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Questa è la Versione finale referata (Post print/Accepted manuscript) della seguente pubblicazione:

Original Citation:

Biological invasions in inland waters: an overview / F. GHERARDI. - STAMPA. - (2007), pp. 3-25.

Availability:

This version is available at: 2158/258021 since:

Publisher:

Springer

Terms of use:

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Biological invasions in inland waters: an overview

Francesca Gherardi

INTRODUCTION

The value of inland waters to humankind is obviously infinite and the induced changes in the goods and services they provide have a strong impact on human welfare. Lakes/ivers and wetlands currently contribute 20% to the estimated annual global value of the entire biosphere amounting to US\$33 trillion per year (Costanza *et al.* 1997). These elevated numbers may justify the present general concern about the increasing degradation of freshwater systems, associated with the rapid extinction rate of their biodiversity – in some cases even matching that of tropical forests (Ricciardi and Rasmussen 1999).

Together with other anthropogenic sources of disturbance, such as the impoundment of rivers (e.g. dams and weirs, water removal), water quality deterioration (e.g. pollution, eutrophication, acidification), habitat degradation and fragmentation (e.g. channelization and land use change), and over-exploitation, the introduction of non-indigenous species (NIS) into fresh waters is today regarded as the main driver of biodiversity change (Millennium Ecosystem Assessment 2005). The effects of such a driver has been estimated to be greater in freshwater than in terrestrial ecosystems (Sala *et al.* 2000). This is particularly apparent in lakes where biological invaders have been recognized as one of the greatest causes of species extinctions (Lodge 2001).

THE VULNERABILITY OF INLAND WATERS TO INVASIONS

Inland waters have been the theatres of spectacular biological invasions. Well-known cases are the introduction of the Nile perch *Lates niloticus* (Linnaeus) into Lake Victoria followed by the elimination of about 200 species of haplochromine cichlids (Craig 1992), the alteration of the Laurentian Great Lakes communities and ecosystems by sea lamprey *Petromyzon marinus* Linnaeus, zebra mussel *Dreissena polymorpha* (Pallas), and other invaders (MacIsaac *et al.* 2001), and the complete domination of lowland rivers in the western USA by non-indigenous fish and invertebrates (Moyle and Light 1996a). In several freshwater systems, other less celebrated dramas are however ongoing with the intervention of several, previously unsuspected actors, such as *Lepomis gibbosus* (Linnaeus) (Chapter 15) and *Carassius auratus* (Linnaeus) (Chapter 13) among fish, *Dikerogammarus villosus* (Sowinsky) (Chapters 12 and 27), *Gmelinoides fasciatus* (Stebbing) (Chapter 26), and *Pontogammarus robustoides* (Sars) (Chapter 25) among crustaceans, and *Rana catesbeiana* Shaw among amphibians (Chapters 7 and 38). This confirms that invasions by NIS are pervasive and highly diffused phenomena in fresh waters but also that our predictive ability may be weak. Meanwhile, other apparently harmless NIS are spreading (see potamid crabs in southern France, Chapter 3).

The reasons that freshwater systems are vulnerable to NIS are several, including the higher intrinsic dispersal ability of freshwater species compared with terrestrial organisms (Beisel 2001). Lakes and some streams are comparable to islands in that their geographic isolation has led to local adaptation with the evolution of many endemisms and sometimes to a low biodiversity (Lodge 1993). The extensive introduction of organisms in inland waters, either inadvertent (e.g. via ship ballast, artificial/natural canals, or estuarine saline-bridges, Chapters 17, 21, and 22; as parasites of other introduced species, such as the oomycete *Aphanomyces astaci*, Chapter 6) or deliberate (e.g. stocking of fish and crayfish, Chapters 20 and 31; intentional releases of pets or farm organisms, Chapters 8 and 9), is a direct consequence of the intensity with which humans utilize these systems for recreation, food sources, and commerce (Rahel 2000, Ricciardi 2001). Human-mediated dispersal of crustacean zooplankton, for instance, might exceed the natural rate by up to 50,000-fold (Hebert and Cristescu 2002). And the frequency of species invasions in freshwater systems is likely to continue to grow commensurate with enhanced global commerce and human exploitation of these communities.

Finally, freshwater systems are subject, especially at higher latitudes, to altered seasonal temperature regimes due to global climatic warming and, especially in developed countries, to strong human disturbance. In fact, many NIS are migrating to new areas where the climate has warmed, such as some introduced warm-water fish [e.g. *Micropterus salmoides* (Lacepède), *Lepomis macrochirus* Rafinesque, and *Lepomis cyanellus* (Rafinesque)] that are spreading in North America into higher latitudes and altitudes (Eaton and Scheller 1996,

Chapter 35). Disturbed ecosystems and communities attract biological invasions more than pristine systems; disturbance results in the resharing of space and energy resources that are available to indigenous and non-indigenous species and may open new vacant niches for the most adaptable and tolerant invaders (Ross *et al.* 2001).

