dangers posed by *P. clarkii* as a vector of *A. astaci* (Diéguez-Uribeondo and Söderhäll 1993). Notwithstanding that *P. clarkii* is today more diffused in lentic, rather than in lotic waters, in Italy, mixed populations composed of *P. clarkii* and the endemic decapods inhabitants of streams and rivers (*A. pallipes* and *P. fluviatile*) have been documented in an increasing number of catchments (Gherardi et al. 1999).

In a laboratory study, Gherardi and Cioni (2004) tested the hypothesis that agonistic behavior and interference competition may induce species replacements in freshwater decapods. A first experiment showed that, while river crabs dominated over the two crayfish species, *P. clarkii* outcompeted *A. pallipes*, as expected from field distributions (Figure 6). In nature, the nonindigenous species might even reach higher levels of dominance over *A. pallipes*. In fact, both the larger body size and the “stronger” chelae of *P. clarkii* can induce asymmetries in fighting ability. In a second set of experiments, the agonistic behavior of the three species combinations was studied in the presence of either food or an artificial shelter. Resources clearly influenced fighting, and dominance translated into a differential capability to compete. In a competitive-free context, shelters were more extensively occupied by *A. pallipes* (which is dependent on natural crevices as hiding places) than by *P. clarkii* (which usually digs burrows). So, *P. clarkii*, which gained less from occupying the offered shelter than *A. pallipes*, was expected to defend it less vigorously. On the contrary, the presence of a rival strengthened its attraction to the shelter, reproducing the behavior shown in the presence of the other North American species *P. acutus acutus* (Gherardi and Daniels 2004).

Finally, several laboratory experiments proved the wide behavioral flexibility of *P. clarkii* when coping with new types of predators. This species appeared to use a broader range of information about increased predation risk than native species, reacting more strongly to heterospecific alarm cues (Hazlett et al. 2003). Assuming that the quick detection of alarm substances alerts an animal to the presence of a predator and hence increases its probability of avoiding it, this ability might contribute to the success of the species in new environments that may contain novel predators. As a confirmation, *P. clarkii* showed that it is capable of learning and remembering associations between different predation-risk cues. When trained to associate a novel cue (i.e. goldfish odor) with predation risk following pairing with conspecific alarm odor, individuals of the invasive species remembered that association longer than *A. pallipes* did (Acquistapace et al. 2003). However, “alarm” substances were found to stimulate feeding-related activities in *P. clarkii* cultivated in aquaculture ponds (Acquistapace et al. 2004). This phenomenon suggests that this crayfish, once reared in an environment where predation risks are reduced, can respond differently to cues that in more risky habitats inform of danger and further underlines the extreme flexibility of the behavior of this species.

All these studies demonstrate that *P. clarkii* should be added to the ever lengthening list of species that have invaded European fresh waters. It is, in fact, a “nonindigenous species that spreads from the point of introduction and becomes abundant” (Kolar and Lodge 2001), but it is also an alien species “which becomes established in natural or semi-natural ecosystems or habitats, is an agent of change, and threatens native biological diversity”

