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CRAYFISH

FRANCESCA GHERARDI
University of Florence

There are over 600 species of crayfish in the world, taxonomically organized into two superfamilies, Astacoidea in the northern hemisphere with the two families of Cambaridae and Astacidae, and Parastacoidea in the southern hemisphere with the single family of Parastacidae. Although quite large, crayfish native diversity is unequally distributed across the world. Over 380 species occur in the nearctics, and 150 are found in the Australasian ecoregion, but only about 60, 30, and 10 occur in the neotropical, palaearctic, and Afrotropical ecoregions, respectively. Crayfish are naturally absent from the Antarctic continent, continental Africa, and much of Asia and South America, while Europe has only five native species. Superimposed on this natural distribution, however, is one orchestrated by humans and is the product of a massive translocation of species between and within continents.

A HISTORY OF CRAYFISH INTRODUCTION

Crayfish introduction has a long story: even the distribution of species of current conservation concern seems to owe much to human intervention. For instance, as suggested by historical records and genetic studies, the European *Austropotamobius pallipes*, now protected under the EU Habitats Directive, was introduced into Ireland from France by monastic orders in the twelfth century. During the last few decades, however, the human-aided movement of nonindigenous crayfish species (hereafter referred to as NICS) has increased as a result of the exponential growth in the volume and complexity of international trade. Ten and 21 crayfish species have been introduced outside their native ranges between and within continents, respectively (Table 1), but most introductions are of six species now widely diffused in the world (*Astacus leptodactylus*, *Cherax destructor*, *Orconectes limosus*, *Orconectes rusticus*, *Pacifastacus leniusculus*, and *Procambarus clarkii*); one of them, *P. clarkii*, accounts for over 40 percent of all introduction events recorded (56).

In some cases, introductions have been accidental (e.g., through ballast, canals, escapes from holding facilities), but the majority of them have been deliberate (for aquaculture and both legal and illegal stocking, for live food trade, as aquarium pets, as live bait, for snail and weed control, and as supplies for science classes). Some were driven by narrow objectives: *P. clarkii*, for instance, was imported to Japan in 1927 as a food for the bullfrog, *Rana catesbeiana*. Sometimes, on the contrary, introductions were intended to ameliorate human conditions: in Africa many releases into the wild of *P. clarkii* from the 1960s onward were aimed at controlling freshwater snails that carry human schistosomiasis. Most often, however, crayfish introductions were motivated by our desire to eat them, which in turn generates economic interests and stimulates further human-assisted dispersal; *C. destructor*, for instance, after its first introduction to Western Australian farm dams for aquaculture in 1932, rapidly spread, now threatening the over ten endemic crayfish species of this state. A handful of other species are highly valued as gourmet food, and in locations such as Scandinavia and Louisiana, feasting on them has become a cultural icon. As a consequence, some NICS are commercially harvested from wild stocks or have become aquaculture commodities in countries such as Australia, China, and the United States. The aquarium and pond trade has been another powerful vector of NICS; it represents a great threat to regions, such as southern Europe, where the climate is today amenable to species from tropical regions—and it will be more so in the near future with the projected global warming. Finally, the use of live bait has also aided the spread of NICS, particularly in North America in the case of *O. rusticus*.

Indeed, some introductions may have provided socioeconomic benefits. However, once introduced for stocking and aquaculture and kept in outdoor ponds, crayfish almost inevitably escape and easily establish self-sustaining populations in the colonized habitats. Because of their ability to integrate into the food web at many levels and to travel long distances even overland, a large majority of the naturalized populations have the potential to become noxious and to spread widely from their points of introduction. Additions of crayfish species may significantly affect the structure of freshwater food webs, which ultimately affect ecosystem services and, as a consequence, human well-being.

