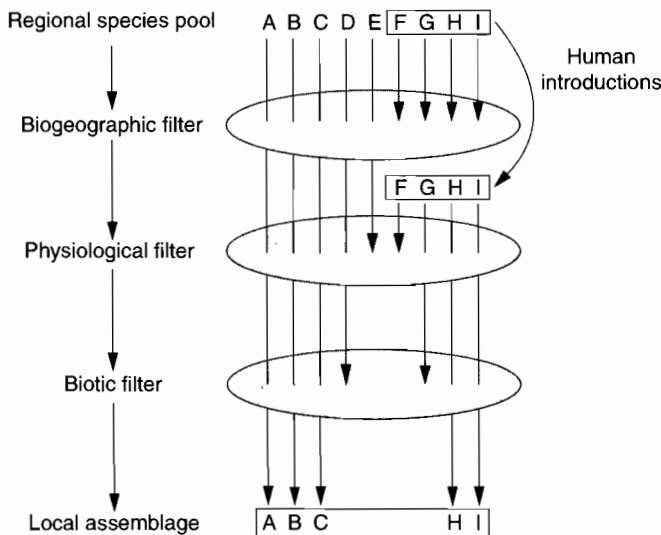


# Modeling biological invasions of inland waters

Hugh J. MacIsaac, Leif-Matthias Herborg, and  
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## INTRODUCTION

The discipline of invasion biology suffers from a number of problems, not least of which is a lack of a central, organizing paradigm. Ecologists have for decades sought to relate invasion success both to characteristics of invaded communities and to those of the invading species (see references in Davis 2005), the results of which have only served to demonstrate the highly system- or species-specific nature of many invasions. One recent development that holds promise for resolving this problem has been a recognition that successful invasions result from a series of inter-connected stages: introduction effort across biogeographic barriers, suitability of physiochemical conditions in the new environment, and survival in the local biota; each of these stages may pose differing demands on entrained species and may be studied independently (Carlton 1985, Williamson and Fitter 1996, Richardson *et al.* 2000, Kolar and Lodge 2001, 2002, Colautti *et al.* 2006). While many patterns in nature may have alternate explanations, none of which takes logical precedence for testing over any other, the same cannot be said for hypotheses that may account for success of non-indigenous species (NIS). All invasions begin with the introduction of NIS propagules, which may vary in number, quality, sex ratio, age, or number of introduction events (Fig. 1). Propagules are then subject to prevailing conditions of the host lake, which may reduce or eliminate effective propagule pressure depending on the species' ability to tolerate these conditions. Only at this stage does the possibility of positive or negative biological feedback between the NIS and host community occur (Fig. 1). So, for example, an introduced mollusk like *Dreissena polymorpha* Pallas could fail to establish in a new lake owing to stochastic or



**Fig. 1** Transportation of species (F, G, H, I) beyond historic biogeographic barriers to new ecosystems, where sequential filters reduce the number that successfully establish (H, I) as NIS. An introduction effort or 'propagule pressure' filter reduces both the number of species and individuals within particular species that reach the physiological filter. Modeling techniques may help identify physiological and/or constraints that further restrict establishment of NIS in novel ecosystems. (Modified from Rahel 2002)

deterministic processes (e.g. small population size; all larval or post-reproductive propagules), because of insufficient calcium in lake water to allow shell formation, or because predation by molluskivorous waterfowl increased the species' death rate. While this model suggests that introduction effort (i.e. propagule pressure) hypotheses be tested first and biological interaction questions last, we recognize that invasions could fail at any stage (see Colautti *et al.* 2006). Additionally, cases might occur where, under the same biological conditions (e.g. predators), NIS introduction can either succeed or fail depending upon physiological conditions. Indeed, evidence exists supporting the importance of all three stages in failed invasions by various species. If this order of hypothesis testing is accepted, then methodologies must be developed for examining propagule pressure. Unfortunately, formal tests of the importance of propagule pressure have been few in number until quite recently (see Lockwood *et al.* 2005, Colautti *et al.* 2006). For species that pass through the introduction effort filter, other methods are required to determine the suitability of water in newly colonized lakes and ecological conditions therein. In this paper, we begin by reviewing mechanisms of natural dispersal, following which we consider human introductions of species to lakes. As much as possible, we follow the sequence of hypothesis testing outlined above.