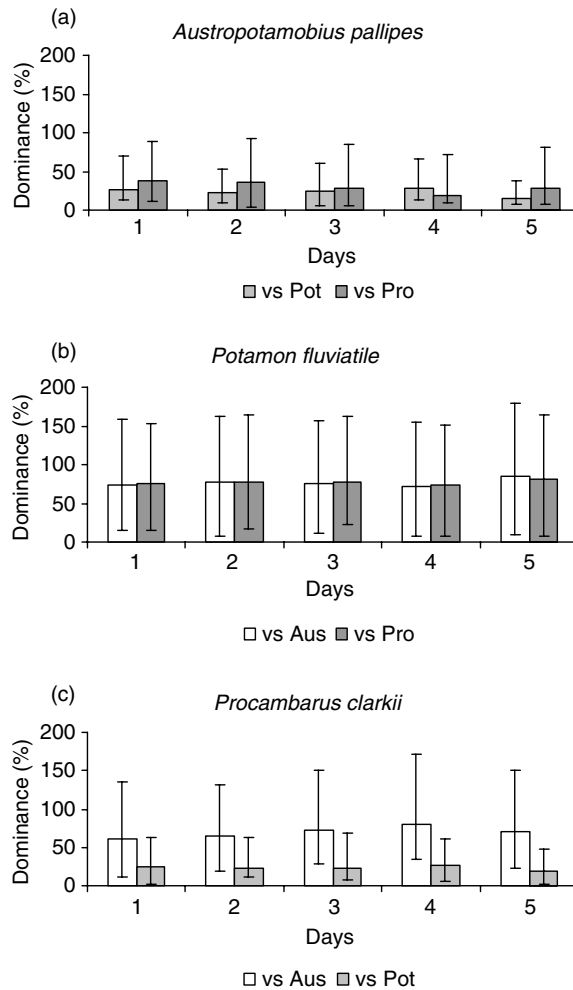


Figure 6. Median values (and interquartile ranges) of dominance (victories over the total number of fights battled in percentage) by each analyzed decapod species (*A. pallipes*, Aus; *P. clarkii*, Pro; *P. fluviatile*, Pot) over the two rival species throughout five days of combat. Dominance remained constant with time in every species combination ($P > 0.1$). Dominance by *P. clarkii* was significantly lower when opposed to *P. fluviatile* than to *A. pallipes* ($P < 0.002$). On the contrary, dominance by *A. pallipes* ($P > 0.1$) and by *P. fluviatile* ($P > 0.1$) was independent of the rival species.

(IUCN 2000) and “whose introduction does or is likely to cause economic or environmental harm or harm to human health” (Executive Order 13112, Clinton 1999).

Today, research is mainly directed to exploring the methods for controlling this nuisance species. Ideally, these methods should be safe for the environment and for humans, inexpensive, and justifiable to the public (Holdich et al. 1999b). Unfortunately, several attempts to date to reduce the impact of *P. clarkii* and of the other invasive crayfish in Europe, *P. leniusculus* (e.g. Frutiger and Müller 2002; Stebbing et al. 2003), have failed, suggesting that, once this species is established, eradication may be impossible, and that mitigation and control are difficult and expensive. Preventing the introduction of potentially

invasive species is, therefore, “the only environmentally sound approach” (Gollasch and Leppäkoski 1999).

Sometimes, it is even difficult to justify the need of decision makers to contain the spread of these species and to mitigate the environmental risks they pose. In fact, a number of issues have been raised in favor of the outcomes of their introduction (Gherardi et al. 2002b). First, in the absence of indigenous species, invasive crayfish were claimed to occupy vacant niches, constituting the unique large macro-consumer within highly “stressed” habitats (Gherardi et al. 2000). They can also be, it has been said, the unique macro-grazer, for instance *P. leniusculus* in Swedish and Finnish lakes where they help keep water bodies clear from the overgrowth of water plants and recycle energy, inorganic, and organic material (Ackefors 1999). The second claim is that they constitute abundant prey for rare or threatened birds and mammals. Though no quantitative study has been yet made, the appearance of high densities of *P. clarkii* has been considered responsible for the increase in the number of avian species, like the Ardeidae *Botaurus stellaris*, *Egretta garzetta*, and *Ardea purpurea*, together with cormorants, in some European areas, as in the Massaciuccoli Lake (Tuscany) and Ebro region (Spain) (Barbaresi and Gherardi 2000; Rodríguez et al. 2005). In Doñana National Park it has become the most common prey category of the otter, *Lutra lutra* (Delibes and Adrian 1987).