The vulnerability of inland waters to biological invasions is a cause of the complete domination of vast waterscapes in certain regions by NIS, such as water hyacinth [*Eichornia crassipes* (Martius) Solms] in many tropical lakes and rivers (Chapter 10) and the red swamp crayfish [*Procambarus clarkii* (Girard)] in several waterbodies of southern Europe (Gherardi 2006, Chapter 2). Xenodiversity may be extraordinarily high in, for instance, large rivers of developed countries that usually host dozens to hundreds of NIS (Mills *et al.* 1996, Chapter 12). The Hudson River, for instance, contains more than 100 species of non-indigenous fish, vascular plants, and large invertebrates, a considerable fraction of which are ecologically important – such as Eurasian watermilfoil (*Myriophyllum spicatum* Linnaeus), purple loosestrife (*Lythrum salicaria* Linnaeus), zebra mussel (*D. polymorpha*), Atlantic rangia (*Rangia cuneata* Gray), and common carp (*Cyprinus carpio* Linnaeus) (Strayer *et al.* 2005). Some taxa are particularly affected by species introductions: the New Zealand fish fauna contains 30 NIS (53% of the total) (Vitousek *et al.* 1997); isolated islands often have more non-indigenous than indigenous fish species (Hawaii: 19 vs. 6), but also continental areas have relatively large numbers of non-indigenous fish species (California: 42 vs. 76, Brazil: 76 vs. 517; references in Vitousek *et al.* 1996); at least 76 fish species belonging to 21 families have been introduced into European fresh waters (Lehtonen 2002), of which 51 have become established.

Species originating from diverse biogeographical areas now coexist in several basins; in the Rhine, indigenous crustaceans [*Gammarus pulex* (Linnaeus)] occur with North American species [*Gammarus tigrinus* Sexton and *Orconectes limosus* (Rafinesque)], Mediterranean species (the freshwater shrimp *Atyaephyra desmaresti* Millet), and Ponto-Caspian species [*Gammarus roeseli* Gervais and *Dikergammarus villosus* (Sowinsky)] (Beisel 2001). Biotic homogenization is constantly increasing; freshwater fish similarity among the States of the USA amounts today to 7% (Rahel 2000) and some of them, such as Arizona and Montana, which previously had no fish species in common, now share more than 30 species. National borders are obviously irrelevant and they provide no barrier to the natural dispersal of NIS: the Nile perch released in Tanzania spread to other countries bordering Lake Victoria (Welcomme 1988) and *P. clarkii* introduced into Spain invaded Portugal via the common hydrographic basins (Gherardi 2006).

Some freshwater systems function as “hotspots” where NIS accumulate. The Great Lakes system contains over 145 non-indigenous invertebrates, pathogens, algae, fish, and plants, with approximately 75% originated from Eurasia of which 57% are native to the Ponto-Caspian region (Mills *et al.* 1993,

Ricciardi and Rasmussen 1998, MacIsaac *et al.* 2001). These species include a wide array of taxa, such as mussels [*D. polymorpha*, *Dreissena bugensis* (Andrusov)], amphipods (*Echinogammarus ischnus* Stebbing), cladocerans [*Cercopagis pengoi* (Ostroumov)], harpacticoid copepods [*Nitocra incerta* (Richard) and *Schizopera borutzkyi* (Monchenko)], and fish [*Neogobius malanostomus* (Pallas)], *Proterorhinus marmoratus* (Pallas), *Gymnocephalus cernuus* (Linnaeus)]. It has been ascertained that Ponto-Caspian species reach the Great Lakes in ballast along five shipping “corridors” (MacIsaac *et al.* 2001). Four of these corridors require the first transfer of species via rivers and canals to ports in the North and Baltic seas that, in their turn, function as “hubs”, acting as the donor for other ships that transport these species in secondary invasions to ports in North America and, potentially, in East Asia, San Francisco Bay, and Australia (e.g. Cohen and Carlton 1998, Ruiz *et al.* 2000).

Finally, many freshwater invaders are moved among biogeographic regions within continents and are transported among continents in association with economic activity and trade globalization that benefit millions worldwide (Lodge and Shrader-Frechette 2003). The inevitable tension between two often competing goals – increasing economic activity and protecting the environment from invasive species – make it difficult to justify the need for decision-makers to contain the spread of these species and to mitigate the environmental risks they pose. For instance, a number of issues has been raised in favor of the outcomes of introducing crayfish (Gherardi 2006, Chapter 28). First, in the absence of indigenous species, invasive crayfish were claimed to occupy vacant niches, constituting the unique large macro-consumer within polluted or eutrophicated waters, where the native fauna has already been severely decimated (Gherardi *et al.* 2000). The second claim is that they constitute abundant prey for rare or threatened birds and mammals, like several Ardeidae and the otter (e.g. Barbaresi and Gherardi 2000, Rodríguez *et al.* 2005). Third, from a socio-economic perspective, introduced crayfish 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 netsmen; (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 and extra-European countries (Ackefors 1999).

