

Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions

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SUMMARY

1. Quantitative models of impact are lacking for the vast majority of known invasive species, particularly in aquatic ecosystems. Consequently, managers lack predictive tools to help them prioritise invasion threats and decide where they can most effectively allocate limited resources. Predictive tools would also enhance the accuracy of water quality assessments, so that impacts caused by an invader are not erroneously attributed to other anthropogenic stressors.
2. The invasion history of a species is a valuable guide for predicting the consequences of its introduction into a new environment. Regression analysis of data from multiple invaded sites can generate empirical models of impact, as is shown here for the zebra mussel *Dreissena polymorpha*. *Dreissena's* impacts on benthic invertebrate abundance and diversity follow predictable patterns that are robust across a range of habitat types and geographic regions. Similar empirical models could be developed for other invaders with a documented invasion history.
3. Because an invader's impact is correlated with its abundance, a surrogate model may be generated (when impact data are unavailable) by relating the invader's abundance to environmental variables. Such a model could help anticipate which habitats will be most affected by invasion. Lack of precision should not be a deterrent to developing predictive models where none exist. Crude predictions can be refined as additional data become available. Empirical modelling is a highly informative and inexpensive, but underused, approach in the management of aquatic invasive species.

Keywords: Nonindigenous species, exotic species, prediction, risk assessment, *Dreissena polymorpha*

Introduction

Predictive models are needed to manage the ecological and technological impacts of species invasions (Byers *et al.*, 2002). To date, there has been meagre progress in developing generalisations about the establishment and consequences of introduced species (Williamson, 1999; Kolar & Lodge, 2001). Some scientists doubt that we will ever be able to predict the outcome of a species' introduction (Gilpin, 1990),

and have suggested that the occurrence and timing of individual invasions (which are largely stochastic) are perhaps as unpredictable as earthquakes (Williamson, 1999). However, a predictive understanding of the impacts of a *known* invader might be attainable if the impacts are a function of quantifiable interactions between the invader and its new environment.

There have been very few attempts at developing quantitative predictions of impact for known invaders (Parker *et al.*, 1999), particularly in aquatic systems. Consequently, managers lack tools, such as predictive models, to decide where to allocate limited resources for prevention and mitigation. Even crude models, if they are based on reliable data, could provide valuable

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criteria for prioritising invasion threats. They would also enhance the accuracy of water quality assessments, given that the changes caused by an invader might otherwise be erroneously attributed to different anthropogenic stressors. Using aquatic examples, I demonstrate a simple, inexpensive approach to developing predictive models of impact for known invaders.

Identifying patterns of impact for species with an invasion history

Predictions are perhaps best developed empirically from a synthesis of data (Peters, 1991). A straightforward method is to compare the invader's impacts in different ecosystems and geographic regions in which it has been introduced (e.g. Crivelli, 1983; Grosholz & Ruiz, 1996). This allows us to determine whether the effects of an invader are consistent, and therefore predictable, in different environments. The zebra mussel, *Dreissena polymorpha* Pallas, can be used to illustrate this method, because the species has invaded numerous lakes and rivers in Central Europe and eastern North America (Mellina & Rasmussen, 1994; Karatayev, Burlakova & Padilla, 1997), and several studies have examined its impact on biotic and abiotic properties of aquatic ecosystems.

Dreissena polymorpha is a fresh and brackish water mussel native to the basins of the Black and Caspian Seas. The larvae are pelagic, whereas the adults attach to hard substrata like many marine bivalves. Over the past 200 years, *Dreissena* has spread across Europe via canals and shipping traffic (Karatayev, Burlakova & Padilla, 1998). In the mid-1980s, it was introduced to the North American Great Lakes, apparently as larvae released with ship ballast water (Hebert, Muncaster & Mackie, 1989), and now inhabits several major rivers and inland lakes in eastern North America. In both Europe and North America, *Dreissena* preferentially colonises solid substrata in calcium-rich waters (i.e. $[Ca] > 15 \text{ mg L}^{-1}$; Ramcharan, Padilla & Dodson, 1992; Mellina & Rasmussen, 1994; Karatayev *et al.*, 1998), and has become a common constituent species of invertebrate communities in these environments. Significant ecological changes have often been attributed to *Dreissena* invasions (e.g. Karatayev *et al.*, 1997; Ricciardi, Whoriskey & Rasmussen, 1997; Ricciardi, Neves & Rasmussen, 1998; Vanderploeg *et al.*, 2002).