Third, from a socio-economic perspective, the introduction of nonindigenous crayfish was assumed to have contributed to: (1) the restoration of traditional habits, e.g., by crayfishing in Sweden and Finland (Kirjavainen and Sipponen 2004), (2) economic benefits for local crayfishermen, e.g. the Spanish netmen, (3) diversification of agriculture to include astaciculture, e.g. by crayfish farmers in Britain and in Spain, and (4) increased trade between countries inside Europe as well as between European countries and countries outside Europe (Ackefors 1999).

Conclusions

Moyle et al. (1986) held that deliberate introductions of nonindigenous species are often made to solve some local or regional problems, but, if the broad-scale consequences of each introduction are not considered, they may ultimately cause more problems than they solve. They described this as the Frankenstein Effect: attempts to improve on nature – in Mary Shelley’s story (1818) Count Frankenstein attempted to create an improved human – may turn out to be a monster. So, the introduction of *P. clarkii* into Europe adds to the many examples of this phenomenon already told by invasion biologists (Holdich et al. 1999a).

This retrospective analysis of the story of invasion by *P. clarkii* shows that several life-history traits (early maturity, rapid growth, large number of offspring, and plastic life cycle) and biological features (tolerance to extreme environments, dispersal, polyphagy, predatory and competitive ability, and behavioral flexibility) predispose this species to spread and to become invasive. Can these results be used to generalize about the invasive potential of crayfish, and to predict the identity of future Frankensteins? Indeed, invasion is a multifactorial process, and the identification of species characteristics is only one component that might explain its potential success. The others include traits of the locality of introduction (e.g. disturbance, anthropogenic impacts, available resources, or the so-called empty niches), the interaction between species and environment that accounts for habitat and climate match, and propagule pressure (i.e. size and number of initial populations) (Ruesink 2005). Furthermore, several confounding variables may hamper any predictive effort, such as the natural variability of the environment in space and time,

synergistic effects of other established invaders, and the variable time lag between initial introduction and detectable impact (Gherardi 2006a). This means that generalizations cannot be made from a single case study, and predictions cannot be based on experiments and observations conducted at small temporal and spatial scales. However, a recent review of the crayfish literature has shown that the scientific interest in crayfish is increasing, and that quantitative methods are developing rapidly (Gherardi 2006b). There is therefore the hope that the intensification of scientific research on crayfish today may soon lead to a broader understanding of invasions in this taxon, providing the quantitative data needed to predict future crayfish invaders and, therefore, to reduce their occurrence and impact.