INVASIVE CRAYFISH OF THE WORLD

Crayfish species that today cause major concern in the recipient areas include the Ponto-Caspian *A. leptodactylus* in some European countries, the Australian *C. destructor*

TABLE 1
Crayfish Species Moved between or within Continents outside Their Native Ranges

Family	Species	Common Name	From	To
Astacidae	*Astacus astacus* (Linnaeus)	Noble crayfish	Europe	Africa, Europe
	Astacus leptodactylus (Eschscholtz)	Narrow-clawed crayfish	Asia, Europe	Asia, Europe
	Austropotamobius pallipes (Lereboullet)	White-clawed crayfish	Europe	Europe
	Pacifastacus gambelii (Girard)	Pilose crayfish	N. America	N. America
	Pacifastacus leniusculus leniusculus (Dana)	Signal crayfish	N. America	Asia, Europe, N America
	Pacifastacus leniusculus trowbridgii (Stimpson)	Columbia River signal crayfish	N. America	N. America
Cambaridae	*Cambarus longirostris* (Faxon)	Atlantic slope crayfish	N. America	N. America
	Cambarus rusticiformis (Rhoades)	Depression crayfish	N. America	N. America
	Orconectes causeyi (Jester)	Western plains crayfish	N. America	N. America
	Orconectes immunis (Hagen)	Calico crayfish	N. America	Europe, N. America
	Orconectes juvenilis (Hagen)	Kentucky river crayfish	N. America	Europe
	Orconectes limosus (Rafinesque)	Spinycheek crayfish	N. America	Africa, Europe, N. America
	Orconectes neglectus neglectus (Faxon)	Ringed crayfish	N. America	N. America
	Orconectes palmeri creolanus (Creaser)	Creole painted crayfish	N. America	N. America
	Orconectes rusticus (Girard)	Rusty crayfish	N. America	N. America
	Orconectes sanbornii (Faxon)	Sanborn's crayfish	N. America	N. America
	Orconectes virilis (Hagen)	Virile crayfish	N. America	Europe, N. America
	Procambarus sp.	Marbled crayfish	N. America	Africa, Europe
	Procambarus acutus (Girard)	White river crawfish	N. America	N. America
	Procambarus clarkii (Girard)	Red swamp crawfish	N. America	Africa, Asia, Europe, C., N. and S. America
	Procambarus zonangulus (Hobbs and Hobbs)	Southern white river crawfish	N. America	N. America
Parastacidae	*Cherax destructor* (Clark)	Yabby	Oceania	Europe, Oceania
	Cherax quadricarinatus (von Martens)	Redclaw	Oceania	Africa, Asia, C., N. and S. America
	Cherax tenuimanus (Smith)	Marron	Oceania	Oceania

NOTE: After Hobbs, et al., 1998; Souty-Grosset, et al., 2006; Taylor, et al., 2007; and Gherardi, 2010.

in Africa and Western Australia, and four North American species: *O. limosus* in Europe, *O. rusticus* in the midwestern United States and Canada, *P. leniusculus* in California, Europe, and Japan, and *P. clarkii* in Africa, California, Europe, and Japan (Figs. 1 and 2). Other species, such as the Australian *Cherax quadricarinatus* in South America and the parthenogenetic North American "marbled crayfish" (*Procambarus* sp.) in Europe and Madagascar, are expected to generate problems in the near future.

Illustrative in this respect is the story of the human-assisted movement of the red swamp crayfish, *P. clarkii*, one of the 100 worst invasive species in Europe. This species occurs naturally in northeastern Mexico and in the south-central United States, extending westward to Texas, eastward to Alabama, and northward to Tennessee and Illinois. It has been extensively cultivated since the 1950s in the southern United States, reaching a maximum production of 3,000 kg ha^{-1}. Because of its commercial value, it has been introduced into several U.S. states; its current range now includes the east and west coasts and extends northward into the states of Idaho and Ohio. Outside the continental United States, *P. clarkii* has been successfully introduced to Hawai'i, western Mexico, Costa Rica, the Dominican Republic, Belize, Brazil, Ecuador, Venezuela, Japan, mainland China, Taiwan, the Philippines, Egypt, Uganda, Kenya, Zambia, South Africa, Israel, and several European countries. Strong economic and social reasons apparently led to its first introduction to a European country, Spain, in 1973. This introduction