Ecological changes associated with *Dreissena* in European and North American lakes are remarkably

similar, implying a predictable consistency (Table 1). The only noteworthy difference is *Dreissena*'s impact on native freshwater mussels in the family Unionidae. Unionid mussels spend their adult life buried in soft sediments with their posterior shell exposed to the water column, providing a colonisable surface for *Dreissena* larvae. The attachment of dense clusters of *Dreissena* may smother and critically impair a unionid, depriving it of sufficient energy stores to survive harsh seasons (Haag *et al.*, 1993; Ricciardi, Whoriskey & Rasmussen, 1996). Having evolved without dominant fouling organisms like *Dreissena*, North American unionid mussels have not adapted mechanisms to mitigate *Dreissena*'s effects. Native mussel assemblages declined rapidly following *Dreissena* invasion in the Great Lakes, St Lawrence River, Hudson River, Illinois River, some of their tributaries and several inland lakes (Schloesser & Nalepa, 1994; Nalepa *et al.*, 1996; Strayer, Smith & Hunter, 1998; Ricciardi *et al.*, 1996, 1998; Martel *et al.*, 2001). This decline is attributable primarily to the effects of fouling, and, secondarily, to competition between these suspension feeders for seston. By contrast, mass mortalities of native mussels have rarely been reported for European lakes invaded by *Dreissena* (Karatayev *et al.*, 1997; Ricciardi *et al.*, 1998), possibly because (1) few European studies have examined changes in mussel communities following invasion and some major declines may have been undocumented; (2) population densities and fouling levels of *Dreissena* on native mussels are generally lower in Europe than in North America; and (3) the European

Table 1 Documented impacts of the Ponto-Caspian zebra mussel, *Dreissena polymorpha*, on invaded lakes in inland Europe and North America. Direction of effect is indicated by positive and negative signs. Weak or moderate effects are indicated by parentheses. Data sources: Karatayev *et al.* (1997), Ricciardi *et al.* (1997), Ricciardi *et al.* (1998), Vanderploeg *et al.* (2002), and references therein

Parameter	European lakes	North American lakes
Transparency	+	+
Seston	-	-
Phytoplankton production	-	-
Zooplankton biomass	(-)	(-)
Macrophyte biomass	+	+
Epibenthic macroinvertebrate abundance	+	+
Native mussel richness	(-)	-
Benthic fish diets	+	+
Waterfowl density	+	+

freshwater mussel fauna, which is depauperate compared with the North American fauna (~12 spp. versus 297 spp.), has previously been exposed to *Dreissena* – whose distribution expanded into northern and Central Europe prior to the last glaciation before retreating to the Ponto-Caspian basins (Ricciardi *et al.*, 1998). Thus, European species may have already experienced selection pressures to adapt to *Dreissena* (e.g. avoidance behaviour through deeper burial in sediment) and may not have retained the same ecological sensitivity to fouling as their North American relatives.

By plotting the results of field experiments and surveys from multiple invaded sites, we can identify predictable patterns of *Dreissena*'s impact on other benthic invertebrates. This information is essential for the accurate interpretation of water quality assessments and indices of biotic integrity, which are commonly based on the composition of benthic macroinvertebrate communities. In the presence of *Dreissena*, the density of other macroinvertebrates increases two to 10 times (Fig. 1). By contrast, macroinvertebrate density declines at deepwater sites, possibly in response to a reduced influx of food particles caused by the filtration activity of nearshore *Dreissena* populations (Nalepa *et al.*, 1998; Strayer *et al.*, 1998). At sites in the Great Lakes-St Lawrence system, the mean taxonomic richness of macroinvertebrates consistently increases following *Dreissena* invasion (Fig. 2a). The largest increases in richness coincided with the largest increases in *Dreissena* density (Fig. 2b), as deposit-feeding and carnivorous invertebrates benefit from enhanced spatial heterogeneity and biodeposits provided by expanding zebra mussel beds (Botts, Patterson & Schloesser, 1996; Ricciardi *et al.*, 1997; Stewart, Miner & Lowe, 1998). In particular, expanding *Dreissena* populations promote increased densities of the amphipod crustacean *Gammarus fasciatus* Say (Fig. 3), an important food item in the diets of several benthic fishes (Boisclair & Leggett, 1989). Thus, these aggregate data reveal a pattern of increased macroinvertebrate density and diversity following *Dreissena* invasion of littoral sites.