THE CURRENT STATE OF RESEARCH

Studies on the identity, distribution, and impact of freshwater NIS and on the dynamics of their invasion have increased exponentially since the 1990s, resulting in a flood of publications particularly abundant in the last decade (Fig. 1). This pattern of growth in the literature is a reflection of the rise in popularity that invasion biology has gained as an appealing area of research

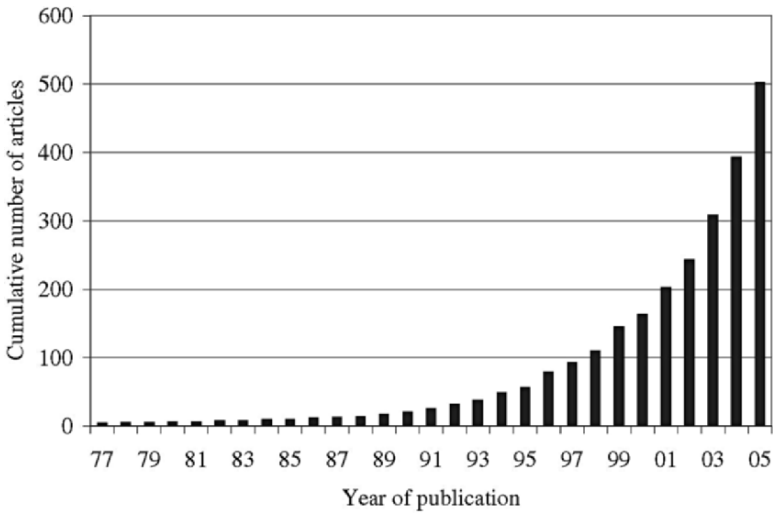


Fig. 1 Cumulative number of publications dealing with non-indigenous species (total number = 502). Papers were identified via keywords from Biosis analyzed between 1967 and December 2005.

among ecologists (Kolar and Lodge 2001). The overall number of published articles is, however, significantly biased towards terrestrial invaders (Fig. 2). This is not surprising: terrestrial systems are the most visible and accessible habitats for humans and, as such, have received the preponderance of ecological attention.

The majority of studies of freshwater invaders has been conducted in North America, and mostly in the Great Lakes (Fig. 3A), and centered on animals (74%) more than on plants (20%), whereas a small fraction (6%) analyzed both kingdoms simultaneously. Of all the animal taxa, fish, particularly salmonids, have received the greatest scientific attention (Fig. 3B), as the result of their

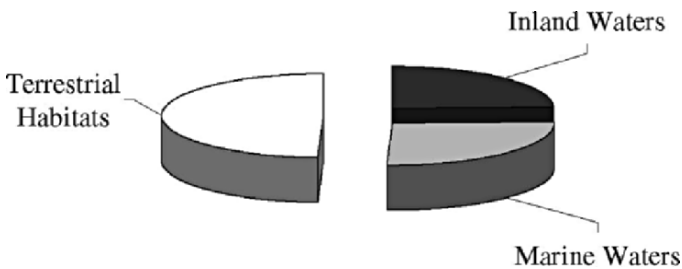


Fig. 2 Frequency distribution of research articles published in the journal *Biological Invasions* (Springer) since 1999 distinguished among habitats (total number = 354).

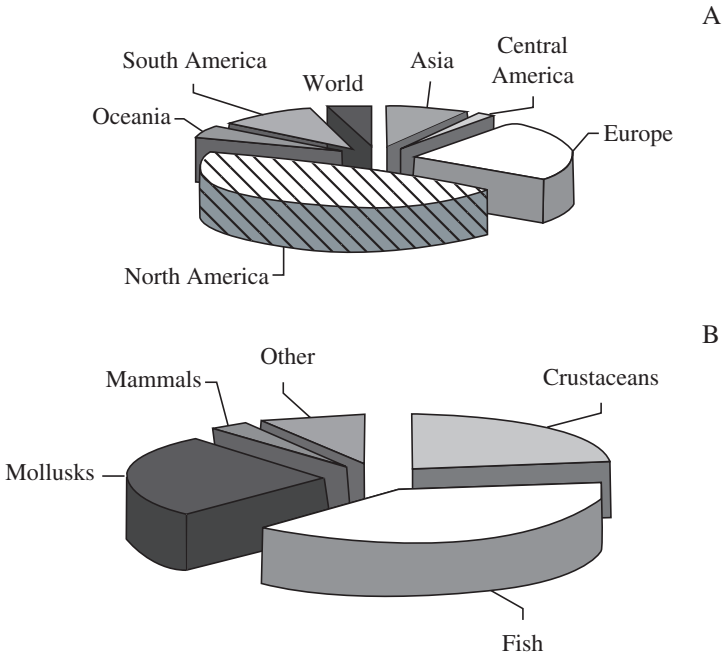


Fig. 3 Frequency distributions of research articles published in the journal *Biological Invasions* (Springer) since 1999 dealing with inland waters distinguished among continents (A) and animal taxa (B) (total number = 69).

perceived ecological role in aquatic food webs and their economic importance to humans. In the other taxa, dreissenids among mollusks and crayfish among crustaceans had been most often studied. Only recently has been the taxonomic coverage of freshwater invaders broadened. New privileged study animals have been Eleotridae and Poeciliidae among fish (e.g. Bedarf *et al.* 2001, Laha and Mattingly 2006, Pusey *et al.* 2006); the Asian clam [*Corbicula fluminea* (Muller)], the golden mussel [*Limnoperna fortunei* (Dunker)], and the golden apple snail [*Pomacea canaliculata* (Lamarck)] among mollusks (e.g. Darrigran 2002, Carlsson and Lacoursière 2005, Boltovskoy *et al.* 2006, Oliveira *et al.* 2006, Yusa *et al.* 2006); and the spiny waterflea (*Bythotrephes longimanus* Leydig) and cladocerans among crustaceans (e.g. Çelik *et al.* 2002, Shurin and Havel 2002, Branstrator *et al.* 2006).

