

Measuring the impact of freshwater NIS: what are we missing?

Francesca Gherardi

There is no data like more data
(Mercer 1998)

INTRODUCTION

Within the last two decades, the dangers that some non-indigenous species (NIS) pose to indigenous species, ecosystem functioning, economic interests, and public health have been abundantly publicized in both the scientific and the popular literatures. A flood of publications, under the format of both synthetic overviews and detailed accounts of some species, accompanied the heightened interest in biological invasions (e.g. Williamson 1996, Mack *et al.* 2000, Cox 2004). Several underlined the dramatic effects that these species induce to the recipient environment and ascribed them to the potential of NIS to (1) alter and disrupt the biotic structure of ecosystems; (2) affect the wellbeing of other species; (3) push many species toward extinction; (4) reduce the productivity of agriculture and aquaculture; and (5) pose threats to human health and to the health of domesticated or semidomesticated plants and animals (Cox 2004). The media often featured both general problems (e.g. Bright 1998, Devine 1999, Di Justo 2006) and “the invader of the week” (Simberloff 2003a). Many nations (e.g. New Zealand, South Africa, USA, Canada, European Union) and international organizations (e.g. IUCN) began to consider the ecological impact of some NIS as one of the world’s most serious conservation issues and several

attempted to improve administrative and legal solutions (Simberloff 2003a). Meanwhile, two points have become universally clear: (1) the introduced species already established in natural areas are far more numerous than managers can really control and (2) their number is inevitably destined to increase as a consequence of the exponential growth of transport and commerce (Ewell *et al.* 1999).

Luckily, not “every barrel contains bad apples” (Sagoff 1999) and not necessarily “the worst of species” are “the ones that are alien and numerically successful” (Slobodkin 2001). On the contrary, the enormous benefits of some of the introduced species are universally recognized. Humans, it has been claimed, depend heavily on several non-indigenous organisms for food, shelter, medicine, ecosystem services, aesthetic enjoyment, and cultural identity (Ewell *et al.* 1999). Also among those species that have been inadvertently introduced by man, as many as 80–90%, according to the “tens rule” (Williamson 1996) – or less than 75%, at least for some taxa, according to Jerscke and Strayer (2005) – may actually have minimal detectable effects on the environment.

Indeed, the classification of NIS in function of the good and the bad they provide to both the environment and humans is implicit in the formal definition of “invasive species” first given by the 1992 Rio Convention on Biological Diversity (CBD 2001) – “alien species which threaten ecosystems, habitats, or species” – and then by 1999 President Clinton’s Executive Order 13112 – “alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health” (Clinton 1999). Unfortunately, in the “continuum of kaleidoscopic interactions” that characterizes the natural world (Carlton 2002), the attribute “invasive” does not divide conveniently species into taxa that have an impact and those that do not but needs to be assessed on a case-by-case basis.

It is certainly critical to face this recognized difficulty in classifying NIS when the purpose is to stimulate management options and policy actions. Priorities based on assessment of impacts need to be set at all scales, from management of local reserves to national and international policy decisions. So, impact measurements may allow for generating a rank-ordering of major risks to ecosystems and natural communities and for guiding ecosystem restoration efforts. But they also help test hypotheses about how communities function and what factors inhibit or facilitate invasions. Ultimately, the availability of quantitative data will make scientists able to generalize, and even predict, which species will most likely be “invasive” (Parker *et al.* 1999).

MULTILEVEL IMPACTS

Since 1984, the research focused on the impact of freshwater NIS on species, communities, and ecosystems has expanded greatly, especially in North America, New Zealand, Australia, and Western Europe (Fig. 1). Introduced plants, bivalves, and fish were the privileged organisms for impact studies in the 1980s,

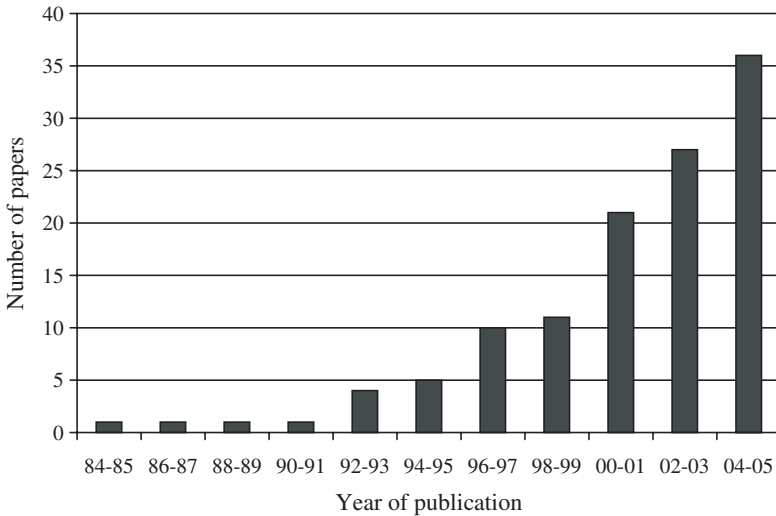


Fig. 1 The rise in the number of publications focused on the impact of freshwater non-indigenous species (NIS). Papers were identified via keywords from Biosis (from 1969 to April 2006) and later selected, reaching a total of 123. Only papers published before 2006 (118) are included here.

but the diversity of the analyzed taxa widened with time, including today also several arthropods (mainly crustaceans) and a few amphibians, e.g. *Bufo marinus* (Linnaeus), reptiles, e.g. *Trachemys scripta elegans* (Wied), and mammals, e.g. *Mustela vison* Schreber (Fig. 2). However, also within the taxa that have been subject to a more extensive research, only a narrow range of genera and families was used as paradigms of freshwater invasions, namely dreissenids (83%), gammarids (38%), and salmonids (50%). Obviously, this concentrated effort on a few organisms is not the reflection of the lack of ecological impacts by other taxa, but the result of some idiosyncratic factors, often interacting (e.g. productivity of laboratories, scientific or economic interest, and easiness of experimentation).

A similar unequal distribution of studies is to be found among the biological levels at which the impact has been measured. Under the classification of Parker *et al.* (1999), five levels of biological complexity may be affected by NIS, namely: (1) individuals (life history, morphology, behavior); (2) population dynamics (abundance, population growth, etc.); (3) genetics (including hybridization); (4) communities (species richness, diversity, trophic structure); and (5) ecosystem processes (nutrient availability, primary productivity, etc.). To these levels a sixth may be added, the “societal” level of impact, in which the focus is on the economic damage that introduced species may inflict to human societies, including social and ethical problems associated with their possible harm to human health.

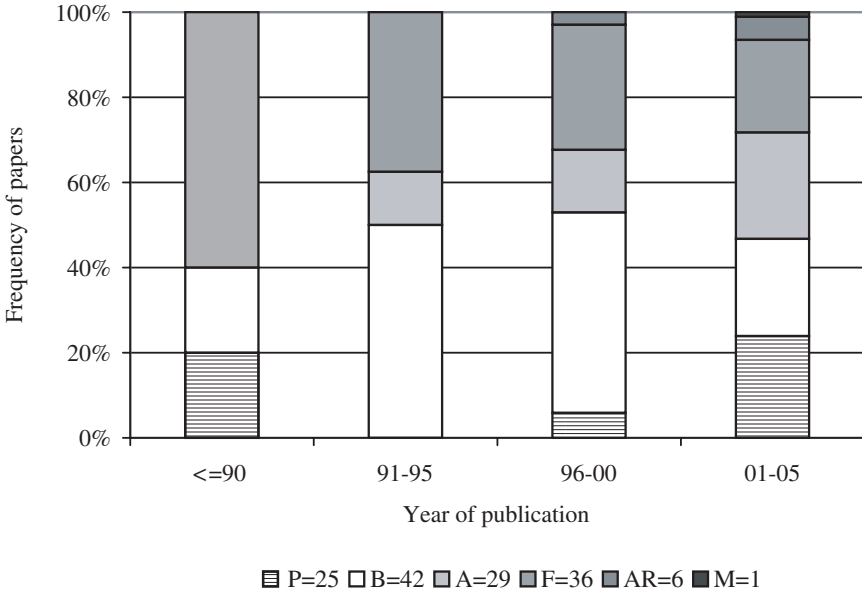


Fig. 2 Distribution per taxon (P = plants, B = bivalves, A = arthropods, F = fish, AR = amphibians and reptiles, and M = mammals) of the articles published before 2006 describing the impact of NIS (see Fig. 1 for the used method of retrieval) classified per periods of 5 years. Before 1990: *n* = 5, 1991–1995: *n* = 8, 1996–2000: *n* = 34, 2001–2005: *n* = 92. Single studies that reported the impact of more than one NIS were tallied more than once.