Regression analysis of data from invaded sites can generate statistical models of impact. For example, the level of infestation (fouling) on unionid mussels is strongly correlated with *Dreissena* population density in the Great Lakes-St Lawrence River basin and in the Mississippi River basin (Fig. 4), which contains the most diverse and endangered unionid assemblages on

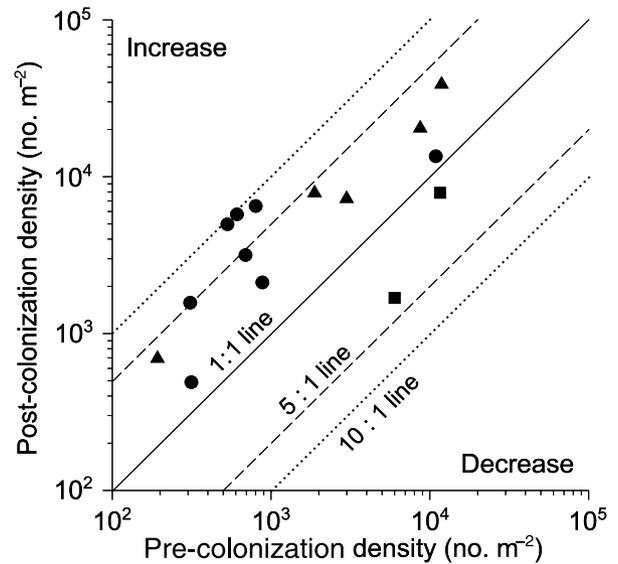


Fig. 1 Changes in the density of macroinvertebrates (excluding *Dreissena*) before and after *Dreissena* colonisation. Points above the 1 : 1 line indicate a positive change. Data include field surveys of littoral rocky substrata (●) and deepwater sediments (■), and experiments using artificial substrata (▲). Data sources are Griffiths (1993), Stewart & Haynes (1994), Ricciardi *et al.* (1996), Botts *et al.* (1996), Strayer *et al.* (1998), Stewart *et al.* (1998), Nalepa *et al.* (1998), Horvath *et al.* (1999), and Kuhns & Berg (1999).

the planet. Although the regression models derived for the Great Lakes-St Lawrence River and Mississippi River basins have significantly different slopes (ANCOVA, $P < 0.0001$), most of the Mississippi data fall within the 99% confidence limits of the Great Lakes-St Lawrence model, suggesting that the latter could provide useful predictions for Mississippi unionid populations. Despite heterogeneity in sampling protocols, geographic location, and species composition, the general model constructed from the entire dataset explains a large proportion (82%) of the variation in unionid infestation level from *Dreissena* population density.

It should be noted that *Dreissena* density is well-correlated with physical habitat variables (Ramcharan *et al.*, 1992; Mellina & Rasmussen, 1994), and adverse physiological effects on unionids have been linked to high *Dreissena* infestations (Haag *et al.*, 1993; Ricciardi *et al.*, 1996; Baker & Hornbach, 2000; Hallac & Marsden, 2000). Therefore, given the strong correlation between *Dreissena* infestation and density (Fig. 4), it may be possible to predict changes in unionid fitness based on the physical conditions of a habitat before it is invaded. Such information could be used