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References

- Ackefors H. 1999. The positive effects of established crayfish. In: Gherardi F, Holdich DM, editors. Crayfish in Europe as alien species. How to make the best of a bad situation? Rotterdam: A.A. Balkema. pp 49–61.
- Acquistapace P, Cacchiani A, Gherardi F. 2006. The impact of the introduced crayfish *Procambarus clarkii* on a lake community in Tuscany. *Biologia Ambientale* 20:45–47.
- Acquistapace P, Hazlett BA, Gherardi F. 2003. Unsuccessful predation and learning of predator cues by crayfish. *J. Crustacean Biol.* 23:364–370.
- Acquistapace P, Daniels WH, Gherardi F. 2004. Behavioral responses to “alarm odors” in potentially invasive and non-invasive crayfish species from aquaculture ponds. *Behaviour* 141:691–702.
- Alvarez-Buylla ER, Garay AA. 1994. Population genetic structure of *Cecropia obtusifolia*, a tropical pioneer tree species. *Evolution* 48:437–453.
- Anastácio PM, Correia AM, Menino JP. 2005a. Processes and patterns of plant destruction by crayfish: Effects of crayfish size and developmental stages of rice. *Arch. Hydrobiol.* 162:37–51.
- Anastácio PM, Parente VS, Correia AM. 2005b. Crayfish effects on seeds and seedlings: Identification and quantification of damage. *Freshwat. Biol.* 50:697–704.
- Aquiloni L, Ilhéu M, Gherardi F. 2005. Habitat use and dispersal of the invasive crayfish *Procambarus clarkii* in ephemeral water bodies of Portugal. *Mar. Freshw. Behav. Physiol.* 38:225–236.
- Axelsson EP, Nyström P, Didenmark J, Brönmark C. 1997. Crayfish predation on amphibian eggs and larvae. *Amphibia-Reptilia* 18:217–228.
- Barbaresi S. 2003. Biological invasions in fresh water: *Procambarus clarkii* as a case study. PhD Dissertation, University of Florence, Italy.
- Barbaresi S, Fani R, Gherardi F, Mengoni A, Souty-Grosset C. 2003. Genetic variability in European populations of an invasive American crayfish: Preliminary results. *Biol. Invas.* 5:269–274.
- Barbaresi S, Gherardi F. 2000. The invasion of the alien crayfish *Procambarus clarkii* in Europe, with particular reference to Italy. *Biol. Invas.* 2:259–264.
- Barbaresi S, Gherardi F. 2006. Experimental evidence for homing in the red swamp crayfish, *Procambarus clarkii*. *Bull. Franç. Pêche Piscic.* 380–381:1145–1154.
- Barbaresi S, Tricarico E, Gherardi F. 2004a. Factors inducing the intense burrowing activity by the red swamp crayfish, *Procambarus clarkii*, an invasive species. *Naturwissenschaften* 91:342–345.
- Barbaresi S, Tricarico E, Santini G, Gherardi F. 2004b. Ranging behaviour of the invasive crayfish, *Procambarus clarkii*. *J. Nat. Hist.* 38:2821–2832.
- Beisel J-N. 2001. The elusive model of a biological invasion process: Time to take differences among aquatic and terrestrial ecosystems into account? *Ethol. Ecol. Evol.* 13:193–195.
- Blake MA. 1995. The vulnerability of juvenile signal crayfish to perch and eel predation. *Freshwat. Biol.* 33:233–244.
- Bolser RC, Hay ME, Lindquist N, Fenical W, Wilson D. 1998. Chemical defenses of freshwater macrophytes against crayfish herbivory. *J. Chem. Ecol.* 24:1639–1658.

