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Invasive crayfish and freshwater fishes of the world

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Summary

After habitat destruction, invasive alien species are the second leading cause of biodiversity loss, particularly in freshwater ecosystems. They also alter the structure and functioning of ecosystems, lead to biotic homogenisation, and eventually threaten human economies and health. This review aims to synthesise some of the existing information about the world distribution, vectors of spread, and impacts of two important components of freshwater ecosystems, crayfish and fishes. Analysis of the available literature shows that crayfish and fish species, once moved outside their native range, are likely to establish self-reproducing populations, spread from the point of introduction and become invasive. Efforts to manage these populations are difficult and expensive, which warrants the provision of effective preventative measures. Unfortunately, the state of our knowledge of the mechanisms in play in crayfish and fish invasions is still limited, which suggests that much greater attention and investment should be directed to studies in this field.

Keywords

Biological invasion – Crayfish – Freshwater fish – Inland water – Introduction – Translocation – Vector.

Introduction

Invasive alien species are amongst the world's most significant, least controlled, and least reversible causes of impact on the planet's ecosystems (e.g. 45). Particularly threatened are inland waters, which are now suffering a rate of biodiversity loss (63, 24) that even matches that of tropical forests (60). Obviously, this generates concern. Rivers, lakes, freshwater marshes, and other inland wetlands are of infinite value to humankind. They contribute 20% (about US$6.6 trillion) to the estimated annual global value of the entire biosphere (15). High-quality water has also become a strategic factor that allows for the viability and development of an increasing number of countries affected by both climate change and rising water demand.

The high susceptibility of inland waters to species invasions is principally the result of a thousand years of human exploitation of these waterways for food, commerce, and recreation (55). The common carp (*Cyprinus carpio*), for instance, which is widespread today, was introduced into Western Europe approximately 2,000 years ago and was most probably facilitated by the Romans and later by monastic activities (14). Even the distribution of species that are today regarded as native to a given region seems to owe much to human intervention. For instance, historical records and genetic studies (67) suggest that the crayfish *Austropotamobius pallipes*, which is now protected under the European Union (EU) Habitats Directive, seems to have been moved to Ireland from France by monastic orders in the 12th Century. In more recent times, the introduction of freshwater animal alien species, mainly fishes, intensified after the mid-19th Century under the promotion of the 'acclimatisation' societies' (societies which introduced species with the purpose of 'enriching' environments that were considered 'deficient'; they were particularly popular with European colonists, who introduced familiar species into their new environments) (14). It is, however, the exponential growth in the volume and complexity of the international trade of the 20th Century that led to a sharp increase in the overall number of freshwater species moved by humans across the world (30).

The vulnerability of inland waters to invasive alien species depends on many factors, including the higher intrinsic dispersal ability of freshwater species compared with terrestrial organisms (2) and the strong impact of both human disturbance (61) and altered seasonal temperature regimes (18). The ability of today's aquatic species to circumvent natural barriers, following the various pathways artificially built by human activities, highly threatens the many endemisms and local adaptations that have characterised freshwater communities for millennia (56).

This review attempts to summarise the current knowledge about the distribution, vectors of spread, and impacts of alien crayfish and fishes, two taxa that are important components of freshwater communities. Here, alien species are defined as species that do not occur naturally in a given area; instead, their introduction into that area is mediated or facilitated directly or indirectly by humans, whether deliberately or unintentionally. The pathways of introduction range from shipping (via ship hulls and in ballast water or sediments) to biocontrol, aquaculture, aquarium trade, and stock enhancement (29). Invasive alien species are alien species that spread, with or without the aid of humans, in natural habitats and produce significant changes in the composition of communities and in ecosystem processes, or cause severe economic losses to human activities and threats to human health.

Crayfish and fish on the move

The existing inventories of alien crayfish and fish species at both global (37, 41) and regional scale (29, 30, 67) support the idea that the world's fresh waters have been extensively subject to invasions by these taxa. Alien species include species imported from other ecoregions or continents (introduced species) and species that have been introduced into drainage areas belonging to the same continent or ecoregion (translocated species). Movements of marine fish are much rarer than those of freshwater fish but they do occur: the Banggai cardinalfish (*Pterapogon kauderni*), for example, which was once only found in the waters around the Banggai islands, has also become established in the Lembeh Strait (a popular diving area) after having been introduced by tropical fish enthusiasts.

Out of the 644 described crayfish species, only 28 (about 4%) have established self-reproducing populations outside their native range. Of these, 9 (1.4%) have been introduced into a new ecoregion and 19 (2.9%, including four species subject also to introductions) have been translocated within the native ecoregion (Table I). Over all, seven of the introduced/translocated species (1.1%) show scientifically proven invasive potential. Of the crayfish species known to have been introduced outside their native country, a single species, *Procambarus clarkii*, accounted for over 40% of the 57 introduction events recorded (28). The Nearctic ecoregion has the largest number of described native crayfish species in the world, and it is the area that has been least subject to introductions (if we exclude Antarctic and Australasian ecoregions), with only *Cherax quadricarinatus* introduced into Mexico. Events of translocation, however, are many and involve at least four invasive species (*Orconectes limosus, O. rusticus, Pacifastacus leniusculus*, and *P. clarkii*). The Palaearctic ecoregion, containing relatively few native species, has been subject to the largest number of introductions/translocations, including six invasive species. This is clearly shown in Europe, where there are almost twice as many alien crayfish species as there are native species (9 vs. 5; 67).