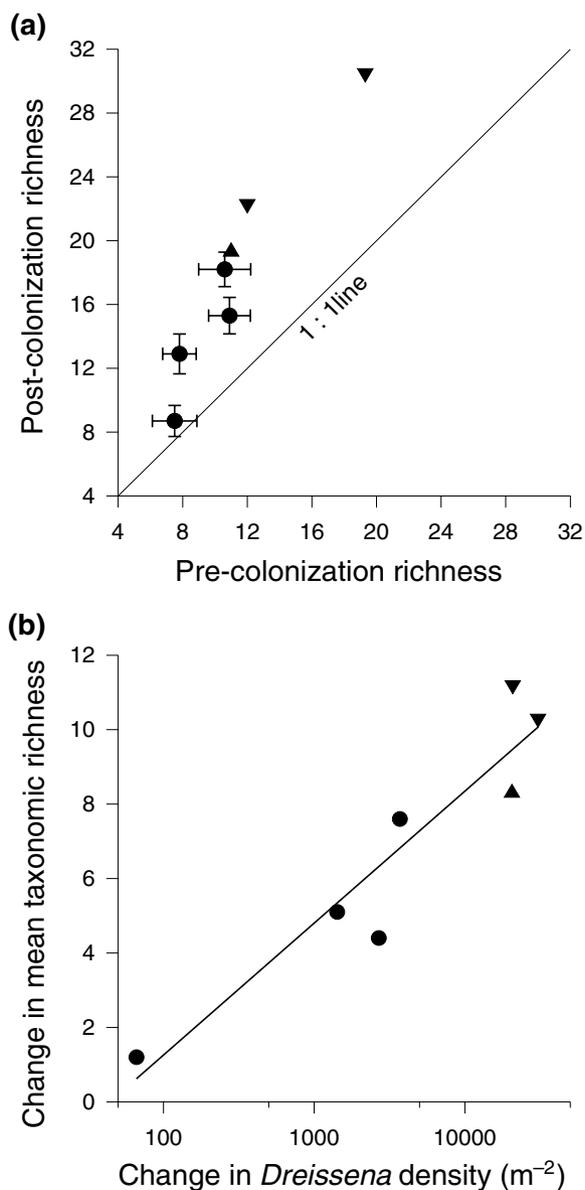


Fig. 2 (a) Mean taxon (primarily genera) richness in macro-invertebrate communities on rocky substrata before and after *Dreissena* colonisation. Points above the 1 : 1 line indicate a positive change. (b) Change in mean taxon richness (arithmetic difference between past and present values) as a function of change in *Dreissena* density. Line fitted by least-squares regression (SAS, 1988): $y = -5.8 + 3.6 \log x$ (Adj. $R^2 = 0.85$, $P < 0.002$, $n = 7$). Data are from the St Lawrence River (●) (Ricciardi *et al.*, 1996; A. Ricciardi, unpublished data), south-eastern Lake St Clair (▲) (Griffiths, 1993), and Lake Ontario (▼) (Stewart & Haynes, 1994).

to select habitat refugia for relocation of endangered unionid populations (Newton *et al.*, 2001).

Another conservation strategy is to reduce *Dreissena* infestations on unionids by periodic manual removal

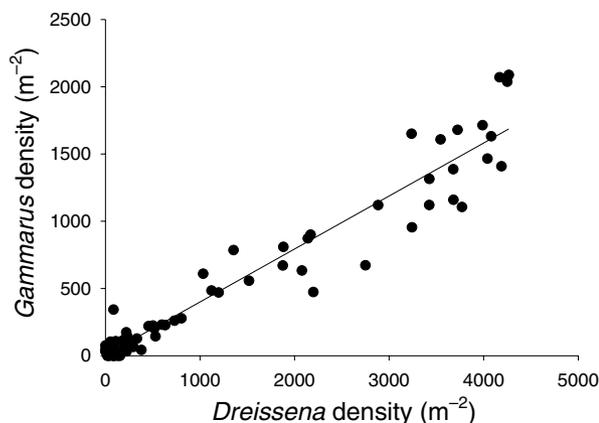


Fig. 3 Amphipod (*Gammarus fasciatus*) density in relation to *Dreissena* density on rocky substrata in the upper St Lawrence River, 1992–95. Each point represents a single stone. Line fitted by least-squares regression (SAS, 1988): $y = 0.39x$ (Adj. $R^2 = 0.93$, $P < 0.0001$, $n = 73$).