- Carmichael WW. 1988. Toxins of freshwater algae. In: Tu AT, editor. Handbook of Natural Toxins, Vol. 3, Marine Toxins and Venoms. New York: Marcel Dekker. pp. 121–147.
- Charlebois PM, Lamberti GL. 1996. Invading crayfish in a Michigan stream: Direct and indirect effects on periphyton and macroinvertebrates. *J. North Am. Benthol. Soc.* 15:551–563.
- Clinton WJ. 1999. Executive Order 13112. Invasive species. Washington, DC: The White House.
- Correia AM, Ferreira O. 1995. Burrowing behavior of the introduced red swamp crayfish *Procambarus clarkii* (Decapoda: Cambaridae) in Portugal. *J. Crustacean Biol.* 15:248–257.
- Covich AP, Palmer MA, Crowl TA. 1999. The role of benthic invertebrate species in freshwater ecosystems. *BioScience* 49:119–127.
- Cox GW. 2004. Alien species and evolution. Washington, DC: Island Press.
- Cox PA, Banack SA, Murch SJ, Rasmussen U, Tien G, Bidigare RR, Metcalf JS, Morrison LF, Codd GA, Bergman B. 2005. Diverse taxa of cyanobacteria produce β -N-methylamino-L-alanine, a neurotoxic amino acid. *Proc. Nat. Acad. Sci. USA* 102:5074–5078.
- Cristescu MEA, Hebert PDN, Witt JDS, MacIsaac HJ, Grigorovich IA. 2001. An invasion history for *Cercopagis pengoi* based on mitochondrial gene sequences. *Limnol. Oceanogr.* 46:224–229.
- Cronin G, Lodge DM, Hay ME, Miller M, Hill AM, Horvath T, Bolser RC, Lindquist N, Wahl M. 2002. Crayfish feeding preferences for freshwater macrophytes: The influence of plant structure and chemistry. *J. Crustacean Biol.* 22:708–718.
- Crooks JA. 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos* 97:153–166.
- Delibes M, Adrian I. 1987. Effects of crayfish introduction on otter *Lutra lutra* food in the Doñana National Park, SW Spain. *Biol. Cons.* 42:153–159.
- Diéguez-Uribeondo J, Söderhäll K. 1993. *Procambarus clarkii* Girard as a vector for the crayfish plague fungus, *Aphanomyces astaci* Schikora. *Aquacult. Fish. Manag.* 24:761–765.
- Enserink M. 1999. Biological invaders sweep in. *Science* 285:1834–1836.
- Ewel JJ, O'Dowd DJ, Bergelson J, Daehler CC, D'Antonio CM, Gomez D, Gordon DR, Hobbs RJ, Holt A, Hopper KR, Hughes CE, Lahart M, Leakey RRB, Lee WG, Loope LL, Lorence DH, Louda SM, Lugo AE, Mcevoy PB, Richardson DM, Vitousek PM. 1999. Deliberate introductions of species: Research needs. *BioScience* 49:619–630.
- Feminella JW, Resh VH. 1989. Submersed macrophytes and grazing crayfish: An experimental study of herbivory in a Californian freshwater marsh. *Holarc. Ecol.* 12:1–8.
- Frutiger A, Müller R. 2002. Controlling unwanted *Procambarus clarkii* populations by fish predation. *Freshw. Crayfish* 13:309–315.
- Gamradt SC, Kats LB. 1996. Effect of introduced crayfish and mosquito fish on California newts (*Taricha torosa*). *Cons. Biol.* 10:1155–1162.
- Geiger W, Alcorlo P, Baltanas A, Montes C. 2005. Impact of an introduced Crustacean on the trophic webs of Mediterranean wetlands. *Biol. Invas.* 7:49–73.
- Gherardi F. 2000. Are non-indigenous species 'ecological malignancies'? *Ethol. Ecol. Evol.* 12:323–325.
- Gherardi F. 2006a. The impact of freshwater NIS: What are we missing? In: Gherardi F, editor. *Biological invaders in inland waters: Profiles, distribution, and threats*. Invading Nature: Springer Series in Invasion Ecology. Dordrecht: Springer (In press).
- Gherardi F. 2006b. Understanding the impact of invasive crayfish. In: Gherardi F, editor. *Biological invaders in inland waters: Profiles, distribution, and threats*. Invading Nature: Springer Series in Invasion Ecology. Dordrecht: Springer (In press).
- Gherardi F, Baldaccini GN, Barbaresi S, Ercolini P, De Luise G, Mazzoni D, Mori M. 1999. The situation in Italy. In: Gherardi F, Holdich DM, editors. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema. pp 107–128.
- Gherardi F, Barbaresi S. 2000. Invasive crayfish: Activity patterns of *Procambarus clarkii* in the rice fields of the Lower Guadalquivir (Spain). *Arch. Hydrobiol.* 150:153–168.
- Gherardi F, Barbaresi S, Vaselli O, Bencini A. 2002a. A comparison of trace metal accumulation in indigenous and alien freshwater macro-decapods. *Mar. Freshw. Behav. Physiol.* 35:179–188.
- Gherardi F, Cioni A. 2004. Agonism and interference competition in freshwater decapods. *Behaviour* 141:1297–1324.
- Gherardi F, Daniels WH. 2004. Agonism and shelter competition between invasive and indigenous crayfish species. *Can. J. Zool.* 82:1923–1932.
- Gherardi F, Holdich DM, editors. 1999. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema.