## NATURAL DISPERSAL

Passive (e.g. wind) and active (e.g. animal-vectored) transport of propagules has long been recognized as important to regional dispersal of species (see reviews Bilton *et al.* 2001, Havel and Shurin 2004, Green and Figuerola 2005). The simplest and most predictable form of dispersal occurs via advection of propagules in currents. Zooplankton and planktonic larval stages of benthic species may be readily dispersed to connected waterbodies, though depending on the life stage involved, mortality during transport may be high. For example, Horvath *et al.* (1996) determined that presence of zebra mussels in upstream lakes was a strong predictor of mussel presence downstream, although abundance of mussel veliger larvae fell exponentially with distance from the source. The same pattern also holds on a broader scale: lakes in the midwestern USA that were connected by streams to invaded lakes were more likely to be invaded than those connected to non-invaded lakes (Bobeldyk *et al.* 2005). A similar pattern was observed in Belarus, where isolated lakes were much less likely to be invaded by zebra mussels than clustered lakes (Kraft *et al.* 2002). Although the generality of these patterns must be tested for species other than zebra mussels, upstream sources of propagules of NIS place downstream ecosystems at high risk of invasion. Western and northern European river systems have become invaded with a succession of NIS from the Black Sea owing to construction of canals that permit passive transfer in currents or active transport in or attached to vessels (Bij de Vaate *et al.* 2002). Likewise, the Volga River has been colonized by a number of species from the Black Sea, placing the Baltic Sea at risk; the Caspian Sea, in turn, has been invaded by NIS from the Black and Azov seas (see Leppäkoski *et al.* 2002). While some of these transfers were undoubtedly made via ships, all of these ecosystems are now linked either directly or indirectly by canals, thus opening the possibility of passive transfers of NIS. Reservoirs are often created by damming rivers, one consequence of which may be greater susceptibility to invasion, in particular for passive dispersing species that cannot persist in strong unidirectional flow (e.g. zooplankton, aquatic weeds, planktonic larvae; Havel *et al.* 2005). These reservoirs may, in turn, serve as 'stepping stones' for secondary spread of NIS to both connected and disconnected aquatic habitats (Havel *et al.* 2005). As an example, the quagga mussel *Dreissena rostriformis bugensis* Andrusov is spreading up the Volga River system after having been introduced in or near Kubyshev Reservoir, Russia (Therriault *et al.* 2005).

Wind and rain also may transport NIS locally or between watersheds, particularly those species capable of producing diapausing eggs (Bilton *et al.* 2001). However, the importance of these mechanisms to overall dispersal patterns remains unclear. On the one hand, Louette and De Meester (2005) observed 20 different colonizing species, averaging 4.2 cladoceran species per pond after a 15-month period, in 25 freshly dug and isolated pools in Belgium, and suggested that dispersal of cladocerans was high. Cohen and Shurin (2003)

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also suggested that zooplankton species were vagile over short distances in their North American study. On the other hand, Jenkins and Underwood (1998) observed only two bdelloid rotifer species in experimental wind socks and four rotifer species from samples of rain, and Havel and Shurin (2004) suggested that zooplankton dispersal might become limiting beyond 20 km.