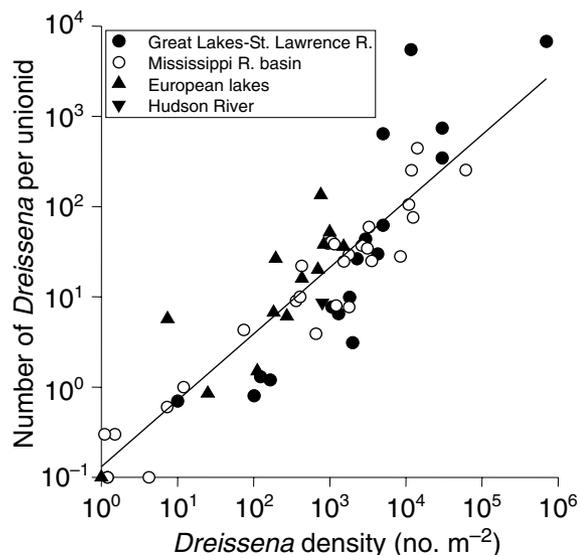


Fig. 4 Infestation level of *Dreissena* on unionid mussels as a function of local *Dreissena* population density. Line fitted by least-squares regression: $\log y = 0.74 \log x - 0.88$ (Adj. $R^2 = 0.82$, $P < 0.0001$, $n = 62$). Data sources are Harman (1994), Ricciardi *et al.* (1996), Whitney *et al.* (1996), Ricciardi *et al.* (1998), and Burlakova, Karatayev & Padilla (2000).

or by applying disinfectants (Waller & Fisher, 1998; Hallac & Marsden, 2001). This treatment requires considerable labour and is effective only if unionids have not been exposed to lethal levels of infestation. Treatment efforts could be prioritised if guided by a statistical relationship between unionid mortality and infestation level, which can be generated using our empirical approach. Here, I choose an alternative

measure of infestation that more accurately represents the encumbrance on unionids: the ratio of the mass of attached *Dreissena* to that of their unionid host (Ricciardi *et al.*, 1996). This variable is a good predictor of unionid population mortality (Fig. 5). The regression model predicts that populations carrying a mean mass of *Dreissena* exceeding ~40% of their own fresh mass will decline in size by at least half, and those populations with mass ratios greater than 1.0 are likely to become extirpated or nearly so.

In support of these predictions, a recent study from the Rideau River (a small impounded watercourse in Ontario, Canada) found that unionids were extirpated soon after the mass ratio peaked at 1.8 (Martel *et al.*, 2001). Another study in Lake Champlain (Vermont, U.S.A.) found that glycogen energy stores were nearly depleted within specimens of *Lampsilis radiata* Gmelin that carried the equivalent of their own mass in attached *Dreissena* (Hallac & Marsden, 2000). The relationship in Fig. 5 is modified from Ricciardi *et al.* (1996) by the addition of seven data points from Lake Champlain, the lower Ottawa River (Quebec), and the Richelieu River (Quebec). When validating the model with these additional data, we find a close correspondence between observed and predicted estimates of

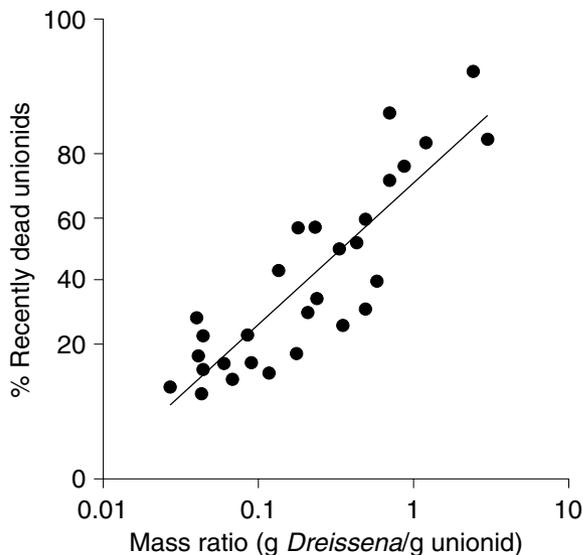


Fig. 5 Proportion of freshly killed unionids as a function of the *Dreissena*–unionid mass ratio (wet weights) for North American unionid populations. Line fitted by least-squares regression: $\sin^{-1}(y^{0.5}) = 0.48 \log x + 1.0$ (Adj. $R^2 = 0.75$, $P < 0.0001$, $n = 29$). Modified from Ricciardi *et al.* (1996) by the addition of data from Hallac & Marsden (2000) and A. Ricciardi & L.E. Johnson (unpublished data).