Table I
Number and type of crayfish species per ecoregion

Ecoregion	Native spp.	Introduced spp.	Translocated spp.	Invasive spp.
Afrotropical	9 (1)	3 (2)	0	*Procambarus clarkii, Procambarus* sp.
Antarctic	0	0	0	
Australasian	151 (9)	0	2 (1)	*Cherax destructor*
Nearctic	382 (12)	1 (1)	16 (4)	*Orconectes limosus, O. rusticus, Pacifastacus leniusculus, Procambarus clarkii*
Neotropical	64 (7)	2 (2)	0	*Cherax destructor, Procambarus clarkii*
Oriental	0	2 (2)	0	*Procambarus clarkii*
Pacific Oceanic Islands	0	2 (1)	0	*Cherax destructor*
Palaearctic	38 (6)	8 (4)	3 (2)	*Astacus leptodactylus, Cherax destructor, Orconectes limosus, Pacifastacus leniusculus, Procambarus* sp., *Procambarus clarkii*
Total number of species	**644**	**18**	**21**	**7**

Source: native species (16); introduced and translocated species (28, 37, 67, 68)
The number of genera is in parentheses; the most widely spread species are underlined

Table II
Global freshwater fish introductions* (10)

Donor areas	Recipient areas							
	Africa	Asia	EU	F-USSR	North and Central America	South America	Oceania	Total
Africa	49	12	2	2	9	4	3	81
Asia	20	70	14	18	24	9	27	182
EU	31	24	60	6	11	8	9	149
F-USSR	0	9	19	22	8	0	0	58
North and Central Americas	23	34	29	8	69	29	25	217
South America	2	6	4	1	21	13	8	55
Oceania	0	8	1	0	1	0	18	28
Unknown	40	194	95	74	79	46	67	595
Total	**165**	**357**	**224**	**131**	**222**	**109**	**157**	**1,365**

* Since records began until 2004
EU: European Union
F-USSR: Former Union of Soviet Socialist Republics

Much more numerous are the human-aided movements of freshwater fishes (Table II, data from FishBase, after 10). The introduced species totalled 568 (from 104 families) in 2006 (with a total of 3,072 events of introduction), representing approximately 4.5% of the described species (12,740; 43). About 50% (1,674 in 2006) of the overall events of introduction were followed by the establishment of self-reproducing populations in the wild (10). The most widely introduced species with a high success of establishment (Table III, data from the United Nations Food and Agriculture Organization [FAO] Database on Introductions of Aquatic Species, after 22) constituted less than 2% of the introduced species, but accounted for about 30% of the introduction events (22). Invasion hotspots, in which alien fishes represent more than a quarter of the fish diversity per basin, have been identified on the Pacific coast of North and Central America, southern South America, western and southern Europe, Central Eurasia, South Africa and Madagascar, and southern Australia and New Zealand (41). These areas are also characterised by the highest proportion of fish species having a high risk of extinction, thus raising concern about the conservation of native assemblages. Introductions and translocations of fish species have been particularly numerous at the European scale: fishes constitute 32% of a total of 296 introduced freshwater animal species and 43% of a total of 136 translocated freshwater animal species (30) (Fig. 1). No European country seems to be immune to the colonisation of alien fish but their diversity varies widely across Europe, ranging from four species in Iceland to 129 in Ukraine. At the country level, alien fishes can constitute a considerable proportion of the total number of fish, with peaks that reach 45% in Spain (33 aliens versus 40 natives) and 46% in Italy (38 aliens versus 44 natives) (14, 29).

Table III
Most frequently introduced fish species in the world (22, modified)

Species	Number of countries in which the species has been introduced	Number of countries in which the species has become established	Percentage of introduction events that have had an impact
Oreochromis mossambicus	172	148	81
Cyprinus carpio	124	102	86
Oncorhynchus mykiss	99	53	88
Ctenopharyngodon idella	91	10	60
Hypophthalmichthys molitrix	79	21	75
Oreochromis niloticus	78	55	75
Gambusia spp.	67	65	50
Micropterus salmoides	64	47	86
Aristichthys nobilis	55	11	80
Carassius auratus	54	50	75