FIGURE 1 Invasive crayfish species of the world (in clockwise order from top left): *Astacus leptodactylus*, *Cherax destructor*, *Cherax quadricarinatus*, and *Orconectes limosus*. (Photographs courtesy of Chris Lukhaup.)

was even solicited by local institutions striving to satisfy, with a "plague-resistant" species, the large demand of crayfish by the European market. The native crayfish production, in fact, had been drastically reduced since the mid-1800s by the spread of the oomycete *Aphanomyces astaci*, the causative agent of a lethal disease for indigenous species, the "crayfish plague." All the legal procedures were followed and respected; there was even the consensus of American experts who had previously visited Spain to identify zones appropriate for crayfish introduction. Because the native *A. pallipes* had never been present in nor was suited to the areas of introduction, and because its potential to transfer *A. astaci* was unknown, there was confidence that *P. clarkii* would be innocuous to the native stocks and would provide great economic benefits to the local population. The habit of selling it alive as a food item or as an aquarium pet accelerated the successful invasion of this species into natural waters. However, the exact trajectory of its rapid spread across Europe is still unknown; recent genetic studies even suggest that multiple introductions have occurred since the 1970s from source areas other than Spain or Louisiana, including the Far East and Kenya.

THE SUCCESS OF CRAYFISH INVADERS

Once added to a system, some NICS have the potential to pose considerable environmental stress, and in most instances, they may induce irreparable shifts in species diversity. In areas without any native ecological equivalent, the changes caused by NICS introductions usually affect all levels of ecological organization. The modes of resource acquisition by crayfish and their capacity to develop new trophic relationships, coupled with their action as bioturbators, may lead to dramatic direct and indirect ecosystem effects.

When NICS replace native crayfish, their ecological effects should not be novel to the colonized community, and so the resulting impact is expected to be weak. But their overall effect can be strong if, once introduced, they are capable of building high densities or achieving large size. Several NICS often reach much higher densities than native crayfish: more than 70 m^{-2} for *O. limosus* in Poland, over 20 m^{-2} for *O. rusticus* in North America,

FIGURE 2 Invasive crayfish species of the world (in clockwise order from top left): *Orconectes rusticus*, *Pacifastacus leniusculus*, the "marbled crayfish" (*Procambarus* sp.), and *Procambarus clarkii*. (Photographs courtesy of Chris Lukhaup.)

and 30 m^{-2} for *P. leniusculus* in the United Kingdom. On the contrary, reported densities of the native species range from 1 m^{-2} for *Pacifastacus fortis* in California to 3 m^{-2} for *Paranephrops planifrons* in New Zealand, 4 m^{-2} for *Cambaroides japonicus* in Japan, and 14 m^{-2} for *Astacus astacus* in Sweden.

Several biological traits contribute to the achievement by crayfish of high densities and large size. Compared to native crayfish, some NICS are characterized by higher fecundity (more than 500 pleopodal eggs in *P. clarkii*), protracted spawning periods, faster growth rates (50 g in three to five months in *P. clarkii*), and maturity reached at relatively small size (10 g in *P. clarkii*). They are also extremely plastic in their life cycle and are 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 and dry conditions in burrows; it tolerates elevated turbidity and a wide range of water temperatures and salinities. A higher survival rate is also expected when a species is introduced without a full complement of specific parasites, pathogens, and enemies. And large sizes, in turn, make crayfish both resistant to gape-size limited predators (such as many fishes) and agonistically superior in resource fights. As a consequence, NICS exert a greater direct (through consumption) or indirect (through competition) effect on the other biota, particularly on other crayfish species, benthic fishes, mollusks, and macrophytes. Invasive crayfish seem also to be affected by the so-called aggression syndrome that makes them highly abundant and active at the same time, despite the elevated intraspecific aggression exhibited. Obviously, large size usually translates into a higher energy and nutrient demand, but NICS may also be more efficient energy converters and may display higher metabolic rates when compared with similarly sized native species.