unionid mortality (Adj. $R^2 = 0.84$; slope of relationship = 1.23 ± 0.22), in spite of the heterogeneity of the data and the effects of various other stressors responsible for unionid mortality in North America (Ricciardi & Rasmussen, 1999). This robust relationship would not have been revealed from a single experiment and thus demonstrates the value of statistical synthesis. Furthermore, it can be progressively refined with the addition of data from a broader range of infestations. This modelling approach could be valuable to conservation managers who need to know the level at which an invader must be maintained to minimise its impact on native species (Byers *et al.*, 2002).

Can we predict the impact of species lacking invasion histories?

For many (if not most) known invaders, insufficient quantitative data are available to make useful comparisons among ecosystems. An increasing number of species are moved outside of their natural range for the first time and thus have no invasion history from which to draw predictive information (Welcomme, 1988). Unfortunately, the impacts of these species cannot be reliably predicted from their effects in their native ranges. For example, some of the most devastating terrestrial invasions have been of herbivorous insects and plant pathogens that were apparently benign or unimportant in their native habitats; these include the European and Asian gypsy moths, chestnut blight fungus, Dutch elm disease, and white pine blister rust (Cox, 1999). Similarly, a fungal parasite, *Aphanomyces astaci* Schikora introduced with North American crayfish into Europe caused a large-scale plague that eliminated most native crayfish populations, and yet the parasite is innocuous in North America (Reynolds, 1988).

An alternative approach might be to predict the impact of an introduced species from the invasion history of functionally similar organisms (Byers *et al.*, 2002). If species that use resources in similar ways exert similar impacts, then management decisions may be guided by a broader set of data than would otherwise be available. Consider the current invasion of South America by the Asian freshwater mytilid mussel, *Limnoperna fortunei* Dunker. This species has a limited and poorly studied invasion history in Hong Kong and Japan (Ricciardi, 1998) and impact studies from South America are just beginning to emerge (e.g.

Darrigran *et al.*, 1998). These studies suggest that many of *Limnoperna's* ecological impacts are nearly identical to those of *Dreissena*, e.g. its positive effect on macroinvertebrate density and taxonomic richness, its enhancement of diets of benthic fishes, and its negative effect on native bivalves (Darrigran *et al.*, 1998; Penchaszadeh *et al.*, 2000). Owing to the entrainment of its larvae in water conduits, and the dense accumulation of its shells attached to hard substrata by byssal threads, *Limnoperna* also has impacts on technical facilities similar to those caused by *Dreissena*, including the infestation of water supply systems and power plants (Ricciardi, 1998; Magara *et al.*, 2001). The life histories of invasive fouling bivalves, such as *D. polymorpha*, *L. fortunei*, *Mytilopsis sallei* Reclúz, *Modiolus striatulus* Hanley, *Perna viridis* L., and *Xenostrobus securis* Lamarck, are remarkably similar (Morton, 1997) and therefore could serve as a template to prioritise other potential pest bivalves that do not have an invasion history.

It is intuitively appealing to assume that closely related species are functionally similar and thus produce similar impacts. Indeed, most invasive fouling bivalves belong to the same family, the Mytilidae (Morton, 1997). Two widely introduced confamilial fishes, smallmouth bass, *Micropterus dolomieu* Lacepède, and rock bass, *Ambloplites rupestris* Rafinesque, both reduce the diversity and abundance of littoral forage fishes, thereby altering the diets of lake trout, *Salvelinus namaycush* Walbaum, in Canadian lakes (Vander Zanden, Casselman & Rasmussen, 1999). The common carp, *Cyprinus carpio* L., and its smaller cousin, the goldfish, *Carassius auratus* L., similarly alter ponds and lakes through turbidity generation and the uprooting of vegetation (Crivelli, 1983; Richardson, Whoriskey & Roy, 1995).