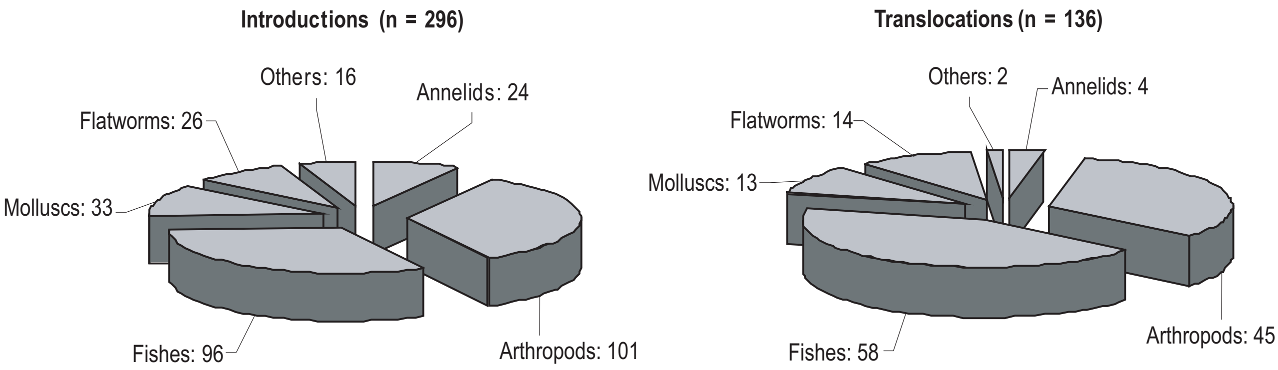

Fig. 1
Frequency per taxon of the animal alien species recorded in European inland waters: introduced and translocated species (30)

The human-aided movement of fish species is even more widespread if we count the many translocation events between geographically distinct drainage basins within each country, such as in southern European peninsular countries (Spain, Portugal, Italy, western Balkans, Greece), the British Isles, Russia, Canada, and the United States. Indeed, freshwater fish translocations have been so common in some countries (e.g. Italy) for so long (numerous decades if not centuries) that it is difficult in some cases to determine the natural post-glacial ranges of some species (14). For example, eight decades of translocations in Italy (totalling approximately 11.9 billion fishes from 32 species, of which 16 were native) resulted in several endemic species, such as the alpine bleak (*Alburnus arborella*), spined loach (*Cobitis taenia*) and lasca (*Chondrostoma genei*), achieving nearly pan-Italian distributions (4).

The distribution of crayfish and fishes, both native and alien, and the composition of freshwater communities are also heavily subject to the impact of climate change, as already documented in the last two decades in five lakes of Wisconsin (74). Unfortunately, to date, there is still poor scientific knowledge about the effects on freshwater ecosystems of altered thermal and streamflow regimes, reduced ice cover, increased salinity, and other correlates of climate change, such as increased water development activities (5). We expect, for instance, that many warm-water species, which were introduced for aquaculture or for the aquarium trade (e.g. the Australian crayfish *C. quadricarinatus* and catfish *Ictalurus punctatus*) and which escaped from captive-breeding facilities, will be able to establish self-reproducing populations in temperate regions. Similarly, it is thought that species able to survive desiccation by burrowing, such as the globally invasive *P. clarkii*, will better cope than native species with the expected prolonged droughts. Milder winters will increase the survival of invaders, such as smallmouth bass (*Micropterus dolomieu*) and walleye (*Sander vitreum*) in some North American drainage basins, and prolong their growing seasons, ultimately magnifying their impact on native prey (reference in 57). The effects of climate change may be even more pervasive when we consider that many native species will shift their geographic distributions and eventually become invasive (36). Finally, some management options increasingly adopted to preserve threatened species, such as the so-called 'assisted migration', may produce additional threats to native biodiversity, since the assisted species might in turn become invasive and negatively affect the taxa native to the recipient region.

The establishment of globally spread aliens, which are associated with the eventual extirpation of endemic species, is often followed by 'biotic homogenisation', a phenomenon leading to the loss by disparate biota of their biological distinctiveness at various levels of organisation, including their genetic, taxonomic, and functional characteristics (51). Homogenisation is well illustrated by the comparison of fish faunas from widely separated countries in different zoogeographic regions, e.g. Sweden in the Palaearctic ecoregion, the United States in the Nearctic ecoregion, and New Zealand in the Australasian ecoregion (56). Sweden and the United States historically had six freshwater fish species in common, Sweden and New Zealand zero, and the United States and New Zealand zero; now each pair of countries shares a total of 16, 9, and 15 species, respectively. As a group, the three countries had no species in common but now share eight species. Even within the same ecoregions, movement of organisms across basin divides has contributed to the process of homogenisation (56). Across the United States, for instance, the average similarity of fish faunas among states has increased by 7%, and pairs of states now share 15% more species on average than they did prior to European colonisation of North America (55). Even higher is the similarity of fish species among basins affected by a more extensive introduction of species, such as those in the Iberian Peninsula (11) and California (48), with an increase of 17% and 20%, respectively, in the overlap of fish fauna across regions.

The first step of the invasive process: introduction

To become invasive, a species must take three sequential steps, (i) introduction, (ii) establishment, and (iii) spread. To pass the first step, a species should be taken by a transport pathway and should be deposited, alive, in a receptive area outside its native range. Several human activities are responsible for the transport of crayfish and fish species. Interestingly, the inadvertent dispersal in ships' ballast and as hull fouling, which is one of the main pathways for other aquatic organisms (33), is less frequent for these taxa: of the 59 freshwater fish species introduced into North America, for instance, only five followed these pathways (56). The transport of the large majority of crayfish and fishes is, on the contrary, associated with purposive modes of dispersal, with crayfish and fish sometimes being contaminants of the transported commodity.