Population-level effects, eventually leading to a decline in the abundance and diversity of indigenous biota, have been documented much more extensively in the literature than the other biological effects (Fig. 3). Conversely, the most understudied impacts are genetic effects, notwithstanding their potential to provide insights about the still controversial role of NIS to speciation (e.g. Rosenzweig 2001).

There is a nearly unanimous belief that several NIS contribute to the threatening of an ever increasing number of indigenous species. In their analysis of the causes of threat for 1,880 of the nearly 2,500 species now imperiled in the USA, Wilcove *et al.* (1998) clearly showed that introduced species are the second leading factor (after habitat degradation/loss); they endanger, alone or in conjunction with other causes, a total of 49% of species – more than the next three categories (overexploitation, pollution, and disease) combined. This is true also for freshwater indigenous taxa, which were found to suffer from competition with, and/or from predation by introduced species, at percentages that reach 27, 53, 17, and 4 in amphibians, fish, mollusks, and crayfish, respectively. However, NIS are not viewed as the only responsible for biodiversity loss;

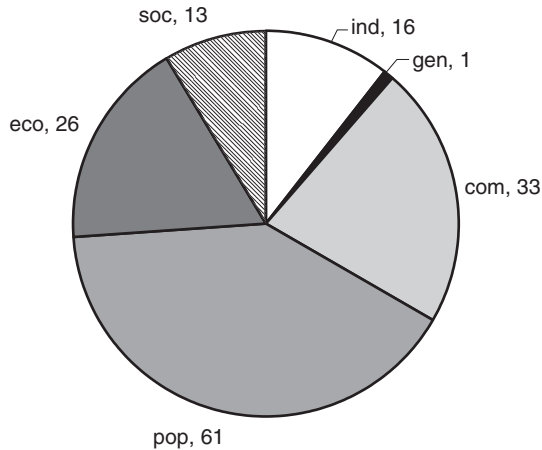


Fig. 3 Number of articles published until April 2006 describing the impact of NIS (see Fig. 1 for the method of retrieval) at six different levels of biological complexity: individual (ind), genetic (gen), population (pop), community (com), ecological (eco), and societal (soc). Single studies that reported the impact of more than one biological level were tallied more than once.

much stress has been recently given to their ancillary role in inducing extinctions or, in the words of Gurevitch and Padilla (2004), to their being “the final nail in the coffin” and “the bouquet at the funeral”.

Surprisingly few are those freshwater organisms whose impacts have been analyzed at multiple biological levels. One is the Ponto-Caspian zebra mussel, *Dreissena polymorpha* (Pallas), certainly the most striking example of a species that has been able to change the nature of entire communities. Since the 1980s, after its introduction to the North American Great Lakes, the invasive potential of *D. polymorpha* has attracted much scientific attention, soon becoming the most thoroughly investigated freshwater invader. Today we dispose of an enormous amount of information about its wide-reaching effects on several invaded lakes and rivers in eastern North America (e.g. Nalepa and Schloesser 1993, Strayer *et al.* 1999) and central Europe (Karatayev *et al.* 1997). The invasiveness of this species is widely facilitated by various biological characteristics (i.e. high fecundity, planktonic veliger larvae enabling its fast diffusion, and byssal threads permitting firm attachment to hard substrates) so that, once introduced into a new system, it soon becomes abundant, even exceeding 10 times the biomass of all other indigenous benthic invertebrates. Its rapid population growth makes this species competitively dominant over resident benthic fauna, including several endangered or threatened bivalves. In conjunction with its close relative, the quagga mussel, *Dreissena bugensis* (Andrusov), zebra mussel colonization has highly accelerated the local extinction of unionid

species as an effect of fouling (i.e. growing in dense clusters on unionid shells) or competing for seston (Strayer 1999). In Lake St. Clair, all the indigenous freshwater mussels were eliminated by 1997 after the appearance of zebra mussel in the early 1980s (Ricciardi *et al.* 1998, Nalepa *et al.* 2001). By contrast, there are few reports of mass mortalities of resident mussels in the European invaded lakes and rivers (e.g. Lake Balaton in Hungary, Lake Bourget in France, Lake Mikolajskie in Poland, and Lake Hallwill in Switzerland; references in Ricciardi *et al.* 1998). A plausible explanation of this different behavior between continents might be that in Europe indigenous bivalve fauna had been previously exposed to *D. polymorpha* during the Pleistocene era and had already acquired counteradaptations to it (e.g. avoidance behavior through deeper burial in sediment, less ecological sensitivity to fouling) (Ricciardi *et al.* 1998).

Functioning as an “ecosystem engineer” – i.e. a species that “directly or indirectly controls the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials” (Jones *et al.* 1994), *D. polymorpha* can affect all components of the invaded freshwater systems at multiple levels (MacIsaac 1996, Strayer *et al.* 1999, Karatayev *et al.* 2002), as synthesized in Fig. 4. It increases water transparency (by 1.5–2 or more times) and the rate of conversion from organic to inorganic matter; it decreases the amount of seston in the water column (by 1.5–10 times), together with organic matter, biochemical oxygen demand (up to 1.5 times), and the biomass of phytoplankton (1–5–4 times); it affects bacterioplankton by e.g. consuming large bacteria and facilitating growth of small bacteria with excretion and release from protozoan predators; it favors growth and production of macrophytes, periphyton, and benthic algae by increasing water transparency; it changes the abundance and diversity of zooplankton community by preying on microzooplankton and offering refuges to large cladocerans; it alters the abundance and diversity of zoobenthos by offering shelters to e.g. snails and gammarid amphipods, competing for food and space or fouling them (e.g. macrophytes, indigenous mollusks); it enhances abundance of benthivorous and, potentially, planktivorous fish; it transfers the accumulated organic pesticides and polychlorinated biphenyl compounds to their predators, mostly waterfowl, fish, and crayfish; and it diverts production and biomass from pelagic to benthic food webs, shifting ecosystems to an alternative state. A gross estimate of *D. polymorpha*'s monetary cost has been recently provided by Pimentel *et al.* (2005): in the USA alone direct costs, mostly due to its fouling and clogging water intake pipes, water filtration, and electric generating plants, amounted to about US\$1 billion per year. If added to the indirect and non-market costs associated with the altered ecosystem processes and reduced indigenous biodiversity, the overall damage inflicted to the human economy by zebra mussel should be enormous. However, notwithstanding this, prevention seems to be currently underfunded. A recent analysis (Leung *et al.* 2002) suggested that it would be beneficial to spend up to US\$324,000 per year to obtain a modest reduction in the probability of zebra mussel invasion into a single lake. For

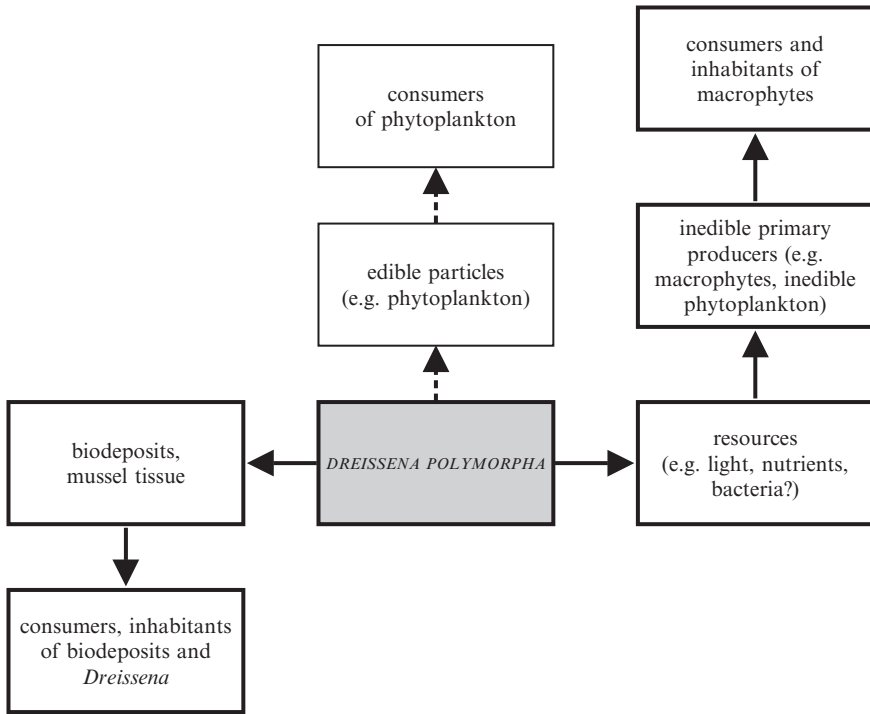


Fig. 4 Ecological changes induced by increasing populations of the zebra mussel (*Dreissena polymorpha*). Bold boxes and lines denote components that tend to increase with the bivalve population, and thin boxes and dotted lines denote components that tend to decrease. (Modified after Strayer *et al.* 1999)

comparison, in 2001 the US Fish and Wildlife Service distributed to all States combined a total of US\$825,000 for prevention and control efforts for all aquatic NIS in all lakes.