However, there are exceptions that show that taxonomic similarity is not a consistent predictor of impact potential. One example is the near-simultaneous introduction of two gobiid fishes into the North American Great Lakes around 1990. More than a decade after they were introduced, populations of the tubenose goby, *Proterorhinus marmoratus*, have remained small and isolated, while the round goby, *Neogobius melanostomus* Pallas, has expanded its range into Lake Michigan, Lake Erie, Lake Ontario and into the St Lawrence River. The round goby's expansion has been accompanied by concomitant local declines in other benthic fishes such as mottled sculpin, *Cottus*

bairdi Girard, and logperch, *Percina caprodes* Rafinesque, possibly as a result of predation by the larger round goby and by competition with this species for food and shelter (Jude, Janssen & Crawford, 1995; Janssen & Jude, 2001). Even congeneric species may differ greatly in invasiveness and impact, as has been shown by crayfishes; *Orconectes rusticus* Girard has expanded its range and displaced native crayfishes in North American lakes and streams (Lodge *et al.*, 2000), while several other *Orconectes* species are declining (Taylor *et al.*, 1996). Similarly, brown trout, *Salmo trutta* L., is highly invasive and is implicated in the extirpation of native fishes in various regions of the world, while Atlantic salmon, *Salmo salar* L., is a poor coloniser and has rarely been associated with species loss (Welcomme, 1988). A rigorous statistical synthesis is needed to determine the value of using taxonomic/functional similarity as a predictor of impact.

Challenges and impediments to prediction

The ecological impact of an invasion can be defined as the measurable change to the properties of an ecosystem. The impact is the outcome of the interaction between the invader and its new environment:

$$\text{Impact} = A \times F \times C$$

where *A* is the abundance of the invader, *F* is its ecological function (per capita effect), and *C* is the composition of the recipient community.

Because each of these variables is dependent on the abiotic and biotic properties of the invaded habitat, predictions of impact will be confounded to some extent by the environmental variability in time and space (e.g. productivity, community composition, climate, other anthropogenic disturbances, and the natural disturbance regime). Additionally, because impacts vary with both the physical environment and the composition of the invaded community, generalisations cannot be made from single experiments at small temporal or spatial scales. The apparently higher impact of *D. polymorpha* on native mussels in the North American Great Lakes compared with European lakes (Karatayev *et al.*, 1997) might be due to the order of magnitude difference in fouling intensity (Fig. 4) as well as selection pressure in European mussel communities (Ricciardi *et al.*, 1998). The higher impact of carp, *C. carpio*, on submerged

vegetation in North American versus European lakes is due to the difference in fish biomass attained on both continents (Crivelli, 1983). Regression models directly relate both the destruction of submerged vegetation and increased turbidity to carp biomass, with good precision (Crivelli, 1983; Lougheed, Crosbie & Chow-Fraser, 1998). Thus, the problem of environmental variability can be addressed by combining models that predict impacts from an invader's abundance to models that relate abundance to environmental parameters.