- Gherardi F, Lazzara L. 2006. Effects of the density of an invasive crayfish (*Procambarus clarkii*) on pelagic and surface microalgae in a Mediterranean wetland. *Arch. Hydrobiol.* 165:401–414.
- Gherardi F, Raddi A, Barbaresi S, Salvi G. 2000. Life history patterns of the red swamp crayfish, *Procambarus clarkii*, in an irrigation ditch in Tuscany, Italy. *Crustacean Issues* 12: 9–108.
- Gherardi F, Renai B, Corti C. 2001. Crayfish predation on tadpoles: A comparison between a native (*Austropotamobius pallipes*) and an alien species (*Procambarus clarkii*). *Bull. Franç. Pêche Piscicult.* 361:659–668.
- Gherardi F, Smietana P, Laurent P. 2002b. Interactions between non-indigenous and indigenous crayfish species. *Bull. Franç. Pêche Piscicult.* 367:899–907.
- Gherardi F, Tricarico E, Ilhéu M. 2002c. Movement patterns of an invasive crayfish, *Procambarus clarkii*, in a temporary stream of southern Portugal. *Ethol. Ecol. Evol.* 14:183–197.
- Gollasch S, Leppäkoski E. 1999. Initial risk assessment of alien species in Nordic coastal waters – Nord 1999:8. Copenhagen: Nordic Council of Ministers.
- Guan R-Z, Wiles PR. 1997. Ecological impact of introduced crayfish on benthic fishes in a British lowland river. *Cons. Biol.* 11:641–647.
- Gutiérrez-Yurrita P, Montes C. 1999. Bioenergetics and phenology of reproduction of the introduced red swamp crayfish, *Procambarus clarkii*, in Doñana National Park, Spain, and implications for species management. *Freshw. Biol.* 42:561–574.
- Gutiérrez-Yurrita PJ, Martínez JM, Bravo-Utrera MÁ, Montes C, Ilhéu M, Bernardo JM. 1999. The status of crayfish populations in Spain and Portugal. In: Gherardi F, Holdich DM, editors. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema. pp 161–192.
- Gutiérrez-Yurrita PJ, Sancho G, Bravo MÁ, BaltanásÁ, Montes C. 1998. Diet of the red swamp crayfish *Procambarus clarkii* in natural ecosystems of the Doñana National Park temporary fresh-water marsh (Spain). *J. Crustacean Biol.* 18:120–127.
- Hasburgo-Lorena AS. 1986. The status of the *Procambarus clarkii* population in Spain. *Freshw. Crayfish* 6:131–136.
- Hazlett BA, Burba A, Gherardi F, Acquistapace P. 2003. Invasive species use a broader range of predation-risk cues than native species. *Biol. Invas.* 5:223–228.
- Henttonen P, Huner JV. 1999. The introduction of alien species of crayfish in Europe: A historical introduction. In: Gherardi F, Holdich DM, editors. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema. pp 13–30.
- Hobbs Jr HH. 1972. Biota of freshwater ecosystems, identification manual 9: Crayfishes (Astacidae) of North and Middle America. *Water Pollution Control Research Series*. Washington DC: US Environmental Protection Agency.
- Hobbs III HH, Jass JP, Huner JV. 1989. A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). *Crustaceana* 56:299–316.
- Holdich DM, Ackefors H, Gherardi F, Rogers WD, Skurdal J. 1999a. Native and alien crayfish in Europe: Some conclusions. In: Gherardi F, Holdich DM, editors. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema. pp 281–292.
- Holdich DM, Domaniewski JCJ. 1995. Studies on a mixed population of the crayfish *Austropotamobius pallipes* and *Pacifastacus leniusculus* in England. *Freshwat. Crayfish* 10:37–45.
- Holdich DM, Gydemo R, Rogers WD. 1999b. A review of possible methods for controlling nuisance populations of alien crayfish. In: Gherardi F, Holdich DM, editors. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema. pp 245–270.
- Horwitz P. 1990. The translocation of freshwater crayfish in Australia: Potential impact, the need for control and global relevance. *Biol. Conserv.* 54:291–305.
- Huner JV. 1977. Introductions of the Louisiana red swamp crayfish, *Procambarus clarkii* (Girard): An update. *Freshw. Crayfish* 3:193–202.
- Huner JV. 2002. *Procambarus*. In: Holdich DM, editor. *Biology of freshwater crayfish*. Oxford: Blackwell. pp 541–584.
- Huner JV, Avault Jr JW. 1979. Introductions of *Procambarus* spp. *Freshw. Crayfish* 4:191–194.
- Huner JV, Barr JE. 1984. *Red swamp crayfish: Biology and exploitation*. Baton Rouge, Louisiana: Louisiana Sea Grant College Program.
- IUCN. 2000. IUCN guidelines for the prevention of biodiversity loss caused by alien invasive species. Auckland, New Zealand: Species Survival Commission (SSC), Invasive Species Specialist Group (ISSG).
- Jerscke JM, Strayer DL. 2005. Invasion success of vertebrates in Europe and North America. *Proc. Nat. Acad. Sci. USA* 102:7198–7202.