A second celebrated case of freshwater invader is the Nile perch, *Lates niloticus* (Linnaeus), purposively introduced into Lake Victoria in the 1950s to boost fisheries (Seehausen *et al.* 1997). The dramatic result of this introduction is universally recognized as “the first mass extinction of vertebrates that scientists have never had the opportunity to observe” (Kaufman 1992). Only in the early 1980s was an explosive increase of this species observed leading to a rapid collapse of the species-rich Lake Victoria ecosystem and its replacement by a highly simplified, largely exotic-based community. Nile perch population explosions were accompanied by the disappearance, mostly occurring between 1975 and 1982, of about 200 endemic haplochromine cichlids of the 300+ species that previously were known to occupy a great variety of niches in the lake. By 1983 in Kenya and by 1986 in Tanzania, the indigenous fish community had

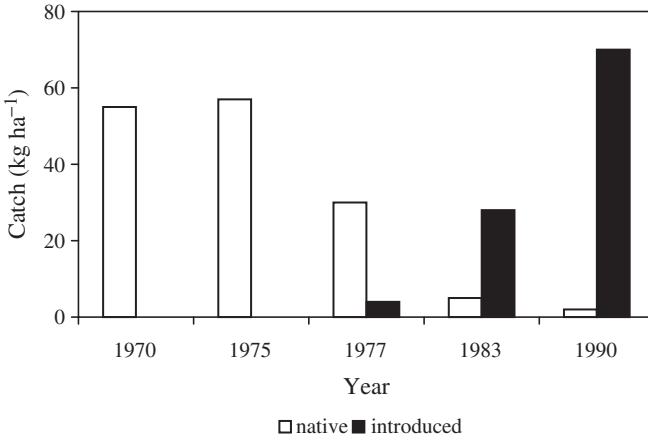


Fig. 5 Demise of the native fish of Lake Victoria, as illustrated by surveys in Kenyan water by the Kenyan Marine and Fisheries Research Institute. Standing stock estimates derived from the following numbers of hauls: 1969–1970 = 19; 1975 = 69; 1982–1990 = 41. (Modified after Kaufman 1992)

been virtually destroyed, while the Nile perch comprised more than 80% of the catch. The remaining 20% consisted of the introduced Nile tilapia, *Oreochromis niloticus* (Linnaeus), an indigenous pelagic minnow, *Rastrineobola argentea* (Pellegrin), and a small remnant of other indigenous fish (Fig. 5).

Coincident with the Nile perch explosion, an abrupt change in the physical environment of the lake was recorded. Today the region between 50 and 25 m in depth is subjected year-round to frequent severe deoxygenation, whereas before 1978 aerobic line penetrated into the lake’s deepest waters. So, indigenous fish, seeking reliable refugia in their seasonal moves between shallow and deep water habitats, “may have faced a choice of death by asphyxiation in deeper water or death by Nile perch predation in the more oxygen-rich shallows” (Kaufman 1992). Among the myriad other aspects of the lake’s ecology that appear to have changed, productivity and turbidity have both increased, papyrus swamps declined, and snails greatly increased in abundance (Kaufman 1992). The recent blooms of blue-green algae have been imputed to the disappearance of phytoplanktivore haplochromines, while the zooplanktivore haplochromines have been replaced by *R. argentea* (Goldschmidt *et al.* 1993). Finally, the indigenous atyid prawn *Caridina nilotica* (P. Roux), a potential consumer of decaying algae, has replaced the bottom-dwelling detritivorous haplochromines, as the result of several concomitant factors, such as the availability of sheltered habitats for prawn juveniles in the increased submerged vegetation and/or the disappearance of their haplocromine predators (Goldschmidt *et al.* 1993).

The story of the Nile perch also highlights the need for a critical evaluation of data in order to properly understand the role of NIS in species extinctions. The decline of cichlids started long before the introduction of the Nile perch, dating back to the 1920s with the development of railroads, erosion, and shoreline destruction. Then, the urbanization of the 1970s increased eutrophication and decreased lake transparency that affected color vision of many cichlids leading to reduced sexual selection, incorrect mate choice, and breakdown of reproductive isolation; increased nutrients produced anoxic events and favored the invader water hyacinth, *Eichhornia crassipes* (Martius). In its turn, this latter species may have altered nursery areas for juvenile fish (reviewed in Gurevitch and Padilla 2004).

Today, an appraisal of the monetary revenues that local people have obtained from the introduction of the Nile perch may be controversial. Certainly, the importance of biodiversity is often questioned when a commodity of immediate value appears in its place (Kaufman 1992). And there is much evidence that local people have taken real profits from the Nile perch commerce. During 1975–1989, the introduction of the Nile perch into Lake Victoria was followed by (1) production gains amounting to about US\$280 million (at 1989 prices); (2) increased number of fishermen and of their dependents by 267% (more than 1.2 million people depend today entirely on fishery); (3) ameliorated food quality for greater numbers of people; (4) intensified exports that reached about 5–10% of the lake's production (Kasulo 2000). However, these estimates do not take into account the changes in the level and distribution of income, and in the ease of entry to fishery. The new fishery that required expensive fishing tools and refrigerating systems has had the effect of concentrating income in the hands of foreign investors and of a small minority of local fishermen (Kasulo 2000).

COMPLEXITY IN THE IMPACTS OF FRESHWATER NIS

Freshwater NIS are well known to exert an immediate impact on the behavior displayed by resident species, which may change their habitat use or activity patterns in response to the new predators or competitors. For instance, in New Zealand, larvae of mayfly *Nesameletus ornatus* Eaton are active on rock surfaces both day and night and drift in the water column when they coexist with indigenous predators (galaxiid fish). Conversely, in rivers invaded by brown trout, they mostly remain beneath rocks during the day and usually only forage on exposed surfaces and drift in the water column at night. This modified behavior was retained when mayflies from brown trout waters were tested in experimental streams without fish or with galaxiids (McIntosh and Townsend 1994). Non-indigenous salmonids also restrict the indigenous fish and amphibians to lesser preferred habitats, where they suffer reduced feeding activity and efficacy (references in Simon and Townsend 2003). Antipredator behaviors

may also quickly evolve in the presence of a non-indigenous predator. In Oregon, when red-legged frog (*Rana aurora* Baird and Girard) tadpoles were exposed to chemical cues of the introduced bullfrog (*Rana catesbeiana* Shaw), individuals that had coexisted with bullfrogs showed strong antipredator responses by hiding or reducing their activity, whereas those from populations without bullfrogs did not (Kiesecker and Blaustein 1997).

When no changes at the individual level occur, when they occur but are insufficient, or when organisms become “trapped” by their evolutionarily responses to formerly reliable cues (Schlaepfer *et al.* 2005), the survival rate of resident species may be affected and the abundance of their populations inevitably decreases. Extreme consequences are the endangerment that indigenous species may suffer from the introduction of NIS or their local or global extinctions (Mack *et al.* 2000). The mass extinctions of endemic fish and mussels recorded in Lake Victoria and in North American lakes and rivers, respectively, are not the only environmental catastrophes to which NIS have contributed. Non-indigenous fish are at least partially responsible for the extirpation of 68% of the 40 fish species and subspecies declared extinct over the past 115 years in North America (Miller *et al.* 1989). The combined pressure of urbanization, overexploitation, and introductions of NIS has led to the global extinction of *Pacifastacus nigrescens* (Stimpson) in northern California (Bouchard 1977) and a similar process is ongoing in the same area for Shasta crayfish, *Pacifastacus fortis* (Faxon), today displaced at several locations by habitat loss and competitive interactions with *Pacifastacus leniusculus* (Dana) (Light *et al.* 1995, Chapter 28).