Many introductions/translocations of species were intended for the development of fisheries and for angling via stock enhancement. Stocking new species was in fact a common practice in the 1960s and 1970s, particularly in Europe. This was aimed at promoting fishery diversity to counterbalance the perceived decline in the status of many native species (72). It was also accompanied by the introduction of large quantities of crustaceans, in particular amphipods, to increase commercial fish production (30). Several introduced species were contaminants of licensed fish consignments (e.g. top-mouth gudgeon, *Pseudorasbora parva*, accidentally imported from Asia in 1960 to a pond in Romania as a contaminant of various Chinese carp species [*Ctenopharyngodon idella, Hypophthalmichthys molitrix*, and *Aristichthys nobilis*]; references in 14) or hosted parasites (e.g. the Platyhelminth *Gyrodactylus salaris*). In the European part of the former Soviet Union (Belarus, Estonia, Latvia, Lithuania, Moldova, Russia, and Ukraine), fish release (under the historical term of 'acclimatisation') was even encouraged by the government. In the 1960s/1970s, there was a dramatic increase in the number of fish introduced, involving up to 400 translocations into up to 370 water bodies each year. Large quantities of crustaceans from the Ponto-Caspian region were also moved between 1940 and 1970 as live food for commercial fish species (references in 14). Several fish species have been illegally translocated across Europe to increase the diversity of the target species for anglers (e.g. large-bodied piscivorous fish species, such as the European catfish *Silurus glanis* and pikeperch *Sander lucioperca*). In both Europe and North America, crayfish and fishes have been released as bait and forage; examples include the rusty crayfish *O. rusticus* and the fathead minnow *Pimephales promelas* in North America (46, 56) and the bleak *Alburnus alburnus* in the Iberian Peninsula (20). Most planned introductions were conducted without any scientific basis: in the Iberian Peninsula, for instance, apparent 'vacant niches' in newly constructed reservoirs were filled by stocking piscivorous fish, such as *Esox lucius* (32). Some introductions were aimed at alleviating poverty in underdeveloped areas, e.g. the red swamp crayfish (*P. clarkii*) released in the rice fields of Andalusia, Spain (23). Unfortunately, several of these attempts to reduce societal problems have had unexpected negative consequences, ultimately causing more problems than they have solved (the 'Frankenstein effect'; 49).

The ornamental industry has been a powerful motive for introductions/translocations of species. For example, 49 of the 59 freshwater fish species introduced into North America and 22 of the 34 introduced into Australia were transported intentionally by humans in association with the aquarium industry (3, 44). As a result of releases of ornamental fishes, the goldfish *Carassius auratus* occurs today in the wild in 42 states of North America (56). Particularly worrying in this respect are the recent reports of *Ameiurus catus* (7) and *A. nobilis* (8) in Britain. The parthenogenetic marbled crayfish (*Procambarus* sp.), found in the wild in Germany, the Netherlands, and Italy (50, 67) and in Madagascar (39), is another popular ornamental species, which can easily be purchased on the internet (50). Species may also have been imported for biological control, e.g. *Gambusia* spp.: the eastern mosquitofish *G. holbrooki*, for instance, was introduced into Spain in 1920, Germany in 1921, and Italy in 1922 to control mosquito larvae and pupae and has since spread to many warm-water systems (14). In Africa, many releases into the wild of the North American *P. clarkii* from the 1960s onwards were aimed at controlling the freshwater snails that carry human schistosomiasis, but the species caused much ecological and economic damage (28). There is also a report of the successful 'assisted migration' of the imperilled Danubian salmon (*Hucho hucho*), intensively stocked outside its native range in Poland (references in 14).

The aquaculture industry, which is related to commercial and sport fishery and to the ornamental industry, has been the cause of most importation of crayfish species from other countries or continents. Once introduced for aquaculture and kept in outdoor ponds, crayfish almost inevitably escape and easily establish self-sustaining populations in the colonised habitats. *Cherax destructor*, for instance, after its first introduction into Western Australian farm dams for aquaculture in 1932, rapidly spread, and it now threatens the 11 endemic crayfish species of this state. Similar phenomena occurred with fish species. Of the 1,205 fish introductions for aquaculture purposes, about 50% were followed by establishment in the wild (10). Interestingly, the aliens that had the highest rate of establishment are also the species with the highest aquaculture production, e.g. grass carp (*C. idella*), with 3,473,051 metric tons (mt), common carp (*C. carpio*) with 2,718,277 mt, and Nile tilapia (*Oreochromis niloticus*) with 904,848 mt (data of 2000; 10).