- Kirjavainen J, Sipponen M. 2004. Environmental benefit of different crayfish management strategies in Finland. *Fish. Manag. Ecol.* 11:213–218.
- Kolar CS, Lodge DM. 2001. Progress in invasion biology: Predicting invaders. *Trends Ecol. Evol.* 16:199–204.
- Lindqvist OV, Huner JV. 1999. Life history characteristics of crayfish: What makes some of them good colonizers?. In: Gherardi F, Holdich DM, editors. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema. pp 23–30.
- Lodge DM, Lorman JG. 1987. Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. *Can. J. Fish. Aquat. Sci.* 44:591–597.
- Lodge DM, Kershner MW, Aloï JE, Covich AP. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology* 75:1265–1281.
- Lodge DM, Stein RA, Brown KM, Covich AP, Bronmark C, Garvey JE, Klosiewski SP. 1998. Predicting impact of freshwater exotic species on native biodiversity: Challenges in spatial scaling. *Aust. J. Ecol.* 23:53–67.
- Lodge DM, Taylor CA, Holdich DM, Skurdal J. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: Lessons from Europe. *Fisheries* 25:7–20.
- Luttenton MR, Horgan MJ, Lodge DM. 1998. Effects of three *Orconectes* crayfish on epilithic microalgae: A laboratory experiment. *Crustaceana* 71:845–855.
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol. Applic.* 10:689–710.
- McKinney ML, Lockwood JL. 1999. Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14:450–453.
- Moyle PB, Li HW, Barton BA. 1986. The Frankenstein Effect: Impact of introduced fishes on native fishes in North America. In: Strond RH, editor. *Fish culture in fisheries management*. Bethesda: American Fisheries Societies.
- Nyström P. 1999. Ecological impact of introduced and native crayfish on freshwater community: European perspectives. In: Gherardi F, Holdich DM, editors. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema. pp 63–85.
- Nyström P. 2002. Ecology. In: Holdich DM, editor. *Biology of freshwater crayfish*. Oxford: Blackwell Science. pp 192–235.
- Nyström P, Brönmark C, Granéli W. 1996. Patterns in benthic food webs: A role for omnivorous crayfish? *Freshwat. Biol.* 36:631–646.
- Nyström P, Strand JA. 1996. Grazing by a native and an exotic crayfish on aquatic macrophytes. *Freshwat. Biol.* 36:673–682.
- Nyström P, Svensson O, Lardner B, Brönmark C, Granéli W. 2001. The influence of multiple introduced predators on a littoral pond community. *Ecology* 82:1023–1039.
- Paglianti A, Gherardi F. 2004. Combined effects of temperature and diet on growth and survival of YOY crayfish: A comparison between indigenous and invasive species. *J. Crustacean Biol.* 24:140–148.
- Pérez JR, Carral JM, Celada JD, Sáez-Royuela M, Munoz C, Sierra A. 1997. Current status of astaciculture production and commercial situation of crayfish in Europe. *Aquaculture Europe* 22:6–13.
- Rahel FJ. 2000. Homogenization of fish faunas across the United States. *Science* 288:854–856.
- Renai B, Gherardi F. 2004. Predatory efficiency of crayfish: Comparison between indigenous and non-indigenous species. *Biol. Invas.* 6:89–99.
- Ricciardi A, Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. *Cons. Biol.* 13:1220–1222.
- Robinson CA, Thom TJ, Lucas MC. 2000. Ranging behaviour of a large freshwater invertebrate, the white-clawed crayfish *Austropotamobius pallipes*. *Freshw. Biol.* 43:509–521.
- Rodríguez CF, Bécares E, Fernández-Aláez M, Fernández-Aláez C. 2005. Loss of diversity and degradation of wetlands as a result of introducing exotic crayfish. *Biol. Invas.* 7:75–85.
- Rodríguez CF, Bécares E, Fernández-Aláez M. 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.
- Ruesink JL. 2005. Global analysis of factors affecting the outcome of freshwater fish introductions. *Cons. Biol.* 19:1883–1893.
- Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sannwald E, Huenneke L, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH. 2000. Biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Shelley MW. 1818. Frankenstein, or the Modern Prometheus. In: Butler M, editor. 1994. Oxford: Oxford University Press.