ARE GENERALIZATIONS POSSIBLE?

A consequence of the concentrated interest on terrestrial biomes and of the limited geographic and taxonomic breadth in fresh waters is that traditional

invasion paradigms have been mostly derived from terrestrial studies and have been rarely tested in aquatic organisms (Beisel 2001). However, a number of generalizations about freshwater invasion is emerging today. They derive from two main approaches (Moyle and Light 1996b): the first analyzes case studies of invaders and their distribution (e.g. *P. clarkii*, Chapter 4; mollusks, Chapter 5; amphibians and reptiles, Chapter 7; plants, Chapter 11), whereas the second approach aims to extend recent developments in ecological theory to freshwater invaders (e.g. Chapters 19 and 23), in which the focus has been mainly directed to the interaction between the invader and the target community and to the biological characteristics of both the invading species and the ecosystem being invaded. Based on the examples provided by the recent literature, a list of 15 general statements characterizing some of the known events of biological invasion in inland waters can be drawn, as follows.

(1) The establishment and spread success of freshwater NIS often exceeds the 10% value predicted by the “tens rule” (Williamson 1996).

This is seen in the results obtained by Jeschke and Strayer (2005), who analyzed the introductions of vertebrates between Europe and North America (USA and Canada). Using corrected data for unrecorded introductions, the authors showed that, of the 220 and 713 fish species native to Europe and North America respectively, 11% and 6% have been introduced into Europe and North America, respectively, and 36% and 49% have become established after slightly longer than a decade, while 56% and 63% of the established fish had spread and become invasive. On a more global scale, Ruesink (2005) used a database of 1,424 intentional international transfers of freshwater fish and found that up to 64% of the introduced fish became established and 22% of the established cases had exerted a documented impact (i.e. changes in food availability, habitat structure, nutrient dynamics, or top-down trophodynamics).

(2) Propagule pressure is often a major predictor of the establishment of freshwater organisms.

Recent findings showed that the large number of propagules present in an inoculating population, such as the thousands of zebra and quagga mussels carried in the ballast of cargo ships, and the frequencies of sequential inoculations, such as multiple introductions of “desired” species, are positively correlated with invasion success (Lonsdale 1999, Kolar and Lodge 2001, Mack *et al.* 2000, Ricciardi 2001). For instance, as showed by Ruesink (2005), introduced fish species were more likely to establish when humans intended their establishment (76%) rather than when fish were cultivated or used with no explicit desire for naturalization (57%).

(3) The often elevated propagule pressures may explain the several instances in which introduced populations appear to be immune from bottlenecks – usually depleting genetic variation (the “genetic paradox”).

Aquatic organisms introduced in large numbers via ballast or subject to multiple introductions can carry a large fraction of the genetic variability of their source populations or bring genetic races from different parts of their native range (Stepien *et al.* 2002). Hence, many colonizers arrive with a high phenotypic and genetic diversity. This adds to other features that may favor their adaptability to the recipient areas, such as the fast acquisition of genetic variability after their arrival that results from such sources as hybridization with closely related organisms, epistasis (i.e. an interaction in which one gene influences the expression of another), or the potential for chromosomal restructuring by inversion, translocation, or duplication (Cox 2004).

(4) Failures of NIS to establish derive most often from their inability to meet the “environmental resistance” on the part of the recipient community – the different regimes of temperature, current, water chemistry, or abiotic resources.

Several examples from different taxa support this statement. Moyle and Light (1996a), for instance, showed that freshwater fish invading North American basins are likely to become established when abiotic conditions are appropriate, regardless of the biota already present. The narrow thermal tolerance of *C. fluminea* may explain its absence from most of the Great Lakes system (Ricciardi 2001), whereas salinity of that system was too low to allow for the successful reproduction of the Chinese mitten crab *Eriocheir sinensis* (Milne Edwards), notwithstanding the frequent introductions of this latter species over the past decades in ship ballast (MacIsaac 1999). The general harshness of the environment may reduce the ability of non-indigenous fish to invade. An example is Eagle Lake, California, which is a highly alkaline (pH: 8–9) terminal lake containing only four indigenous fish species (Moyle and Light 1996b). Any attempt to introduce fish failed in the long term, including the introduction in the early 20th century of the largemouth bass, *M. salmoides*.

(5) As a consequence of (4), success in the establishment of freshwater invaders may depend on a close match between their physiological requirements and the environmental characteristics of the system being invaded.