The mechanisms leading to biodiversity loss are many and abundantly explored in inland waters. They range from predation/parasitism, to competition for resources, interference competition, and transmission of parasites. So, the sharp decline in macroinvertebrates that have been recorded in central-European streams after the appearance of the Ponto-Caspian crustacean amphipod *Dikerogammarus villosus* (Sowinsky) in the early 1990s was imputed to the ability of this invasive species to prey upon more macroinvertebrates than the resident species did (Dick and Platvoet 2000, Krisp and Maier 2005). Invasive amphipods, although under the regulatory control of acanthocephalan parasites (MacNeil *et al.* 2003), are also able to kill and consume individuals of close relative species (Dick and Platvoet 2000). Similarly, the decreased abundance of several dominant species of zooplankton [*Daphnia retrocurva* Forbes, *Bosmina longirostris* (O.F. Müller), and *Diacyclops thomasi* (Forbes)] recorded in Lake Ontario (North America) coincided with the increased occurrence of the introduced predator cladoceran *Cercopagis pengoi* (Ostroumov) (Laxson *et al.* 2003).

Food competition with amphibian and reptile NIS – larvae of *R. catesbeiana* and *Osteopilus septentrionalis* (Duméril and Bibron) or adults of *T. scripta elegans* – was hypothesized to cause decreased survivorship, reduced growth rate, and delayed metamorphosis in the larvae of indigenous anurans – *Rana boylei* Baird, *Hyla regilla* Baird and Girard, *Bufo terrestris* (Bonnaterre), and *Hyla cinerea*

(Schneider) – (Kupferberg 1997, Smith 2005) or was found to determine weight loss and high mortality in the European turtle *Emys orbicularis* (Linnaeus) (Cadi and Joly 2004). Similarly, in the US waters, the plankton feeding, non-indigenous alewife, *Alosa pseudoharengus* (Wilson), heavily competes for prey with indigenous fish. Only a few indigenous fish were able to survive to its competition. Among them, the bloater, *Coregonus hoyi* (Milner), was able to coexist with alewife by shifting its diet from small zooplankton to larger benthic prey (Crowder 1984).

NIS may also outcompete indigenous species through direct aggression and/or transmission to them of diseases and parasites. So, the dominance in agonistic interactions of North American crayfish species over the European indigenous species (e.g. Gherardi and Cioni 2004) and the ability to transmit to them the oomycete *Aphanomyces astaci* Schikora – the etiological agent of the crayfish plague (e.g. Alderman and Polglase 1988, Diéguez-Uribeondo and Söderhäll 1993) – have both contributed to the constant contraction of indigenous crayfish biodiversity in Europe (Chapter 28).

The potential for introgressive hybridization is an additional but still elusive threat posed by NIS to closely related indigenous species. Introgression can increase the likelihood of extinction by reducing fitness and the ability of populations to changing conditions. However, the occurrence and consequences of hybridization between indigenous species and NIS have been overlooked in most freshwater species with the exception of fish. Genetic assimilation has led to the extinction of about 38% of North American indigenous fish species (Cox 2004). Cutthroat trout (*Salmo clarkii* Richardson), Apache trout (*Oncorhynchus apache* Miller), and Gila trout (*Oncorhynchus gilae* Miller) have undergone extensive hybridization with the invading rainbow trout, *Oncorhynchus mykiss* (Walbaum) (references in Simon and Townsend 2003). Stocking of conspecifics or escape of farm individuals may result in disruption of local adaptations and reduction of genetic diversity, as shown in brook trout, *Salvelinus fontinalis* (Mitchill) (Hayes *et al.* 1996), and in the Atlantic salmon, *Salmo salar* Linnaeus (Fleming *et al.* 2000). If hybrid individuals show greater fitness or vigor, the pure indigenous species may become extinct by being absorbed into the gene pool of a NIS with high invasive rates. This phenomenon of “genetic assimilation” has been reported in crayfish. For instance, matings between *Orconectes rusticus* (Girard) females and *Orconectes propinquus* (Girard) males yield a fecund and highly competitive progeny, which is replacing the indigenous species in Trout Lake, Wisconsin, USA (Perry *et al.* 2001, 2002, Chapter 28). Indigenous species are threatened by hybridization with a NIS also when the hybrids do not succeed, simply because crossbreeding reduces the number of new offspring added to the species’ own population. For instance, females of the European mink, *Mustela lutreola* (Linnaeus), hybridize with males of the introduced North American mink, *Mustela vison* (Schreber); embryos are invariably aborted, but the wastage of eggs exacerbates the decline of the indigenous mink (Rozhnov 1993).

Other subtler evolutionary changes (Cox 2004) may influence several life history characteristics of both NIS and indigenous species in a relatively short-time scale. In fact, once established, NIS are freed from the constraints of gene flow from their parent population and from the biotic pressures of former enemies, are subject to altered selection pressures, and impose strong new evolutionary pressures on indigenous species. As an example, Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), native to the Pacific coast of North America, was introduced to New Zealand in 1901–1907. From the initial introduction, the species has colonized several river systems along the eastern coast of the South Island, giving rise to isolated populations. These populations, after about 30 generations, now differ genetically among themselves and from their source population in California by several morphological and reproductive features (Quinn *et al.* 2001).

At the community level, the potential by NIS to alter trophic interactions has been abundantly studied in several salmonids. Brown trout (*Salmo trutta* Linnaeus), introduced into New Zealand in 1867 (Townsend 1996), has been responsible for the local extinction of several indigenous galaxiid fish; it also profoundly affects 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. Several other NIS are reported to induce trophic cascades, e.g. rainbow trout (*O. mykiss*) (Nyström *et al.* 2001) and crayfish (*P. leniusculus*, Nyström 1999, and *O. rusticus*, Charlebois and Lamberti 1996). Similarly, by preying on crustacean zooplankton, the cladoceran *C. pengoi* seems to cascade down the foodweb in Lake Ontario to increase phytoplankton abundance (Laxson *et al.* 2003).

The impact of NIS on ecosystem processes has rarely been analyzed in freshwater habitats, except for invasive plants. Their induced changes to nutrient cycling were found to range from being inconsistent (e.g. Findlay *et al.* 2002) to causing enormous consequences. For instance, purple loosestrife, *Lythrum salicaria* (Linnaeus) was found to accelerate P turnover (twice that of indigenous cattail *Typha angustifolia* Linnaeus) leading to low porewater nutrient concentrations (Templer *et al.* 1998), whereas common reed *Phragmites australis* (Cav.) Trin. ex Steud. is capable to sequester a large amount of nitrogen and to reduce nutrient availability to other organisms (Templer *et al.* 1998).

THE IMPACT ON HUMAN ACTIVITIES

A limited understanding of the inextricable link between nature and economy may be responsible for the often failed attempts of invasion biologists to arouse public and governmental support for the prevention or control of invasions (Mack *et al.* 2000). Indeed, the direct and indirect economic consequences of

the ecological impact of NIS are well acknowledged but as yet poorly quantified. Scientific studies centered on the damage they inflict to human activities are still relatively rare, notwithstanding the increased general interest in the discipline of ecological economics.

Recently, Pimentel *et al.* (2005) attempted to tabulate the damage that NIS inflict to the US economy and the expenses needed for their control. The total cost in 2004 reached US\$120 million per year, which appears to be “a formidable loss” even for a productive industrialized society such as the USA (Mack *et al.* 2000). The introduction of about 40 freshwater fish species alone was estimated to cause US\$5,400 million in losses each year (Pimentel *et al.* 2005). A similar study has been recently conducted in Canada. Colautti *et al.* (2006) attempted to quantify the economic cost associated with 13 nuisance species (freshwater, marine, and terrestrial), including control costs, reduced yield, reduced land use, trade bans on exported goods, compensation paid to farmers, health care costs, and reduced tourism and tourism-related revenues. Comprehensive data were lacking for virtually all the analyzed species, providing relatively modest costs (an overall of CAN\$187 million per year) if compared with two non-indigenous disease outbreaks (SARS and mad cow disease), which posed an additional cost of CAN\$2.5 billion in 2003. Zebra mussels, quagga mussels, and the sea lamprey, *Petromyzon marinus* (Linnaeus) made up the bulk of CAN\$32.3 million per year in characterized costs to aquaculture and aquatic-related industries. Of these species, dreissenid mussels have affected primarily industries and municipalities with a variety of direct costs. The sea lamprey, which attacks salmonids and other valuable fish, costs CAN\$22 million per year to the Great Lakes Fishery Commission – a joint agency administered by the USA and Canadian federal governments – for its control and for research. However, costs incurred through reductions in harvest of commercial and sports fish would likely be much higher without this expenditure.