- Slater FM, Rayner G. 1993. *Austropotamobius pallipes* in otter diet in the mid-Wye catchment of central Wales. *Freshwat. Crayfish* 9:365–367.
- Söderbäck B. 1995. Replacement of the native crayfish *Astacus astacus* by the introduced species *Pacifastacus leniusculus* in a Swedish lake: Possible causes and mechanisms. *Freshw. Biol.* 33:291–304.
- Souty-Grosset C, Holdich DM, Noël PY, Reynolds JD, Haffner P, editors. 2006. Atlas of Crayfish in Europe. Paris: Muséum national d'Histoire naturelle (Patrimoines naturels, 64).
- Stebbing PD, Watson GJ, Bentley MG, Fraser D, Jennings R, Rushton SP, Sibley PJ. 2003. Reducing the threat: The potential use of pheromones to control invasive signal crayfish. *Bull. Franç. Pêche Piscicult.* 370–371:219–224.
- Svärdson G. 1965. The American crayfish *Pacifastacus leniusculus* (Dana) introduced into Sweden. Report of the Institute of Freshwater Research, Drottningholm 46:90–94.
- Svärdson G, Hammar J, Nyberg P, Degerman E. 2001. Human impact on the fish diversity in the four largest lakes of Sweden. *Ambio* 30:522–528.
- Taugbøl T, Skurdal J. 1999. The future of native crayfish in Europe: How to make the best of a bad situation?. In: Gherardi F, Holdich DM, editors. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema. pp 271–279.
- Unestam T. 1973. Significance of diseases in freshwater crayfish. *Freshw. Crayfish* 2:136–150.
- Vogt G. 1999. Diseases of European freshwater crayfish, with particular emphasis on interspecific transmission of pathogens. In: Gherardi F, Holdich DM, editors. *Crayfish in Europe as alien species. How to make the best of a bad situation?* Rotterdam: A.A. Balkema. pp 87–103.
- Whitledge GW, Rabeni CF. 1997. Energy sources and ecological role of crayfishes in an Ozark stream: Insights from stable isotopes and gut analysis. *Can. J. Fish. Aquat. Sci.* 54:2555–2563.
- Williamson M. 1996. *Biological invasions* London: Chapman & Hall.
- Williamson M. 1999. Invasions. *Ecography* 22:5–12.
- Williamson M, Fitter A. 1996. The varying success of invaders. *Ecology* 77:1666–1670.