Species from nearby areas are more likely to be successful invaders than those from more distant locations, as found for fish species in North America that are most likely to be successful if they are adapted to the local, highly seasonal, hydrological regime of the recipient environment (Moyle and Light 1996b). For

instance, two species of Cyprinidae introduced into the Pecos River, Texas, USA from nearby areas became established because the artificial flow regime of the recipient river closely resembled that of their native streams (Bestgen *et al.* 1989). Convergent salinity conditions in donor and recipient ecosystems played a key role in the success of invaders in the Great Lakes (MacIsaac *et al.* 2001). An additional prerequisite for successful invasion that allows a species to survive transportation (e.g. in ballast; Bailey *et al.* 2004) and to become established in a recipient area is its euryoeciousness, i.e. its ability to tolerate wide environmental conditions (Ricciardi and Rasmussen 1998). For instance, the range of salinity in which a species can live and reproduce provides a reliable basis for discrimination between invasive and non-invasive North American and East European gammarid amphipods (Devin and Beisel 2007). In general, areas with a wide salinity gradient, like the Baltic Sea, may offer a range of hospitable conditions for invaders, functioning as hot spots of xenodiversity (Leppäkoski *et al.* 2002). Finally, the increased ionic content of large European rivers as the result of pollution has allowed salt tolerant species to spread in new river basins in recent decades (Ketelaars *et al.* 1999).

(6) Demographic factors (sexual precocity, fecundity, and number of generations per year; Lodge 1993, Chapter 12), biological plasticity (Chapters 14 and 16), and/or the ability to overcome the biotic resistance posed by the recipient community (the complex of native predators, parasites, pathogens, and competitors, and previously introduced species) may be neither essential nor sufficient for freshwater species to become invasive.

Usually, *r*-selected crayfish (e.g. *P. clarkii*) rather than *K*-selected species [(e.g. *Austropotamobius pallipes* (Lereboullet)] have a high probability of spreading. But fecundity and number of generations per year often are not sufficient to explain why the amphipod *G. pulex* has invaded the streams in Northern Ireland where it outcompetes *G. duebeni* Liljeborg (Devin and Beisel 2007). Often, the magnitude of an invader's impact may be predicted by its "taxonomic distinctiveness" within the recipient community (Ricciardi and Atkinson 2004). Indeed, the lack of evolutionary experience with the invader – meaning the absence of competitors, predators, or parasites and the inability to respond to them with an appropriate behavior – may predispose communities to be altered by invasions (e.g. Diamond and Case 1986). For instance, eliminations of indigenous species by *D. polymorpha* have rarely been reported from the invaded European lakes whose native fauna was previously exposed to *Dreissena* during the Pleistocene era (Ricciardi *et al.* 1998). Similarly, the introduced tilapiine species, *Oreochromis niloticus* (Linnaeus), is one of the few fish species to persist in Lake Victoria in large numbers in face of the Nile perch invasion as the result of its past evolutionary experience with similar predators (Moyle and Light 1996b). Sometimes, the interaction between two species that do not share an evolutionary

history leads to the positive outcome for one of the two in a form of “evolutionary release” (Schlaepfer *et al.* 2005). For instance, indigenous prey (e.g. anuran tadpoles and metamorphs) may be unable to recognize introduced predators (e.g. the introduced *R. catesbeiana* in the western USA; Rosen and Schwalbe 2002) and their style of preying. As a result, the naïve predators are released from the difficulties of finding a prey (Kiesecker and Blaustein 1997); they may dispose of a high availability of food during the establishment phase of their invasion, which is a precondition of their fast spread. The phenomenon of evolutionary release might explain the paradox of why invasive species sometimes enjoy a competitive advantage over locally adapted species, although there would be a priority effect for residents (e.g. Shea and Chesson 2002, Schlaepfer *et al.* 2005). Also a reduced attack from natural enemies (predators and parasites) encountered outside their natural range gives some species the ability to spread and to become invasive, as predicted by the “enemy release hypothesis” (ERH) (e.g. Torchin *et al.* 2003). However, generalizations about the role of the naïveté of introduced species and of their potential lack of enemies in the recipient community may not be possible in freshwater systems. Several examples, in fact, provide contrasting evidence. The sea lamprey, *P. marinus*, eliminated large fish from Lake Michigan even if some of these species [e.g. the lake trout *Salvelinus namaycush* (Walbaum)] coexisted with the lamprey in other lakes where the species have been together for thousands of years (Moyle 1986). In addition, the ERH has been verified in relatively few organisms and subject to limited criticism (Colautti *et al.* 2004), being only one of the several hypotheses that can explain the abundance and/or the impact of a given invader (Enemy Inversion Hypothesis, climatic variables, selection for “invasive” genotypes, human disturbance, etc.).

(7) In fresh waters, species-rich communities may be as vulnerable to invasion as less speciose, less biologically “sophisticated” communities.