The residents of a community can modify the impact of an invader by altering its abundance or function, as illustrated by several examples: (1) the suppression of the Asiatic clam, *Corbicula fluminea* Müller, by predators in a Texas reservoir (Robinson & Wellborn, 1988), (2) the effect of resident herbivores and native vegetation on seedling establishment of invading purple loosestrife, *Lythrum salicaria* L., in North American wetlands (Rachich & Reader, 1999), (3) the effect of *D. polymorpha* on other invertebrates in the presence of introduced round gobies, *N. melanostomus*, in the Great Lakes (Kuhns & Berg, 1999) and (4) the effect of *D. polymorpha* on the replacement of a North American amphipod, *G. fasciatus*, by a Ponto-Caspian amphipod, *Echinogammarus ischnus* Stebbing, in the Great Lakes (Dermott *et al.*, 1998). The latter example, involving *Dreissena* and an exotic amphipod, demonstrates that invaders may interact in synergistic ways. Through mutualistic and commensalistic interactions, one introduced species may facilitate the establishment (or enhance the survival and/or population size) of another introduced species, with significant consequences for the entire community (Simberloff & Von Holle, 1999; Ricciardi, 2001). For example, intense filtration by zebra mussels increases water transparency, thereby stimulating the growth of exotic and native macrophytes (Skubinna, Coon & Batterson, 1995), which in turn provide substrate for settling mussel larvae. In some areas of the Great Lakes, these physical changes have led to the replacement of commercially important walleye *Stizostedion vitreum* Mitchell, which are adapted to turbid water, by bass *Micropterus* spp. and muskellunge *Esox masquinongy* Mitchell, which inhabit macrophyte beds (Vanderploeg *et al.*, 2002). In the Potomac River, the invasion of the Asiatic clam, *C. fluminea*, caused a tripling of water clarity and subsequent growth of submerged macrophytes (includ-

ing an exotic weed, *Hydrilla verticillata*), followed by increased populations of exotic largemouth bass, *Micropterus salmoides* Lacepède, and waterfowl that used the macrophyte beds; later, a population decline by *Corbicula* triggered system-wide changes in each of these biotic components (Phelps, 1994). Because an invader's impact is largely dependent on its abundance, facilitative interactions between introduced species may not only pave the way for invasions but may also magnify their consequences. These synergisms can be expected to increase with the number of species introduced over time, implying that impact predictions will become increasingly difficult for systems subject to a high frequency of introductions.

Williamson (1999) discusses reasons why attempts at predicting the outcome of introductions often fail. He cites the problem of 'statistical shrinkage', in which the fit of a regression model to new data is worse than the fit to the original data. This occurs as new sources of variability are added to the model. However, despite loss of precision, patterns that emerge from this 'statistical noise' should be valued as robust generalisations.

One biological reason for failed prediction is the time lag between initial introduction and detectable impact. When populations undergo exponential or logistic growth, an initial lag period corresponding to slow growth and spread may last years to decades, presumably because of a number of factors including density-dependent effects and genetic selection (Shigesada & Kawasaki, 1997). For example, the Nile perch, *Lates niloticus* L. was introduced to Lake Victoria in about 1954, but remained a minor component of the community until the 1980s when it underwent a population explosion. The combined stresses of organic pollution and indiscriminate predation by this species are assumed to be responsible for the loss of perhaps hundreds of endemic species of cichlids (Kaufman, 1992). The results of short-term initial studies would not have predicted the outcome of this invasion. Furthermore, the scarcity and brevity of preinvasion data sets severely limits our ability to measure invasion impacts against a background of temporal variability. Using a 15-year preinvasion data set, Yan & Pawson (1997) demonstrate the value of long-term monitoring in isolating the effects of a non-indigenous planktonic predator from other anthropogenic perturbations such as nutrient loading, fish stocking, and chemical pollution.

Conclusions

The impact history of a species is a valuable guide for predicting the consequences of its introduction into a new environment. An invader's impact is, among other factors, a function of the properties of the invaded ecosystem; therefore, generalisations cannot be made from only a few sites. The synthesis of data from multiple invaded sites can reveal predictable patterns at various spatial scales. The simplest, fastest, least expensive and most effective way to determine predictive relationships is through statistical analysis of existing data (Peters, 1991). Although precise predictions are often elusive, lack of precision should not be viewed as a deterrent to developing predictive models where none exist. Even crude models (constructed from reliable data) have potential value and can be refined as additional data become available.

Where possible, models that relate an invader's abundance to physical environmental variables should be linked with models that relate the invader's impact to its abundance. The resulting composite models would allow us to predict, prior to invasion, which habitats would be vulnerable to high impacts and thus should be a priority for management. However, empirical approaches are only effective when applied to invaders with a well-documented invasion history (e.g. zebra mussel, common carp, rainbow trout). For many invaders, valuable data sets have not been published; this information should be made broadly accessible via Internet web sites, which ultimately could be linked within a global information system (Ricciardi *et al.*, 2000).

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