The interconnection of river basins by canals has facilitated the expansion of many species, because it has enabled aquatic animals to move freely between the basins or be transported by ship (e.g. 52). Numerous canals have been constructed over the last two centuries in Europe to promote trade. They form complex networks of inland waterways that connect 37 countries in Europe and beyond (21): in Germany alone, for instance, there are 1,770 km of inland waterways (69). Several studies showed the penetration of Ponto-Caspian species via three important canal corridors along which animals were able to spread, either actively or passively, throughout Europe (6, 21). Sprat (*Clupeonella cultriventris*) and needle fish (*Syngnathus abaster*), for example, migrated through the Volgo-Don Canal. The canals have also facilitated the expansion of introduced species (e.g. Chinese sleeper, *Perccottus glenii*). The arrival of the Ponto-Caspian round goby (*Neogobius melanostomus*) in the late 1980s in the Baltic Seas was followed by its 'jump' in ships' ballast to the Laurentian Great Lakes, where it was first reported in June 1990 (14). After having rapidly spread across the Great Lakes–St Lawrence river province, the round goby began spreading in the Mississippi province via the Chicago Sanitary and Shipping Canal system, opened in 1900 and connecting Lake Michigan and the Des Plaines River of the Mississippi province (56).

Interestingly, the reasons behind introductions/translocations may vary between countries for each species. For instance, as reported by Copp *et al.* (14), the introduction of pumpkinseed (*Lepomis gibbosus*) in the late 19th Century and early 20th Century resulted from deliberate releases for angling in France, but in England, Slovenia, and Spain it was the result of escaping ornamental fish.

Establishment and spread

The success of a crayfish or fish species in progressing to the second step of the invasion process, i.e. establishment (the formation of self-reproducing populations), most often depends on the intensity and diversity of imports as a consequence of 'propagule pressure', i.e. the number of individuals released and the frequency of release in a given area (12, 73). Introduced fishes, for instance, were more likely to establish when humans intended their establishment (76%) rather than when fish were cultivated or used with no explicit desire for naturalisation (57%) (62). Indeed, the most widespread alien fishes are those that have an elevated value for angling, aquaculture, biocontrol, etc. The most diffused species in Europe, the rainbow trout (*Oncorhynchus mykiss*), supports a significant recreational fishery. The fish is native to regions west of the North American continental divide (Rocky Mountains) and has been also extensively translocated in North America (into 77 drainages and now occurring in 89 drainages out of the 125 examined). A second widely introduced species in both Europe (31 countries) and North America (34 drainages) is the Asian grass carp (*C. idella*), used for aquatic weed control and as food.

That human activities highly facilitate the establishment of alien fish species has been confirmed by Leprieur *et al.* (41): the level of economic activity of a given basin (expressed by the gross domestic product) strongly determines the likelihood of it being invaded by fish species. Three, not mutually exclusive, mechanisms may explain this phenomenon. First, economically rich areas are more prone to habitat disturbances (e.g. dams and reservoirs modifying river flows) that often facilitate the establishment of alien species. Secondly, high rates of economic exchanges increase the propagule fluxes of alien species via sport fishing, aquaculture, and ornamental trade. Thirdly, the increased demand for imported products associated with economic development increases the likelihood of unintentional introductions through the import process.

What makes established populations of alien species able to progress to the third step of the process and to become invasive is known only for a few species. The literature on biological invasions is crowded with studies providing generalisations about traits that make species successful invaders (e.g. high fecundity, small body size, vegetative or asexual reproduction, high genetic diversity, high phenotypic plasticity, broad native range, abundance within native range, physiological tolerance, generalist habitat, human commensalisms) and about what makes habitats highly susceptible to invasions (climatically matched, disturbed, low diversity, absence of predators, presence of vacant niches, low connectance of food web) (23).

The ability to achieve a high biomass and a dominant role in the community is a general characteristic of alien species that have serious impacts on the ecosystem (66). This is well illustrated by the case of invasive crayfish (28). When compared to native species they are characterised by higher fecundity (more than 500 pleopodal eggs in *P. clarkii*), protracted spawning periods, faster growth rates (50 g in 3-5 months in *P. clarkii*), and maturity reached at relatively small sizes (10 g in *P. clarkii*), all properties that make these species able to reach a large number and a high biomass in a short period of time. 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 coloniser 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 salinity levels. The relatively large body size reached makes crayfish both resistant to gape-size limited predators (such as many fishes) and dominant in the competition for access to limited resources. As a consequence, the introduced crayfish may have a greater direct (through consumption) or indirect (through competition) effect on the other biota, particularly on other crayfish species and on benthic fish, molluscs, and macrophytes. Large body size usually translates into a higher energy and nutrient demand, but invasive crayfish are often more efficient energy converters and display higher metabolic rates when compared with similarly sized native species.