This statement contrasts with one of the most well-established generalizations in the invasion literature since Elton (1958), i.e. that communities with high diversity and complexity are the least susceptible to invasion because of the strength of the community interactions (e.g. Lodge 1993, Levine and D’Antonio 1999, Kennedy *et al.* 2002, Shea and Chesson 2002). Numerous examples at both the global and local levels demonstrate that often the opposite occurs in freshwater systems (Moyle 1986, Ross *et al.* 2001). Jeschke and Strayer (2005), for instance, showed that there is no clear difference in the probability of fish species becoming established and spreading once introduced from Europe to North America and *vice versa*, suggesting that, at the global level, the biota of North America do not offer more resistance to invaders, notwithstanding that it is less disturbed by humans and species-richer than Europe. At a local level, Lake Victoria, which once contained the richest endemic fish communities on

the planet, was devastated by a single invader, the Nile perch *L. niloticus*, because it encountered neither predation nor competition from indigenous fish (Goldschmidt *et al.* 1993). Mississippi River, once the most speciose of all temperate rivers, has been invaded by several non-indigenous fish, including common carp *C. carpio*, goldfish *C. auratus*, grass carp *Ctenopharyngodon idella* (Valenciennes), striped bass *Morone saxatilis* (Walbaum), rainbow smelt *Osmerus mordax* (Mitchill), rainbow trout *Oncorhynchus mykiss* Walbaum, and white catfish *Ictalurus catus* (Linnaeus) (Burr and Page 1986). Similarly, the zebra mussel has become established at high densities throughout the Mississippi River basin, which contains the world's richest endemic assemblage of freshwater mussels (Ricciardi *et al.* 1998).

The above examples, however, contrast with the results obtained by employing disturbance treatments in pond zooplankton communities (Smith and Shurin 2006). Shurin (2000) found that reducing the abundance of indigenous species allowed four times as many invaders to establish and to obtain 16 times greater total abundance, therefore showing that in some instances local interactions may be strong enough to exclude a large fraction of potential invaders.

(8) Often, freshwater NIS, instead of interfering with one another, facilitate each other's establishment and/or continued existence, and therefore increase the likelihood and the magnitude of their ecological impact, as predicted by the phenomenon of "invasional meltdown" (Simberloff and Von Holle 1999, Simberloff 2006).

Invasive species may facilitate further invasions by direct effects – providing benefits to another invader – and indirect effects – reducing an invader's enemies or enhancing its prey (Ricciardi 2001). Strong experimental evidence was provided by Adams *et al.* (2003), who showed that introduced fish facilitated invasion by the bullfrog (*R. catesbeiana*) in western North America by preying on native macroinvertebrates (such as dragonfly nymphs) that otherwise precluded establishment or severely limited the numbers of frogs. In the Great Lakes, mutualistic, commensal, and asymmetric exploitative interactions facilitated the survival and population growth of many invaders (Ricciardi 2001). *Dreissena polymorpha* facilitated colonization by several invertebrate NIS (Ricciardi *et al.* 1998) because it increased the surface area and spatial heterogeneity, creating settling sites, providing refuge, and trapping sediment and biodeposits. Additionally, *Dreissena* generates filtration currents that are exploited by other invertebrates (Stewart and Haynes 1994) and it is a food source for several introduced fish, i.e. white bass [*Morone chrysops* (Rafinesque)] and round goby [*Neogobius melanostomus* (Pallas)] (French 1993). Its invasion also increased the spread of Eurasian watermilfoil (MacIsaac 1996). The reduction of piscivores by the parasite sea lamprey was an indirect effect that paved the way for invasion by the planktivore alewife

[*Alosa pseudoharengus* (Wilson)] followed by *Oncorhynchus* spp. (Moyle 1986). Finally, sequential invasions by Ponto-Caspian species completed the life cycle of parasitic organisms, such as the trematode *Bucephalus polymorphus* (Baer) of western Europe origin. The introduction of the first intermediate host (the zebra mussel) of the trematode and its definitive host [the pikeperch *Stizostedion lucioperca* (Linnaeus)] allowed it to spread, causing high mortality in its secondary intermediate hosts, the indigenous cyprinids (Combes and Le Brun 1990).

(9) There is still a poor state of knowledge of whether invasive species are the “drivers” of the extinction of indigenous populations or species, or merely the “passengers” along for the environmental ride (MacDougall and Turkington 2005).

Local and global extinctions frequently overlap invasions in space and time. For instance, the loss of genetically distinct populations of unionids in North America has been accelerated by a factor of 10 after the invasion of zebra mussels (Ricciardi *et al.* 1998). Of the 40 fish species known to have become extinct since 1890 in North America, 27 were negatively affected by the introduction of NIS (Wilcove and Bean 1994). However, the dominance of NIS might be an indirect consequence of habitat modifications that by themselves lead to both indigenous species loss and NIS invasion (Gurevitch and Padilla 2004, Didham *et al.* 2005). For instance, the unionid declines began before the introduction in the mid-1980s of zebra mussels and were caused by several stressors, such as habitat destruction and deterioration resulting from water diversion, erosion, an increase in eutrophication (which causes periods of anoxia), pesticides, loss of host fish for parasitic unionid larvae, historic harvesting for the button industry and harvesting for the pearl industry (reviewed in Gurevitch and Padilla 2004). In some instances, successful freshwater invaders have been integrated without eliminations of species from the communities being invaded. In Lake Malawi, East Africa, 12 species of bottom-feeding haplochromine cichlids from one part of the lake were introduced into another part of the lake in which they were absent without any apparent changes in the abundance of the local species (Trendall 1988). After the completion of the Panama Canal in 1914 and the consequent creation of a freshwater corridor between the Rio Chagres on the Caribbean slope and the Rio Grande on the Pacific slope of the Isthmus of Panama, the freshwater fish assemblages of previously isolated drainage basins were enabled to interchange. However, no cases of local extinctions were recorded but species richness increased by 10% in the Rio Chagres and 22% in the Rio Grande (Smith *et al.* 2004). And there are documented cases (see statement 15) of indigenous species that, given enough time, learn or evolve the ability to escape the “evolutionary trap” caused by an invasive species (Schlaepfer *et al.* 2005).