ECOLOGICAL IMPACTS

The negative impact that invasive crayfish inflict on the environment occurs at multiple levels of ecological organization. NICS may outcompete or prey upon native species, eventually leading to their extirpation and, in at least one case, extinction. For instance, the ability of *P. leniusculus* to outcompete fishes by expelling individuals from their shelters, making them more vulnerable to predators, has contributed to the drastic reduction in abundance of *Cottus gobio* and *Noemacheilus barbatulu* in some rivers of England. Similarly, its heavy predatory pressure upon the eggs of the newt *Taricha torosa*, despite their antipredator chemical defense (tetrodotoxin), allowed *P. clarkii* to extirpate this species from some streams in southern California. Competition and predation, coupled with reproductive interference, enhance the effects of habitat loss, overexploitation, and pollution in inducing a dramatic decline of crayfish diversity. Of the 67 threatened crayfish species in North America, for instance, over 5 percent are subject to interference competition by NICS. Along with urbanization and overexploitation, *P. leniusculus* has contributed to the global extinction of the crayfish *Pacifastacus nigrescens*, once common in the creeks of the San Francisco Bay area; in northeastern California, it is now displacing the Shasta crayfish, *P. fortis*. Similarly, the European native species *A. astacus*, *A. pallipes*, and *A. torrentium* are threatened by *A. astaci*, introduced to Europe via the North American NICS. To make things worse, the parasite does not require its host in order to spread; the spores can be transported on damp surfaces (e.g., on fishing equipment), as is thought to have triggered the crayfish plague outbreak in central Ireland in 1986. Hybridization with invaders is an additional threat for native crayfish species. In Wisconsin, hybrids between the invader *O. rusticus* and the native *O. propinquus* were found to mate with pure *O. rusticus*, which leads to a massive genetic introgression of nuclear DNA from the native to the invasive species and thus to the gradual elimination of *O. propinquus* genes from the population.

At the community level, NICS exert direct and indirect effects on invaded ecosystems. Their intense grazing on aquatic macrophytes, coupled with nonconsumptive plant clipping and uprooting, induces a significant decline in plant abundance. Macrophyte destruction is generally followed by a switch from a clear to a turbid state, dominated by surface microalgae growth with consequent reduction in light penetration and decrease in primary production of benthonic plants.

The biomass and species richness of macroinvertebrates are altered by NICS as the result of consumption, increased drift through prey escape, incidental dislodging by their foraging, and possible inhibition of invertebrate colonization. Mollusks are the taxon most affected: some gastropod species, particularly thin-shelled snails, have sometimes been extirpated. Crayfish predation is weak only on species that move quickly enough to escape tactile-feeding crayfish (e.g., amphipods) and that live in cases (e.g., Trichoptera) or in the sediment (e.g., some Diptera). Through consumption of macrophytes and detritus, crayfish may also lead, indirectly, to the decline of macrophyte-associated taxa, particularly collector-gatherers, while their predation upon other zoobenthic predators such as Odonata larvae causes an increased abundance of their prey. Finally, NICS can be prey items for a large number of fish, bird, and mammal species, such as eels, storks, herons, egrets, and otters, thus representing a new resource for higher trophic levels in the areas of introduction.

At the ecosystem level, NICS may alter pathways of energy flow by augmenting connectance by feeding at several trophic levels and increasing the availability of autochthonous carbon as a food source for higher trophic levels. The intense NICS burrowing activity and locomotion often result in bioturbation: water quality is impoverished, light penetration and plant productivity are reduced, and the benthic community is affected by changes in the riverbed substrate.

EFFECTS ON HUMAN WELL-BEING

Introduction of NICS has sometimes been assumed to have benefited human societies by, fore example, restoring cultural traditions such as crayfishing (in Sweden), producing economic benefits in poorly developed areas (in southern Spain), inducing the development of extensive or semi-intensive cultivation systems (in China), and increasing the volume of international trade (in Spain).