A higher survival rate is also expected when a species is introduced into a new ecosystem without a full complement of specific parasites, pathogens, and enemies, as suggested by the 'enemy release hypothesis' (e.g. 70). For instance, the introduced brown trout (*Salmo trutta*) in New Zealand is associated with only 17 parasites compared with 63 in its native Europe. Several examples, however, provide contrasting evidence. The sea lamprey (*Petromyzon marinus*) has eliminated many fishes from Lake Michigan, whereas in other lakes some of these species, e.g. lake trout (*Salvelinus namaycush*), have co-existed with the lamprey for thousands of years (47). Likewise, the success of an invader should be most severe in communities lacking species similar to it, due to the community's lack of evolutionary experience with them (e.g. 17). Often, however, the colonisation by alien species facilitates, rather than interferes with, the establishment of other alien species, and therefore increases the likelihood and the magnitude of ecological impact on the recipient area ('invasional meltdown theory'; 65). This phenomenon seems to have occurred in the Great Lakes, which have been subject to the sequential invasion of several species, including ruffe (*Gymnocephalus cernuus*) and Ponto-Caspian gobies (in particular *N. melanostomus*) (59).

Often, the 'tens rule' (73) has been invoked to predict the relative number of introduced species that will overcome the numerous barriers encountered in the recipient ecosystem and become invasive. This rule-of-thumb estimates that between 5% and 20% of introduced species become established, and, on average, 10% of those established become invasive. But this rule provides only a rough guideline. A study that compared Europe and North America for the number of fishes moved from one continent to the other (38) revealed that the proportions of species that take each step in the invasion process differ highly; the first step, introduction, being the hardest to take. For either direction of introduction, the proportion of all species that took the second step, establishment, was significantly lower than those that took the third step, spread (establishment: 36% and 49%; spread: 56% and 63%). Both these values, however, far exceed the average of 10%. This anomaly to the tens rule has been confirmed on a more global scale by Ruesink (62): using a database of 1,424 intentional international transfers of freshwater fishes, the author found that up to 64% of the introduced species became established and 22% of the established cases had had a documented impact. Taken together, these results show the critical importance of the first step of the invasion process, introduction. Vertebrates, and in particular fishes, have by far the lowest success rate in taking this step, so the most effective control of their invasion is to prevent them from entering a new area. Once introduced, fishes have a high potential to establish and spread.

The debate about impacts

A multitude of questions has arisen about the potential impacts of crayfish and fish introductions/translocations. The current debate centres on whether these species are to be viewed as advantageous, of neutral value, highly 'undesirable', or even as ecological abnormalities (14). Whereas some authors maintain that the majority of intentional freshwater fish introductions, particularly those associated with aquaculture, have had no proven ecological impact (35), others (1, 22, 26, 42) observe that, since very little is known about impacts of a large number of species, it would be inappropriate to equate a lack of data with 'no impact'. Of the 3,141 fish introduction records in the FAO Database on Introductions of Aquatic Species, whether the species succeeded in establishing is unknown in 13.9% of cases and whether the species had ecological effects is unknown in 80% of cases (22); however, all the most frequently introduced species were more likely to produce detectable ecological effects (Table III). Given that the establishment and spread of freshwater species is extremely likely, as shown above, and most often irreversible, the precautionary approach seems the most appropriate.

A second debated question regards the impact of the new crayfish and fish species on the other species of the same assemblage. Several studies show that invasive crayfish, due to their competitive superiority over native species coupled with reproductive interference, often enhance the effects of habitat loss, overexploitation, and pollution in inducing a dramatic decline of crayfish diversity (25). *Pacifastacus leniusculus*, for instance, has contributed to the global extinction of the crayfish *P. nigrescens*, once common in the creeks of the San Francisco Bay area; in north-eastern California it is now displacing the Shasta crayfish

(*P. fortis*). Similarly, the European native species *Astacus astacus*, *A. pallipes*, and *Austropotamobius torrentium* are under threat from the oömycete *Aphanomyces astaci*, the causative agent of the so-called crayfish plague. This disease was introduced into Europe by the North American crayfish but does not require its host in order to spread; the spores can be transported on damp surfaces, e.g. fishing equipment, as is thought to have happened with the crayfish plague outbreak in central Ireland in 1986. Hybridisation with the invaders is an additional threat for native crayfish species. In Wisconsin, the hybrids of the invader *O. rusticus* and the native *Orconectes 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 (references in 25).

Highly debated are the effects that alien fishes may have on the native fish assemblages. There is at least one paradigmatic example of a fish invader that has changed the nature of a whole community: the Nile perch (*Lates nilotica*), introduced into Lake Victoria in the 1950s to boost fisheries (64), led to 'the first mass extinction of vertebrates that scientists have ever had the opportunity to observe' (40). An explosive increase of this species was observed in the early 1980s; the boom of the Nile perch population was soon accompanied by a rapid collapse of the species-rich Lake Victoria ecosystem and its replacement by a highly simplified, largely exotic-based community. Between 1975 and 1982, about 200 endemic haplochromine cichlids of the more than 300 species that previously were known to occupy a great variety of niches in the lake disappeared, mostly as the result of competition and predation by the Nile perch. By 1983, the indigenous fish community had been virtually destroyed, while the Nile perch comprised more than 80% of the catch.