(10) Among the diverse ways that introduced species threaten the existence of indigenous species (e.g. predation, parasitism, vectoring of pathogens, and competition; Mack *et al.* 2000), the most underestimated is hybridization with indigenous species (Olden *et al.* 2004).

Hybridization is thought to alter the integrity of the endemic gene pools of unionids, crayfish, and fish; it produces hybrid swarms that eliminate indigenous taxa often in a very short time frame (Perry *et al.* 2002). Examples are several, especially in fish. Within a 4-year period following its introduction, the non-indigenous pupfish, *Cyprinodon variegatus* Lacépède, was involved in a large-scale introgressive hybridization event with the endemic *Cyprinodon pecosensis* Echelle and Echelle in New Mexico, USA (Echelle and Connor 1989). Similarly, anadromous populations of wild brown trout (*Salmo trutta* Linnaeus) were highly introgressed by stocking with hatchery fish and eventually reduced their fitness (Hansen 2002).

(11) Introduced species have effects at multiple ecological levels in freshwater systems (Simon and Townsend 2003, Chapter 24), but a few studies, mostly focused on salmonids (Simon and Townsend 2003), have analyzed this multifaceted impact (Parker *et al.* 1999).

At the level of individual organisms, invaders may alter the behavior of native species, influencing habitat use and foraging. At the population and community levels, they may induce changes in the abundance or distribution of other species and affect both direct and indirect interactions among populations, respectively. Finally, at the ecosystem level, invaders may change the pathways and magnitude of movements of energy and nutrients.

(12) A first strong danger posed by freshwater invaders to native biota arises if they are either macro-enemies (predators or grazers) or micro-enemies (pathogens or parasites) (Williamson 1996).

Specifically, the NIS posed on the top of the food web or those that are generalized predators (Williamson 1996) are likely to produce marked effects on ecosystem processes (see the case of *P. clarkii*; Chapters 29 and 30) because their impact can “cascade” through the entire food web, altering both ecosystem processes and the behavior of the indigenous species (Townsend 1996). This is especially true in aquatic systems, in which trophic cascades appear to be more common than in terrestrial biomes (Strong 1992). For instance, in California the most successful fish invaders have been piscivores and omnivores (Moyle and Light 1996a), while detritivorous fish seemed to have little effect on indigenous fish assemblages (Power 1990).

(13) A second strong danger posed by freshwater invaders to native biota is their role of “ecosystem engineers”, i.e. species that “directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials” (Jones *et al.* 1994).

Engineering organisms may cause physical modifications to the environment and influence the maintenance or creation of habitats. Their ecological effects on other species occur because of physical state changes caused, either directly or indirectly, by the engineer, and because, as engineers, they affect the control and use of resources by other species. Zebra mussels have all the properties of ecosystem engineers. They change the characteristics of biotic and abiotic environments by their presence and activities, especially their feeding and filtering. These changes are system-wide, affecting species composition, species interactions, community structure, and ecosystem properties (Karatayev *et al.* 2002, Chapters 32 and 33).

(14) In freshwater systems, as in other biomes, invaders may be subject to evolutionary changes that influence several life history characteristics (Cox 2004).

Once established, NIS are freed from the constraints of the gene flow from their parent population and from the biotic pressures of former enemies, they are subject to altered selection pressures, and they impose strong new evolutionary pressures on the indigenous species. Substantial evolution may take place over relatively short timescales (Carroll and Dingle 1996). For instance, following its introduction to Pacific rivers in North America, the American shad, *Alosa sapidissima* (Wilson), evolved geographic changes in its life history patterns in less than a century (summarized in Dingle 1980). In its native rivers in eastern North America, fecundity and the yearly number of spawns vary as a function of latitude, with reduced clutch size and increased repeat spawning more prevalent in northern versus southern rivers. Fish from Pacific rivers are 32–77% (vs. 20–40% from Atlantic rivers) repeat spawners; their age at maturity varies from 3.3 to 3.8 years for males (vs. 4 years) and from 4 to 4.5 years for females (vs. 4.6 years), and their mean lifetime fecundities range from 321,000 to 500,000 eggs (vs. 300,000–350,000). These variations are a function of latitude and water temperature, reflecting rapid post-invasion evolution under selection by local environmental conditions. The western mosquitofish [*Gambusia affinis* (Baird and Girard)] native to North America has shown rapid genetic changes in several locations into which it has been introduced (references in Cox 2004); a period of about 70 generations was sufficient to induce adaptive changes in the life history of the populations introduced into Hawaii, whereas, in the populations introduced into thermal springs in Nevada, changes in body fat content and size at maturity required about 110–165 generations.

(15) In freshwater systems there is growing evidence for adaptive evolutionary responses by indigenous species to NIS and for the influence of such responses on the community dynamics (Lambrinos 2004).