Several examples, however, show that often the introduction of commercially valuable crayfish has also led to negative results in the marketplace. In Scandinavia, Germany, Spain, and Turkey, the plague led to a loss of over 90 percent in the production of *A. astacus* and *A. leptodactylus*, with considerable economic damage. For instance, when the plague spread to Turkey in the 1980s, the annual catch of *A. leptodactylus* plunged from 7,000 to 2,000 tons, nearly eliminating exports from Turkey to Western Europe. In Africa, very few of the several projects that led to crayfish importations have been successful: in Lake Naivasha, Kenya, only about 40 metric tons of *P. clarkii* are now fished annually for exclusive local consumption (mainly tourism), while crayfish spoil valuable fish species and damage fish nets.

NICS may affect other human activities: *P. clarkii* is a recognized pest in rice cultures in various parts of the world, causing a decrease in profits that amounts to over 6 percent in, for example, Portugal. Burrowing by several species can be a problem in agricultural and recreational areas, such as lawns, golf courses, levees, dams, dykes, and canal irrigation systems, and in rivers and lakes, where NICS may destabilize the banks. The nonmarket economic damage of NICS, owing to their impact on biodiversity, seems to be enormous. For instance, the restitution of *P. fortis* in California cost $4.5 million, and the (unsuccessful) eradication of *P. leniusculus* in Scotland cost about £100,000.

Little attention has been paid until now to the harm that NICS pose to human health. Invasive crayfish often live in areas contaminated by sewage and toxic industrial residues and have high heavy metal concentrations in their tissues. Their potential to transfer contaminants to their consumers, humans included, is obviously high. The finding that *P. leniusculus* and *P. clarkii* may also accumulate toxins produced by cyanobacteria is of increasing concern for human health; *P. clarkii* is also suspected to be an intermediate host for many helminth parasites of vertebrates and a vector of transmission of the bacterium *Francisella tularensis*, the causative agent of human tularemia.

On the other hand, *P. clarkii* may control snails known to host *Schistosoma* spp., the agents of human schistosomiasis. Owing to the quick spread of this crayfish in African water bodies, the epidemiology of schistosomiasis is expected to be significantly altered with time, although the possibility remains that African snails will soon evolve measures to avoid crayfish predation or that the parasite will change its host.

PREVENTION, MANAGEMENT, AND EDUCATION

The "three-stage hierarchical approach" (prevention, early detection/rapid response, and containment/control), recommended by the Convention on Biological Diversity for the management of invasive species, applies well to NICS. The first stage, prevention, is particularly critical in this case. NICS, in fact, can be hard to detect and can disperse rapidly, making eradication or control extremely difficult and expensive. Much effort should therefore be directed at minimizing the risks of intentional and unintentional introductions, as is attempted by the current legislation of some countries. For instance, in the United Kingdom, *A. astacus*, *A. leptodactylus*, and *P. leniusculus* have been designated as pests under the Wildlife and Countryside Act; much of Britain has been declared a no-go area for keeping *P. leniusculus*, and the whole of Britain for keeping all other NICS (except the tropical *C. quadricarinatus*). Similarly, in Japan, *Astacus* spp., *Cherax* spp., *O. rusticus*, and *P. leniusculus* have been classified as invasive alien species under the Invasive Alien Species Act; their import and live keeping are banned except for scientific purposes. In the EU, Council Regulation No 708/07 "concerning use of alien and locally absent species in aquaculture" has been in force since 2007; its novelty is to take a "white list" approach: only the importation of species that have been appropriately screened after a thorough risk assessment analysis can be approved is allowed. This contrasts with the homologous regulation in the United States, which permits the importation of species unless they are on a "black list" (classified as "injurious wildlife species" by the U.S. Fish and Wildlife Service). The above restrictions on import of NICS for aquaculture use, however, seem not to be well harmonized with the legislation concerning the aquarium trade. NICS, such as the parthenogenetic marbled crayfish, are easy to buy for ornamental use, particularly via e-commerce. Finally, illegal importations of NICS are very difficult to police, and their accidental introductions as, for instance, contaminants of fish stockings are common.