A number of studies, however, contrast with the above example, showing an increase rather than a decrease in the variety of fish species following the introduction/translocation of species (11, 31). For instance, only in 21 out of the 125 temperate North American drainage basins analysed was the number of introduced species positively correlated with the native species richness (31). If, on the one hand, these results seem to contradict one of the most well-established generalisations in the invasion literature since Elton (19) – the 'biotic resistance' hypothesis (i.e. communities with high diversity and complexity are the least susceptible to invasion because of the strength of the community interactions) – on the other, they raise doubts about the negative impact that alien fishes have on native species through competition or predation, at least in the short term.

There are, however, other types of impact that alien species can have on native fishes without necessarily leading to their immediate extirpation. The first is genetic introgression, which may increase the likelihood of extinction by reducing fitness and the ability of populations to adapt to changing conditions. In North America, cutthroat trout (*Salmo clarki*), Apache trout (*Oncorhynchus apache*), and Gila trout (*Oncorhynchus gilae*) have undergone extensive hybridisation with invading rainbow trout (*O. mykiss*) (references in 66). Stocking of conspecifics can also result in introgression and loss of genetic information; hybridisation, for instance, occurs between hatchery and wild populations of salmonids, including brown trout (references in 66).

There is also increasing awareness about a second threat to native species, the spread of new diseases or parasites following movements of fish species. Within European fresh waters, over 100 new fish parasite species have been recorded, all introduced along with fish that were not intended for release (34). For example, the nematode *Anguillicola* sp. entered Europe with oriental eels, *Anguilla* spp., intended for human consumption. Its dispersion was probably due to the exchange of water in transporter tanks infested with spores during the journey from the place of capture to the market. Many diseases of salmonids that infect hatchery-reared fish, and which now occur in the wild, have been imported. Rainbow trout, *O. mykiss*, imported from western North America, carried furunculosis to Europe. Similarly, wild Atlantic salmon populations in Norway have suffered massive mortalities and, in some areas, total eradication because of the monogenean fluke *G. salaris*, introduced from infected salmon hatcheries in Sweden. An often overlooked pathogen introduction pathway is transport with ornamental organisms. A recent example is Koi herpes virus, transferred with Koi carp (a domesticated variety of the common carp), first in Israel and later in Europe, Indonesia, the United States, and Japan. The virulence of alien pathogens, such as the European *Myxobolus cerebralis* (the causative agent of whirling disease in salmonids in North America), is expected to increase with climate warming (reference in 57).

A large number of studies also show that alien species may cause some more subtle changes in the behaviour, biology and ecology of native fish, possibly leading to deleterious effects in the medium-long term (26). Alien species may induce changes in the distribution of natives: in North American lakes, lake trout (*S. namaycush*) limit the distribution of bull trout (*Salvelinus confluentus*) by predation (references in 66). They can affect individuals by influencing their habitat use and foraging. Invasive salmonids, for instance, can restrict native fish to less preferred microhabitats, with changes in behaviour that can translate to reduced feeding activity and success (references in 66). Invaders may also cause diet shifts in native species. For instance, native lake trout

(*S. namaycush*) begin eating zooplankton rather than littoral fish in the presence of invading bass *M. dolomieu* and *Ambloplites rupestris* (71). Other negative impacts of colonising species often are not confined to the fish assemblage but extend to other components of the food web that in turn might affect fish communities. Brown trout (*S. trutta*), introduced into New Zealand in 1867, profoundly affect the functioning of stream communities by reducing the biomass of grazing invertebrates, altering their grazing activity, and ultimately releasing algae from top-down regulation by grazers and therefore indirectly increasing their biomass (references in 66); these changes may then indirectly affect the survival of native fish species.

Other important ecological changes following the introduction of crayfish and fish are those related to food web links and ecosystem functioning. Bass (*Micropterus salmoides*) and northern pike (*E. lucius*) in lakes, signal crayfish (*P. leniusculus*) in ponds, and rusty crayfish (*O. rusticus*) in streams all cause increases in primary producers by reducing grazer abundance (references in 66). Invasive crayfish alter the pathways of the energy flux 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. The intense burrowing activity and locomotion of *P. clarkii* and other invasive crayfish often result in bioturbation: water quality may be impoverished and light penetration and plant productivity reduced (28).

Finally, invasive crayfish and fish species inflict a great deal of damage on human well-being. The types of damage they can cause have not been well studied but range from indirect damage (e.g. the loss in crayfish production following the pan-European spread of the plague) to direct damage (e.g. the destruction of crops, such as rice, by *P. clarkii* in Portugal). There can also be substantial indirect costs to society, for example:

– CAN$22 million per year for funded research on the sea lamprey in the Great Lakes (13)

– £100,000 and £190,000, respectively, for the eradication of *P. leniusculus* in Scotland (25) and *P. parva* in England and Wales (9)

– US$4.5 million for the reintroduction of *P. fortis* in California (references in 25).

Total monetary losses may be extremely high. In the United States the annual direct/indirect costs associated with just 40 species of freshwater fish are US$5,400 million (53). However, systematic studies on the overall economic impact of alien species of crayfish and fishes are still missing.