Declines in native populations may be ephemeral if indigenous species are genetically variable in their susceptibility to NIS and can evolve in response to invasion. Alternatively, lack of the ability to evolve in the face of strong selection from invaders can cause extinction (see statement 9). For instance, in 70 years *Rana aurora* Baird and Girard has acquired the ability to recognize the chemical cues emitted by its new predator, the introduced bullfrog *R. catesbeiana*, and behaves accordingly, by reducing their foraging activity and increasing their refuge use, whereas frogs from uninvaded ponds do not change their behavior when presented with bullfrogs (Kiesecker and Blaustein 1997). Evolutionary adaptation may also involve habitat and resource use, leading to the phenomenon of character displacement (i.e. increased difference in quantitative characters of two or more species in areas of syntopy compared to areas of allopatry) (Strauss *et al.* 2006). In the Great Lakes, the bloater [*Coregonus hoyi* (Milner)] is one of the indigenous fish that survived competition with the introduced alewife for zooplankton. Following the explosion of the alewife populations in the 1960s, the bloater shifted its diet from small zooplankton to larger benthic prey (Crowder and Binkowski 1983, Crowder and Crawford 1984). In less than 20 years, this shift was accompanied by an adaptive change of its feeding apparatus that showed a decrease by about 15% in the number of gill rakers (Crowder 1984). Similarly, in North American lakes where bluegill sunfish (*L. macrochirus*) have been absent, the pumpkinseed (*L. gibbosus*) exhibits pelagic and littoral ecotypes as adaptations to the diet of zooplankton (for pelagic forms) and of benthic arthropods and mollusks (for littoral forms). In the lakes where bluegills have been introduced, the pumpkinseed populations exhibited exclusively littoral ecotypes, thus restricting its feeding activity to littoral areas in response to the competition with the dominant newcomer (Robinson *et al.* 2000).

CONCLUSIONS

In recent years, a rising awareness of the economic and ecologic costs caused by invasions in fresh waters has encouraged more proactive research and this has increased our understanding of invasive processes in aquatic systems. Notwithstanding some obvious limitations derived from the relatively small taxonomic coverage of invasion studies and the prevailing focus on certain systems, some general issues regarding freshwater invaders can be raised. First and foremost, predicting the likelihood of the success of a freshwater invader or predicting the invasibility of an aquatic system depends on a detailed understanding of the characteristics of the invader and of the system that is being invaded (Moyle and Light 1996b). But both are likely to be idiosyncratic and complex at the local

level, which makes it difficult to apply some generalized theories of invasion biology. As observed by Simberloff (2006), this is part of the larger problem that “ecology is fundamentally an idiographic science” (p. 917): we will need a large catalogue of case studies in order to generate the level of understanding required to deal with many of the environmental problems (Simberloff 2004).

The “tens rule” does not hold for invasion processes in fresh waters. Introduction is a critical step, so the most effective means of minimizing the adverse impact of freshwater invaders is to prevent species transport in the first place. Once introduced, several species have a high potential to establish, and, once established, eradication is often impossible and mitigation and control are difficult and expensive, if possible at all (Chapters 34, 36, 37, and 38). The successful establishment of a species is positively related to propagule pressure (Chapter 18). A consequence is that the probability of establishment might be lessened by reducing both the number of individuals accidentally released via commerce-related activities and the frequency of such releases. The importance of propagule pressure also alerts us about the need to construct effective legislative barriers against the introduction of “desirable” species that might turn out to be “Frankensteins” (Moyle *et al.* 1986).

The most likely “monsters” in fresh waters are those species whose physiological requirements closely match with the environmental characteristics of the recipient system or those species able to tolerate a wide range of environmental conditions. With some exceptions, the biotic resistance exerted by the recipient community, including its richness in species and complexity, seems to be less effective in countering the establishment of freshwater invaders, while an *r*-selected strategy is only in some cases a prerequisite for a species to become invasive. Similarly, the naïveté of introduced species and the assumed lack of enemies in the recipient community cannot explain *per se* freshwater invasions. Most freshwater communities are not saturated with species (Cornell and Lawton 1992), but instead are capable of supporting greater numbers of them if the pool of potential colonists and the rate of colonization from the pool is increased (Gido and Brown 1999). Introduced species, in fact, often facilitate each other’s establishment and/or their continued existence, therefore increasing the likelihood and the magnitude of the global ecological impact inflicted by biological invasions.

NIS exert multiform effects on the recipient community, most often acting simultaneously at multiple ecological levels. They may pose threats to indigenous species, populations, and genes, and may induce changes to individuals, populations, communities, and ecosystems. The most dangerous species are parasites but also predators or omnivores that may produce trophic cascades in the recipient community, and ecosystem engineers that may cause physical modifications of the environment and may influence the maintenance or creation of habitats. All these recognized impacts of invaders represent, however, only the “tip” of an ecological and evolutionary iceberg (Palumbi 2001). In inland waters, as in the other biomes, the introduction of species may interact

with habitat destruction and degradation, overexploitation of plants and animals, and global climate change to create an “evolutionary revolution” (Cox 2004). And empirical data and theories are urgently needed to enable prediction, understanding, and management of the acute and chronic effects of species invasions (Strayer *et al.* 2006).

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