Other detailed analyses are scarce in the published literature. An example might be the estimated loss of US\$30–45 million per year in Lake Tahoe (California) due to the degradation of resources by the introduced Eurasian watermilfoil (*Myriophyllum spicatum* Linnaeus) (Eiswerth *et al.* 2000). A similar analysis was done by Zavaleta (2000): the invasion of riparian tamarisk led to an increased sedimentation in river channels followed by frequent and severe floods. This translates to an overall cost of US\$280–450 ha⁻¹ that adds to US\$7,400 ha⁻¹ needed to eradicate the invader and to restore indigenous riparian communities. Conversely, still anecdotal is the monetary damage inflicted to water transportation, recreation activities, and hydraulic systems by other infamous invasive species, e.g. the water hyacinth (Gao and Li 2004) and *Limnoperna fortunei* (Dunker) (Oliveira *et al.* 2006).

Even fewer are the studies that have attempted to assign monetary values to species extinctions and losses in biodiversity, ecosystem services, and aesthetics. One example comes from the analysis by Spencer *et al.* (1991) of the impact of

the opossum shrimp, *Mysis relicta* (Loven), on the Flathead Lake in Montana, USA. This species was introduced between 1968 and 1975 by the Montana Department of Fish, Wildlife and Parks to provide a supplemental prey for kokanee salmon, *Oncorhynchus nerka* (Walbaum), the dominant sport fish in the area. However, the shrimp did not become significant components of the kokanee diet, possibly because their vertical migration in deep waters during the daytime precluded fish from exploiting the new prey. On the contrary, they led to marked changes in the community initiating a trophic cascade to higher trophic levels. The density of two cladocerans – *Daphnia longiremis* Sars and *Leptodora kindtii* (Focke) – decreased as an effect of their voracious predation. Consequences were the crash of the population of kokanee, from 26,000–118,000 annual spawners in 1979–1985 to 50 in 1989, and the reduction in the angler catches from 100,000 kokanee through 1985 to fewer than 6000 in 1987 to no reported catches in 1988 and 1989 (Spencer *et al.* 1991). The abundance and diversity of birds and mammals feeding on spawning kokanee, carcasses, and eggs, sharply declined. Among the others, flagship species such as bald eagles and grizzly bears reduced their density. As a result, the number of tourists declined from 46,500 in 1983 to less than 1,000 in 1989 with an obvious economic loss for local activities based on ecotourism (Williamson 1996).

The damage that freshwater NIS may inflict on human health is well exemplified by the 1991 outbreak of cholera in Peru. It caused the death of over 10,000 people after ballast water containing the microbe *Vibrio cholerae* Pacini was released and infected drinking water (Bright 1998). However, conflicting insights emerge from the literature, especially concerning introductions of species into tropical areas. On the one hand, introduced snails may be extremely dangerous, due to their serving as intermediate hosts for some animal or human parasites, as in paragonimiasis. Invasive plants, such as water hyacinth, may also offer protection from predators to some snail species, such as *Biomphalaria sudanica* (Martens), host of *Schistosoma mansoni* Sambon (Plummer 2005). On the other hand, some introduced snails may be also beneficial due to their ability to outcompete indigenous snail vectors of blood and liver flukes (Pointier 1999).

MEASURES OF THE IMPACT

According to Parker *et al.* (1999), much of the discussion about the ecological effects of invasive species has been purely anecdotal in nature. Any conclusions about impacts, or the lack thereof, are often based upon “conjecture, suppositions, and presumptions” (Carlton 2002). The result is that “the case against introducing NIS is often poorly supported even for some of the most infamous invaders” (Parker *et al.* 1999).

This picture seems to be changing in the last few years, at least in the case of freshwater species. More than 100 studies on a total of the 123 here analyzed

provide a quantitative estimate of the different categories of the impacts produced by NIS. Several have adopted a correlative approach making useful diachronic and synchronic comparisons between sites. However, in a few of these studies attempts have been made to control for naturally different responses of the invaded community over space and time or for confounding variables in the environment, such as pollution, harvesting, climate change, or other established NIS (Witt *et al.* 2005).

Many drawbacks of quantitative studies derived from the paucity of historical data needed to compare the same area before and after the invasion event. One of the few examples comes from the study of Wei and Chow-Fraser (2006) on the effects of multiple stressors [water level fluctuations, human population growth, and percent cover of nonindigenous *Glyceria maxima* (Hartman) Holmberg 1919 and *P. australis*] on the indigenous *Typha latifolia* Linnaeus marsh community in Lake Ontario (Canada). Studies of historical records, human population census, and field vegetation maps clearly showed that each stressor, including NIS, may explain alone the observed changes in indigenous *T. latifolia* community but that their synergistic interaction induces even greater detrimental effects on it.

The impact of NIS has been more extensively investigated in multiple sites or, most often, in the same site at different stages of invasion. For instance, field and laboratory studies in Northern Ireland showed that the non-indigenous *Gammarus pulex* (Linnaeus) has a greater impact on the composition of the macroinvertebrate community than the indigenous *Gammarus duebeni celticus* Stock and Pinkster due to its more intense predation on ephemeropterans, dipterans, and plecopterans (Kelly *et al.* 2003, Kelly and Dick 2005). These effects seemed to be independent of other environmental factors (Kelly *et al.* 2003) but they also operated at larger scales than those detected within individual rivers (Kelly and Dick 2005). Often comparisons have been made between sites with and without the invader; e.g. some Canadian lakes invaded by the non-indigenous predatory cladoceran *Bythotrephes longimanus* (Leydig) showed a significantly lower richness in crustacean zooplankton species (for 30%) than the non-invaded lakes (Boudreau and Yan 2003). Surprisingly, the ecological role of a species has never been compared between the indigenous and the colonized communities. Certainly, the impacts of potentially invasive species cannot be reliably predicted from their effects in the native ranges. For instance, the virulence that the oomycete *A. astaci* exerts toward the European crayfish could not have been forecasted from its innocuous effects toward North American species (Reynolds 1988). However, information about the biology of an invader in its native range would, on the one hand, provide a useful baseline for unraveling its ecological role and, on the other, greatly improve our understanding of the factors eliciting its invasive behavior in novel areas.

Still today, few studies are adopting stable isotope techniques to quantify the food-web consequences of invasions. Using this method, Vander Zanden *et al.* (1999) found that the indigenous top predator, the lake trout, *Salvelinus*

namaycush (Walbaum), had more negative $\delta^{13}\text{C}$ values and lower trophic positions (3.3 vs. 3.9) in two Canadian lakes invaded by the introduced small-mouth bass, *Micropterus dolomieu* Lacepède, and rock bass, *Ambloplites rupestris* (Rafinesque) than in two non-invaded lakes, as an indication of the NIS-induced shift from a fish-based to a plankton-based diet in lake trout.

Much more numerous are the studies analyzing differences in diet breadth and/or in the position within the food web between invasive and non-invasive related taxa or between invasive taxa. For instance, laboratory experiments revealed that invasive *Gambusia* species consistently fed at higher rates than two non-invasive congeneric species, although displaying similar feeding preferences (Rehage *et al.* 2005). Multiple methods (stable isotope analysis, feeding experiments, mesocosm experiments, and gut content analysis) showed large differences in the potential impact on aquatic food webs of two non-indigenous decapod crustaceans, the Chinese mitten crab, *Eriocheir sinensis* (H. Milne Edwards) and the red swamp crayfish, *Procambarus clarkii* (Girard), in the San Francisco Bay (USA) (Rudnick and Resh 2005). Conversely, using stable isotope techniques, zebra mussel (*D. polymorpha*) and quagga mussel (*D. bugensis*) were found to share suspended detritus as the main food item and to compete with zooplankton and with each other for seston (Garton *et al.* 2005).

Obviously, both the population dynamics of an NIS and the responses by the recipient community (e.g. its species abundance) are expected to vary over time; therefore, any estimate of the impact of an NIS may greatly depend on the temporal scale of the study. Some successful invaders increase steadily to a stable equilibrium density, but others exhibit a more complex behavior, initially reaching very high densities (“boom”) but then declining to lower levels (“bust”). And the same NIS may show booms and busts in some areas and steady logistic increase in others, as found for the zebra mussel in eastern Europe (e.g. Karatayev *et al.* 1997). Notwithstanding these well-known idiosyncratic dynamics of NIS populations (Williamson 1996), a minority of studies has been conducted on the impact of freshwater NIS over a long-time scale of analysis (e.g. Yan and Pawson 1997, Johannsson *et al.* 2000, Yan *et al.* 2002, Laxson *et al.* 2003, Barbiero and Tuchman 2004). This is not surprising: long-term monitoring requires a pattern of time and money allocation, which is usually extraneous to the rhythms of both academy and funding agencies, except for few cases (e.g. McCarthy *et al.* 2006). Conversely, long-term data sets would provide the indispensable background to help us assess the biotic resilience of the community, predict the restoration potential of the ecosystem, and finally understand the ecological and evolutionary mechanisms accompanying the integration of NIS in the system. By understanding the long-term feedbacks between invasive species and the invaded communities and ecosystems, “we will be able to evaluate alternative management approaches for well-established invaders, and be better able to identify which new invaders should be targeted for early eradication because of unacceptable acute and chronic impacts” (Strayer *et al.* 2006, p. 650).