There are even fewer studies that investigate the harm posed by alien species to human health. Illustrative in this respect is the case of invasive crayfish (25). Often they 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, including people, 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 numerous helminth parasites of vertebrates and to be a vector of transmission of the bacterium *Francisella tularensis*, the causative agent of human tularemia. On the other hand, *P. clarkii* may control the 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.

Possible solutions

The Guiding Principles adopted by the Convention on Biological Diversity suggest a 'three-stage hierarchical approach' as the basis for all action on invasive alien species: (i) prevention of introductions and translocations; (ii) if a species has been introduced, early detection and rapid action followed by quick eradication of the organisms; (iii) where eradication is not feasible or resources are not available, implementation of forms of containment and of long-term control measures. The first stage, prevention, seems to be particularly crucial in the case of crayfish and fish. In fact, these taxa are extremely hard to detect and disperse rapidly, making any subsequent form of management difficult and expensive. There are only a few records of successful eradication of freshwater species (9). The best documented is the eradication of *P. parva* from five lakes in England and Wales: the procedure used was extremely expensive despite the small areas of water being treated and unlikely to be extended to wider water basins.

As a consequence, more attention should be paid to minimising the risks of intentional and unintentional introductions, as in part done by current legislation in some countries (e.g. EC Council Regulation No. 708/2007 concerning use of alien and locally absent species in aquaculture). Despite the economic arguments and political pressures often brought to bear in support of the importation of commercial species, biologists can contribute to the effort to minimise risks by, for instance, identifying pathways of accidental introductions, promoting measures that may reduce them, producing protocols for risk assessment, and, finally, raising public awareness and disseminating information (27, 58).

However, despite the progress made in the last decade in understanding biological invasions, current efforts on this front still suffer from a lack of scientific knowledge about the extent and distribution of alien diversity and about the multiple impacts of many potentially invasive species, particularly in some regions of the world such as Africa and Asia (54). A much greater and more urgently applied investment to address these deficiencies is thus warranted (30).

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■

Espèces envahissantes d'écrevisses et de poissons d'eau douce dans le monde

F. Gherardi

Résumé

Après la destruction des habitats, les espèces exotiques envahissantes sont, par ordre d'importance, la deuxième cause de la perte de biodiversité, en particulier dans les écosystèmes d'eau douce. En outre, ces espèces modifient la structure et le fonctionnement des écosystèmes et favorisent les processus d'homogénéisation biotique qui représentent, à terme, une menace potentielle pour les économies et pour la santé humaine. L'auteur fait le point sur les informations actuelles concernant deux éléments constitutifs des écosystèmes d'eau douce, à savoir les écrevisses et les poissons, en précisant leur distribution mondiale, les vecteurs de leur dispersion et leurs principaux impacts respectifs. Comme le révèle l'analyse de la littérature qui leur est consacrée, les écrevisses et les poissons, une fois déplacés hors de leurs zones de distribution d'origine sont capables de s'établir, de se reproduire librement et de se propager à partir du site d'introduction, selon un processus d'invasion. Les actions permettant de maîtriser ces nouvelles populations s'avèrent difficiles et onéreuses, d'où la nécessité de privilégier les mesures de prévention. Malheureusement, nos connaissances sur les mécanismes à l'œuvre dans les invasions par les écrevisses et les poissons d'eau douce sont encore limitées. Il conviendrait donc d'accorder une plus grande attention à ce domaine en investissant davantage dans des études plus poussées.

Mots-clés

Eaux continentales – Écrevisse – Introduction – Invasion biologique – Poisson d'eau douce – Transfert – Vecteur.

■

Especies invasoras de cangrejos y peces de agua dulce del mundo

F. Gherardi

Resumen

La presencia de especies foráneas invasoras es, después de la destrucción del hábitat, la segunda de las principales causas de pérdida de diversidad biológica, sobre todo en ecosistemas de agua dulce. Esas especies también alteran la estructura y el funcionamiento de los ecosistemas, provocan una homogenización de la biota y a la larga amenazan la economía y la salud de las poblaciones humanas. El autor trata de sintetizar parte de la información existente sobre la distribución mundial, los vectores de propagación y los efectos de dos importantes miembros de los ecosistemas de agua dulce: los cangrejos y los peces. El análisis de la bibliografía existente pone de manifiesto que las especies de peces y cangrejos de río, una vez desplazadas de su área de distribución original, pueden fácilmente fundar poblaciones capaces de reproducirse, extenderse a partir del punto de introducción y cobrar carácter invasor. El control de esas poblaciones exige medidas caras y complicadas, lo que supone un argumento de peso en favor de medidas preventivas eficaces. Lamentablemente, aún no sabemos lo bastante sobre los mecanismos que intervienen en las invasiones por los cangrejos y peces de agua dulce, por lo que es preciso dedicar mucha más atención y recursos a los estudios sobre el tema.

Palabras clave

Aguas continentales – Cangrejo de río – Introducción – Invasión biológica – Pez de agua dulce – Translocación – Vector.

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