Several attempts have been made in different countries to eradicate or to control invasive populations of NICS, and experimentation on different methods is under way. Independently of the method adopted, however, a high rate of failures has generally been lamented. Mechanical removal using baited traps of various design or electrofishing has had some effect only when conducted for an extended period of time, which means considerable cost and human-power; besides, the prevalent removal of large and dominant individuals from the population might reduce their pressure on juveniles that are usually trap-shy, thus allowing them to grow and to give rise to even larger populations. Drainage of ponds, diversion of rivers, and construction of barriers (either physical or electrical) may also be used in the case of confined crayfish populations, but very little is known about their efficacy. Biocides, including organophosphate, organochlorine, pyrethroid insecticides, rotenone, and surfactants, lack specificity: other invertebrates may be eliminated along with crayfish, and, except for natural biocides (such as derivatives of pyrethrum), toxin bioaccumulation and biomagnification in the food chain are likely. Other solutions lie in recourse to two autocidal methods already used with success against insect pests and now under investigation for the control of the *P. clarkii* populations in Italy—the use of sex pheromones and the sterile male release technique (SMRT); both, although expensive, cause no environmental contamination or nontarget impacts. Traditional biological control methods include the use of fish predators, disease-causing organisms (e.g., engineered strains of *A. astaci*), and microbes that produce toxins, such as strains of the bacterium *Bacillus thuringiensis*. Only the introduction of predaceous fish species, however, has provided some positive results, for example in Switzerland; eels, burbot, perch, and pike are well known predators of crayfish, but they are usually gape-size limited, preying only on small crayfish; in some instances, the presence of fish predators induces a change in the behavior of crayfish by reducing their trophic activity and increasing the time spent in shelter. But it is the combination of different methods, such as intensive trapping and an induced increase in predation pressure, that can be followed by some success against invasive NICS. In Sparkling Lake (Wisconsin), *O. rusticus* was mechanically removed from 2001 to 2005, and the harvest of fish species known to consume crayfish was restricted. As a result, crayfish catch rates declined by 95 percent, from 11 crayfish per trap per day in 2002 to 0.5 crayfish in 2005, and the native community showed a slow but steady recovery.

Whatever method is used, however, any intervention against NICS should be based on a thorough understanding of their threats by the general public, decision-makers, and other stakeholders. On the contrary, as recently shown in southern Spain, most stakeholders seem to have a limited knowledge of the nature of invasive species, and have varied perceptions of their impacts and different attitudes toward their introduction or eradication. Education and public awareness campaigns seem thus to be indispensable prerequisites for developing shared responsibility in solving the problems generated by these invaders.

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CRUSTACEANS (OTHER)

ANTHONY RICCIARDI

McGill University

Crustaceans (phylum Arthropoda: subphylum Crustacea) are among the aquatic animals most widely introduced by humans. Their geographic spread is driven by activities such as local and transoceanic shipping, the construction of canals, aquaculture, and the aquarium trade. Although the impacts of most of crustacean invasions are unknown, dozens of nonindigenous species have been observed to be ecologically or economically disruptive—particularly in freshwater and estuarine systems, where they can reduce native biodiversity, alter food webs, and modify the physical structure of habitats. Economic impacts have also been incurred due to biofouling (e.g., by barnacles), damage to river banks and pier pilings by burrowing species (e.g., crayfish, the Chinese mitten crab *Eriocheir sinensis*, the Australasian isopod *Sphaeroma quoyanum*), declines of commercially important fisheries resulting from food web disruptions (e.g., by mysids), and direct predation on cultured bivalves (e.g., by green crabs).

GLOBAL PREVALENCE OF CRUSTACEAN INVADERS

Most large freshwater and coastal marine systems worldwide have been invaded by crustaceans such as amphipods (Amphipoda), mysid shrimp (Mysida), waterfleas (Cladocera), and copepods (Copepoda), among other groups. At least 40 nonindigenous crustaceans have invaded European inland and coastal waters, 70 have invaded North American coastal areas, and 30 have invaded New Zealand coastal areas. Intercontinental transfers of species are common; for example, an African freshwater cladoceran (*Daphnia lumholtzi*) has invaded North American lakes, North American crayfishes have invaded European and African rivers, and Eurasian amphipods, cladocerans,