THE NEED FOR PREDICTIVE MODELS

Related to the exiguous number of pre-colonization data sets and the rarity of long-monitoring researches, there is a general lack of theoretical studies aimed at modeling the effects of NIS on resident communities. This is unfortunate, because models might provide significant insights into the impact of NIS by permitting the calculation and comparison of an essentially unlimited range of measures. They may also help design more effective and efficient empirical studies by providing information about which measures are redundant and which measures identify independent effects. Taking advantage of their ability to vary characteristics of either the NIS or the community independently, models would also enhance the accuracy of water quality assessments by decoupling the environmental effects of NIS from those caused by different anthropogenic stressors. In sum, the modeling exercise may put biologists “in a much better position” in order to understand and to predict the impacts of a wide range of invaders (Parker *et al.* 1999).

Following this rationale, Ricciardi (2003) synthesized the data collected in different ecosystems and geographic regions to generate statistical models of the impacts exerted by the zebra mussel (*D. polymorpha*). This exercise permitted the author to determine whether the effects of *D. polymorpha* are consistent in different environments, and therefore whether they are predictable. For instance, by plotting the results of field experiments and surveys from multiple colonized sites, predictable patterns of *D. polymorpha*'s impact on other benthic invertebrates were identified. In the presence of the zebra mussel, the density of other macroinvertebrates was found to increase 2–10 times, whereas they declined in deepwater sites as a possible response to a reduced influx of food particles caused by the filtration activity of near-shore zebra mussel populations (Fig. 6). This information was found to be essential also for the correct interpretation of water quality assessment and of indices of biotic integrity, which are commonly based on the composition of benthic macroinvertebrate communities.

Recently, Vander Zanden *et al.* (2004) developed models aimed at predicting future occurrences and impacts of the non-indigenous smallmouth bass (*M. dolomieu*) into lakes in central Ontario. To identify “vulnerable” lakes, the authors used a conceptual framework for modeling the occurrence and impact of this species. Its colonization was dissected into three steps or filters. The first filter identified which lakes are accessible to colonists, the second filter identified which lakes are capable of supporting a population of NIS, and the third filter identified which lakes would be adversely impacted if an NIS were to become established. Based on this conceptual approach and using a data set composed of 3,046 lakes in central and northern Ontario, the authors developed two separate lake classification models. The first model, based on artificial neural networks, aimed at predicting the location of future bass invasions based on environmental suitability, and the second, based on known food-web

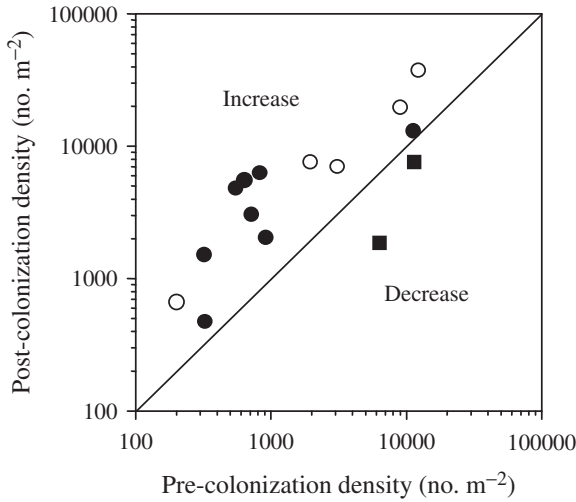


Fig. 6 Changes in the density of macroinvertebrates (excluding *Dreissena*) before and after *Dreissena polymorpha* colonization. Points above the 1:1 line indicate a positive change (increase), points below a negative change (decrease). Data include field surveys of littoral rocky substrata (black circles) and deepwater sediments (black quadrates), and experiments using artificial substrata (white circles). (Modified after Ricciardi 2003)

interactions derived from extensive stable isotope and gut content-based studies, singled out lakes in which bass was expected to have negative impacts on lake trout populations (Vander Zanden *et al.* 1999). By combining the predictions of these two models, along with information about lake remoteness, a subset of lakes in the region was identified, 48 (6%), that were classified as “highly vulnerable”, being both likely to be colonized and impacted by smallmouth bass. These lakes, the authors concluded, should have priority for the efforts aimed at minimizing further impacts of bass introductions in Ontario.

Certainly, the inherent difficulty in incorporating in a model the complexity of the community and the manifold biological relationships between NIS and residents has hampered the adoption of the modeling approach also in freshwater systems (Parker *et al.* 1999). Quantification of impacts may be made particularly complex due to a long list of confounding factors that include: the natural variability of the environment in space and time, other anthropogenic disturbances, synergistic effects of other established invaders (the “invasional meltdown”, Simberloff and Von Holle 1999, see also Dermott *et al.* 1998), the original composition of the invaded community, the extremely variable time lag between initial introduction and detectable impact (Shigesada and Kawasaki 1997), and the “statistical shrinkage” (i.e. the fit of a regression model to new data is worse than the fit to the original data) lamented by Williamson (1999). All these multiple sources of variability influence the observed responses

of a system and may explain why generalizations cannot be made from single experiments at small temporal and spatial scales (Ricciardi 2003). As a consequence, for many, if not most, known NIS, insufficient quantitative data are available to make useful comparisons between systems, times, and geographical areas.

To make the picture worse, when confronted with the increasing number of species that are moved outside their natural range for the first time, most often scientists do not dispose of an invasion history from which to draw predictive information (Ricciardi 2003). An approach might be to predict their impact from the invasion history of functionally similar organisms. For instance, the Asian freshwater mytilid mussel, *L. fortunei*, currently invading South America, displays a number of biological properties that are remarkably similar to those of *D. polymorpha*. Many of these properties are shared with other fouling bivalves, such as *Mytilopsis sallei* (Recluz), *Modiolus striatulus* (Hanley), *Perna viridis* (Linnaeus), and *Xenostrobus securis* (Lamarck). The life history of these species could therefore serve as a template to prioritize other potential pest bivalves without an invasion history (Ricciardi 2003). Taxonomic similarity may be a predictor of impact potential. Indeed, most invasive fouling bivalves belong to the same family, the Mytilidae, and the confamilial fish, smallmouth bass, *M. dolomieu*, and rock bass, *Ambloplites rupestris* (Rafinesque), alter the food web to the same extent by reducing the diversity and abundance of littoral fish. There are however some remarkable exceptions, also within congeneric species. The rusty crayfish, *O. rusticus*, has greatly expanded its range and displaces indigenous crayfish in North American lakes and streams (Lodge *et al.* 2000), whereas several other congeneric species are declining (Taylor *et al.* 1996).

All the above examples and thoughts may support the pessimistic attitude of several ecologists about the role of scientific research in predicting invaders. Research certainly yields major insights into areas of ecology, evolution, and conservation biology, and the frequent “serendipity” in science ensures that some fraction of these insights will ultimately help management (Simberloff 2003b). But most of these findings will have “little direct relevance to the introduced species problem” (Simberloff 2003b) and precise predictions are often expected to be elusive. Agreeing with Ricciardi (2003), the point here is that lack of precision should not be viewed as a deterrent to developing predictive models where none exist. Even “crude” models, obviously based on reliable data, could be extremely helpful in providing valuable criteria for prioritizing invasion threats (Simon and Townsend 2003).

CONCLUSIONS

Several NIS are today affecting freshwater communities, imperiling indigenous species, altering ecosystem processes, and causing damage to human endeavors. Recognizing these threats certainly represents the strongest and possibly the only

“ethical basis” for the concern that scientists, laypeople, and institutions have today about the problem of introduced species (Simberloff 2003a). This general awareness of the detrimental effects of several NIS is expected to translate soon into implemented policies aimed at preventing new undesirable introductions, responding quickly to newly discovered NIS, and controlling the most damaging established NIS. To succeed, however, all management and policy actions should be based on a sound understanding of the impact that target species exert, of their multilevel effects, and of the diverse expression of these effects over space and time. And they should also acknowledge that not all NIS exert a negative impact and the same species may have large effects in some areas and negligible ones in others (Byers *et al.* 2002). The so-often revealed idiosyncratic behavior of NIS can be properly faced – and reliable predictive models of their impact can be developed, only when a large amount of quantitative information is available. And the more idiosyncratic is a species’ behavior, i.e. more noise is in the background, the larger is the information required. That is, in invasion biology, as within the entire scientific realm, “there is no data like more data” (Mercer 1998): the limiting factor for predicting the impact of NIS is the chronic scarcity of “numbers”.

ACKNOWLEDGEMENTS

This paper was written while the author was acting as a Visiting Scholar at the Columbia University in the City of New York (NY, USA). My warmest thanks are directed to Professor Shahid Nahem for his kind hospitality.

REFERENCES

- Alderman, D. J. and J. L. Polglase. 1988. Pathogens, parasites and commensals. Pages 167–212 in D. M. Holdich and R. S. Lowery, editors. *Freshwater crayfish: biology, management and exploitation*. Croom Helm (Chapman & Hall), London, UK.
- Barbiero, R. P. and M. L. Tuchman. 2004. Long-term dreissenid impacts on water clarity in Lake Erie. *Journal of Great Lakes Research* **30**, 557–565.
- Bouchard, R. W. 1977. Distribution, systematics status, and ecological notes on five poorly known species of crayfishes in western North America (Decapoda: Astacidae and Cambaridae). *Freshwater Crayfish* **3**, 409–423.
- Boudreau, S. A. and N. D. Yan. 2003. The differing crustacean zooplankton communities of Canadian Shield lakes with and without the nonindigenous zooplanktivore *Bythotrephes longimanus*. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 1307–1313.
- Bright, C. 1998. *Life out of bounds: Bioinvasion in a borderless world*. Norton, New York, NY.
- Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002. Directing

- research to reduce the impacts of nonindigenous species. *Conservation Biology* **16**, 630–640.
- Cadi, A. and P. Joly. 2004. Impact of the introduction of the red-eared slider (*Trachemys scripta elegans*) on survival rates of the European pond turtle (*Emys orbicularis*). *Biodiversity and Conservation* **13**, 2511–2518.
- Carlton, J. T. 2002. Bioinvasion ecology: assessing invasion impact and scale. Pages 7–17 in E. Leppäkoski, S. Gollasch and S. Olenin, editors. *Invasive aquatic species of Europe: Distribution, impacts and management*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- CBD. 2001. Invasive alien species: report on existing international procedures, criteria and capacity for assessing risk from invasive alien species, Convention on Biological Diversity. Subsidiary body on scientific, technical and technological advice, Sixth meeting, Montreal, Canada, 12–16 March 2001 UNEP/CBD/SBSTTA/6/INF/5.
- Charlebois, P. M. and G. L. Lamberti. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. *Journal of the North American Benthological Society* **15**, 551–563.
- Clinton, W. J. 1999. Executive Order 13112. Invasive species. The White House, Washington, DC.
- Colautti, R. I., S. A. Bailey, C. D. A. van Overdijk, K. Amundsen, and H. J. MacIsaac. 2006. Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions* **8**, 45–59.
- Cox, G. W. 2004. *Alien species and evolution*. Island Press, Washington, Covelo, London.
- Crowder, L. B. 1984. Character displacement and habitat shift in a native cisco in southeastern Lake Michigan: evidence for competition? *Copeia* **1984**, 878–883.
- Dermott, R., J. Witt, Y. M. Um, and M. Gonzalez. 1998. Distribution of the Ponto-Caspian amphipod *Echinogammarus ischinus* in the Great Lakes and replacement of native *Gammarus fasciatus*. *Journal of Great Lakes Research* **24**, 442–452.
- Devine, R. S. 1999. *Alien invasion: America's battle with non-native animals and plants*. National Geographic Society, Washington, DC.
- Dick, J. T. A. and D. Platvoet. 2000. Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society of London B* **267**, 977–983.
- Diéguez-Uribeondo, J. and K. Söderhäll. 1993. *Procambarus clarkii* Girard as a vector for the crayfish plague fungus, *Aphanomyces astaci* Schikora. *Aquaculture and Fisheries Management* **24**, 761–765.
- Di Justo, P. 2006. The alien invasion. *Wired* **14**, 46–47.
- Eiswerth, M. E., S. G. Donaldson, and W. S. Johnson. 2000. Potential environmental impacts and economic damages of Eurasian watermilfoil (*Myriophyllum spicatum*) in Western Nevada and Northeastern California. *Weed Technology* **14**, 511–518.
- Ewel, J. J., D. J. O'Dowd, J. Bergelson, C. C. Daehler, C. M. D'Antonio, D. Gomez, D. R. Gordon, R. J. Hobbs, A. Holt, K. R. Hopper, C. E. Hughes, M. Lahart, R. R. B. Leakey, W. G. Lee, L. L. Loope, D. H. Lorence, S. M. Louda, A. E. Lugo, P. B. Mcevoy, D. M. Richardson, and P. M. Vitousek. 1999. Deliberate introductions of species: research needs. *BioScience* **49**, 619–630.
- Findlay, S. E. G., S. Dye, and K. A. Kuehn. 2002. Microbial growth and nitrogen retention in litter of *Phragmites australis* compared to *Typha angustifolia*. *Wetlands* **22**, 616–625.

- Fleming, I. A., K. Hindar, I. B. Mjolnerod, B. Jonsson, T. Balstad, and A. Lamberg. 2000. Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society of London B* **267**, 1517–1523.
- Gao, L. and B. Li. 2004. The study of a specious invasive plant, water hyacinth (*Eichhornia crassipes*): Achievements and challenges. *Zhiwu Shengtai Xuebao* **28**, 735–752.
- Garton, D. W., C. D. Payne, and J. P. Montoya. 2005. Flexible diet and trophic position of dreissenid mussels as inferred from stable isotopes of carbon and nitrogen. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1119–1129.
- Gherardi, F. and A. Cioni. 2004. Agonism and interference competition in freshwater decapods. *Behaviour* **141**, 1297–1324.
- Goldschmidt, T., F. Witte, and J. Wanink. 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktonivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology* **7**, 686–700.
- Gurevitch, J. and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* **19**, 470–474.
- Hayes, J. P., S. Z. Guffey, F. J. Kriegler, G. F. McCracken and C. R. Rarker. 1996. The genetic diversity of native, stocked and hybrid populations of brook trout in the southern Appalachians. *Conservation Biology* **10**, 1403–1412.
- Jerscke, J. M. and D. L. Strayer. 2005. Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences USA* **102**, 7198–7202.
- Johannsson, O. E., R. Dermott, D. M. Graham, J. A. Dahl, E. S. Millard, D. D. Myles, and J. LeBlanc. 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. *Journal of Great Lakes Research* **26**, 31–54.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* **69**, 373–386.
- Karatayev, A. Y., L. E. Burlakova, and D. K. Padilla. 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. *Journal of Shellfish Research* **16**, 187–203.
- Karatayev, A. Y., L. E. Burlakova, and D. K. Padilla. 2002. Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. Pages 433–446 in E. Leppäkoski, S. Gollasch and S. Olenin, editors. *Invasive aquatic species of Europe: Distribution, impacts and management*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Kasulo, V. 2000. The impact of invasive species in African lakes. Pages 183–207 in C. Perrings, M. Williamson and S. Dalmazzone editors. *The Economics of Biological Invasions*. Edward Elgar, Cheltenham, UK.
- Kaufman, L. 1992. Catastrophic change in species-rich freshwater ecosystems: the lesson of Lake Victoria. *BioScience* **42**, 846–858.
- Kelly, D. W. and J. T. A. Dick. 2005. Effects of environment and an introduced invertebrate species on the structure of benthic macroinvertebrate species at the catchment level. *Archiv für Hydrobiologie* **164**, 69–88.
- Kelly, D. W., J. T. A. Dick., W. I. Montgomery, and C. MacNeil. 2003. Differences in composition of macroinvertebrate communities with invasive and native *Gammarus* spp. (Crustacea: Amphipoda). *Freshwater Biology* **48**, 306–315.

- Kiesecker, J. M. and A. R. Blaustein. 1997. Population differences in responses of red-legged frogs (*Rana aurora*) to introduced bullfrogs. *Ecology* **78**, 1752–1760.
- Krisp, H. and G. Maier. 2005. Consumption of macroinvertebrates by invasive and native gammarids: a comparison. *Journal of Limnology* **64**, 55–59.
- Kupferberg, S. J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California River: The role of larval competition. *Ecology* **78**, 1736–1751.
- Laxson, C. L., K. N. McPhedran, J. C. Makarewicz, I. V. Telesh, and H. J. MacIsaac. 2003. Effects of the non-indigenous cladoceran *Cercopagis pengoi* on the lower food web of Lake Ontario. *Freshwater Biology* **48**, 2094–2106.
- Leung, B., D. M. Lodge, D. Finoff, J. F. Shogren, M. A. Lewis, and G. Lamberti. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London B* **269**, 2407–2413.
- Light, T., D. C. Erman, C. Myrick, and J. Clarke. 1995. Decline of the Shasta crayfish (*Pacifastacus fortis* Faxon) of Northeastern California. *Conservation Biology* **9**, 1567–1577.
- Lodge, D. M., C. A. Taylor, D. M. Holdich, and J. Skurdal. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. *Fisheries* **25**, 7–20.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**, 689–710.
- MacIsaac, H. J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *American Zoologist* **36**, 287–299.
- MacNeil, C., N. J. Fielding, J. T. A. Dick, M. Briffa, J. Prenter, M. J. Hatcher, and A. M. Dunn. 2003. An acanthocephalan parasite mediates intraguild predation between invasive and native freshwater amphipods (Crustacea). *Freshwater Biology* **48**, 2085–2093.
- McCarthy, J. M., C. L. Hein, J. D. Olden, and M. J. Vander Zanden. 2006. Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biology* **51**, 224–235.
- McIntosh, A. R. and C. R. Townsend. 1994. Interpopulation variation in mayfly anti-predator tactics: differential effects of contrasting predatory fish. *Ecology* **75**, 2078–2090.
- Mercer, R. L. 1998. Language modelling for speech recognition, IEEE Workshop on Speech Recognition, Arden House, Harriman, New York, NY, May 1988.
- Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. *Fisheries* **14**, 22–38.
- Nalepa, T. F., D. J. Hartson, D. L. Fanslow, and G. A. Lang. 2001. Recent population changes in freshwater mussels (Bivalvia: Unionidae) and zebra mussels (*Dreissena polymorpha*) in Lake St. Clair, USA. *American Malacological Bulletin* **16**, 141–145.
- Nalepa, T. F. and D. W. Schloesser. 1993. Zebra mussels: biology, impacts and control. Lewis Publishers, Boca Raton, Florida, FL.
- Nyström, P. 1999. Ecological impact of introduced and native crayfish on freshwater communities: European perspectives. Pages 63–84 in F. Gherardi and D. M. Holdich, editors. *Crayfish in Europe as alien species: How to make the best of a bad situation?* A. A. Balkema, Rotterdam, The Netherlands.

- Nyström, P., O. Svensson, B. Lardner, C. Brönmark, and W. Granéli. 2001. The influence of multiple introduced predators on a littoral pond community. *Ecology* **82**, 1023–1039.
- Oliveira de, M. D., A. M. Takeda, L. Fernandes de Barros, D. Savio Barbosa, and E. K. de Resende. 2006. Invasion by *Limnoperna fortunei* (Dunker, 1857) (Bivalvia, Mytilidae) of the Pantanal wetland, Brazil. *Biological Invasions* **8**, 97–104.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**, 3–19.
- Perry, W. L., J. E. Feder, and D. M. Lodge. 2001. Implications of hybridization between introduced and resident *Orconectes* crayfish. *Conservation Biology* **15**, 1656–1666.
- Perry, W. L., D. M. Lodge, and J. E. Feder. 2002. Importance of hybridization between indigenous and nonindigenous freshwater species: an overlooked threat to North American biodiversity. *Systematic Biology* **51**, 255–275.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental costs associated with alien-invasive species in the United States. *Ecological Economics* **52**, 273–288.
- Pointier, J. P. 1999. Invading freshwater gastropods: Some conflicting aspects for public health. *Malacologia* **41**, 403–411.
- Plummer, M. L. 2005. Impact of invasive water hyacinth (*Eichhornia crassipes*) on snail hosts of schistosomiasis in Lake Victoria, East Africa. *EcoHealth* **2**, 81–86.
- Quinn, T. P., M. T. Kinnison, and M. J. Unwin. 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*. populations in New Zealand: pattern, rate, process. *Genetica* **112–113**, 493–513.
- Rehage, J. S., B. K. Barnett, and A. Sih. 2005. Foraging behaviour and invasiveness: do invasive *Gambusia* exhibit higher feeding rates and broader diets than their noninvasive relatives? *Ecology of Freshwater Fish* **14**, 352–360.
- Reynolds, J. D. 1988. Crayfish extinctions and crayfish plague in central Ireland. *Biological Conservation* **45**, 279–285.
- Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: An empirical approach applied to zebra mussel invasions. *Freshwater Biology* **48**, 972–981.
- Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology* **67**, 613–619.
- Rosenzweig, M. 2001. The four questions: what does the introduction of exotic species do to diversity? *Evolutionary Ecology Research* **3**, 361–367.
- Rozhnov, V. V. 1993. Extinction of the European mink: an ecological catastrophe or natural process? *Lutreola* **1**, 10–16.
- Rudnick, D. and V. Resh. 2005. Stable isotopes, mesocosms and gut content analysis demonstrate trophic differences in two invasive decapod crustacean. *Freshwater Biology* **50**, 1323–1336.
- Sagoff, M. 1999. What's wrong with exotic species? Report from the Institute for Philosophy & Public Policy **19**, 16–23.
- Schlaepfer, M. A., P. W. Sherman, B. Blossey, and M. C. Runge. 2005. Introduced species as evolutionary traps. *Ecology Letters* **8**, 241–246.

- Seehausen, O., F. Witte, E. F. Katunzi, J. Smits, and N. Bouton. 1997. Patterns of the remnant cichlid fauna in southern Lake Victoria. *Conservation Biology* **11**, 890–904.
- Shigesada N and Kawasaki K 1997. *Biological invasions: theory and practice*. Oxford University Press, Oxford, UK.
- Simberloff, D. 2003a. Confronting introduced species: a form of xenophobia? *Biological Invasions* **5**, 179–192.
- Simberloff, D. 2003b. How much information on population biology is needed to manage introduced species? *Conservation Biology* **17**, 83–92.
- Simberloff, D. and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* **1**, 21–32.
- Simon, K. S. and C. R. Townsend. 2003. Impacts of freshwater invaders at different levels of ecological organization, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology* **48**, 982–994.
- Slobodkin, L. B. 2001. The good, the bad and the reified. *Evolutionary Ecology Research* **3**, 1–13.
- Smith, K. G. 2005. Effects of nonindigenous tadpoles on native tadpoles in Florida: evidence of competition. *Biological Conservation* **123**, 433–441.
- Spencer, C. N., B. R. McLelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement: cascading interactions in the food web of a large aquatic ecosystem. *BioScience* **41**, 14–21.
- Strayer, D. L. 1999. Effects of alien species on freshwater mollusks in North America. *Journal of North America Benthological Society* **18**, 74–98.
- Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of freshwater ecosystems by bivalves: a case study of zebra mussels in the Hudson River. *BioScience* **49**, 19–27.
- Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution* **21**, 645–651.
- Taylor, C. A., M. L. Warren Jr, J. F. Fitzpatrick Jr, H. H. Hobbs III, R. F. Jezerinac, W. L. Pflieger, and H. W. Robinson 1996. Conservation status of crayfishes of the United States and Canada. *Fisheries* **21**, 25–38.
- Templer, P., S. Findlay, and C. Wigand 1998. Sediment chemistry associated with native and non-native emergent macrophytes of a Hudson River marsh ecosystem. *Wetlands* **18**, 70–78.
- Townsend, C. R. 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. *Biological Conservation* **78**, 13–22.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* **401**, 464–467.
- Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. *Ecological Applications* **14**, 132–148.
- Williamson, M. 1996. *Biological invasions* Chapman & Hall, London, UK.
- Williamson, M. 1999. Invasions. *Ecography* **22**, 5–12.
- Wei, A. and P. Chow-Fraser. 2006. Synergistic impact of water level fluctuation and invasion of *Glyceria* on *Typha* in a freshwater marsh of Lake Ontario. *Aquatic Botany* **84**, 63–69.

- Wilcove, D. S., D. Rothstein, J. Dubow, A. Philips, and E. Losos 1998. Quantifying threats to imperiled species in the United States. *BioScience* **48**, 607–615.
- Witt, A. M., J. M. Dettmer, and C. E. Caceres. 2005. *Cercopagis pengoi* in southwestern Lake Michigan in four years following invasion. *Journal of Great Lakes Research* **31**, 245–252.
- Yan, N. D., R. Girard, and S. Boudreau. 2002. An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness. *Ecology Letters* **5**, 481–485.
- Yan, N. D. and T. W. Pawson. 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following invasion by *Bythotrephes cederstroemi*. *Freshwater Biology* **37**, 409–425.
- Zavaleta, E. 2000. The economic value of controlling an invasive shrub. *Ambio* **29**, 462–467.