Local spread of NIS may be affected by strong winds and the availability of resting stages. For example, extensive foam windrows of the NIS waterflea *Bythotrephes longimanus* Leydig have been observed on leeward shores of Lake Huron after strong winds blew across the lake (D. Garton 1986, personal observation). Diapausing eggs contained in this foam could be moved to seed new populations in waters directly proximal to the lake, or, more likely, coat plumage of dabbling waterfowl that could then introduce the species to other visited lakes in the region. Introductions by local movements of waterfowl are likely confined to proximal systems (e.g. Johnson and Carlton 1996, Bilton *et al.* 2001), while long-distance transport would almost certainly be limited to seasonal migrations (e.g. Proctor 1959, 1964, Swanson 1984). Thus even though Green and Figuerola (2005) proposed that transfer of invertebrates by waterfowl may exceed 1,000 km, from a mass-transfer viewpoint, it is far more likely that flocks of migrating waterfowl would effect transfer of species more readily than could single individuals. Ectozoochorous or endozoochorous transfers by seasonally migrating waterfowl could effect both regional and long-distance introductions of NIS in a non-spatially explicit (i.e. not area specific) yet predictable pattern (Bilton *et al.* 2001, Figuerola and Green 2002). For example, Figuerola *et al.* (2003) identified a broad array of invertebrate eggs in digestive tracts of waterfowl arriving to and departing from wetlands in Doñana, Spain. If this information were combined with that on the primary flight paths of the waterfowl species and the distribution of major stopover sites, general models of possible range extensions of zooplankton could be constructed.

Charalambidou *et al.* (2003) suggested that autumnal migrations of waterfowl were more likely to spread *Bythotrephes* via endozoochory from north to south in Europe. However, they also asserted that dispersal probability would drop sharply beyond 60–80 km, based upon waterfowl flight speed and gut retention time for diapausing eggs of the waterflea. The application of molecular markers may allow identification of source–destination relationships (see Bilton *et al.* 2001, Figuerola and Green 2002), although in the case of NIS this is often simplified since there may be very few putative sources from which new populations could be drawn.

In summary, both wind and directed flights by waterfowl are capable of dispersing propagules – especially resting stages of invertebrates – of NIS in a directional manner, although identifying destinations of these propagules can only be done on a relatively crude, regional basis. Development of models to predict the strength of these vectors also has not yet been accomplished. Even though these vectors have likely played important roles in evolutionary changes to species distributions, their respective roles in effecting dispersal of NIS now

appear swamped by vectors associated with human activities, in part because the number of propagules potentially transported by an individual waterfowl or by wind is much lower than the bulk transfers associated with ballast water discharges or recreational boats trailered between lakes (e.g. Johnson and Carlton 1996, Hebert and Cristescu 2002). The importance of human vectoring over natural mechanisms like wind or waterfowl has been highlighted for the dispersal patterns of non-indigenous macrophytes in New Zealand (Johnstone *et al.* 1985). Indeed, our understanding of human-mediated dispersal of NIS has been enhanced by studies of inter-lake transfers of invasive macrophytes, which many political jurisdictions recognize as problematic and have taken management actions to prevent.

### HUMAN-MEDIATED DISPERSAL

Humans are rapidly changing biological communities of lakes through a combination of habitat change, overexploitation, and species introductions. Biodiversity of lakes appears particularly vulnerable to introduction of NIS (Sala *et al.* 2000, Rahel 2002). Heretics argue that changes to species distributions, including invasions of new habitats, occur naturally. While this is certainly true, the scale by which natural dispersal operates is far lower than that associated with human activities (Hebert and Cristescu 2002, Grigorovich *et al.* 2003), and, in some cases, species are being introduced across biogeographic realms that have, until now, proved resistant to natural dispersal (see Havel and Shurin 2004). For example, the waterflea *Daphnia lumholtzi* Sars was introduced to North America from its native regions of Australasia and northern Africa (Havel and Medley 2006), whereas the signal crayfish *Pacifastacus leniusculus* Dana has been introduced to Europe from North America (Gherardi and Holdich 1999).

Once NIS establish in one location, they may be spread by both natural and human-mediated mechanisms elsewhere in the introduced region. For example, zebra mussels dispersed through the Great Lakes in a pattern consistent with stratified diffusion involving both advective and human-mediated dispersal (Griffiths *et al.* 1991). Buchan and Padilla (1999) developed a diffusion model for zebra mussels that incorporated long-distance movement of trailered boats across Wisconsin and the probability that zebra mussels survive transport and establish in the destination lake. Johnson *et al.* (2001) developed a probability-based model to forecast spread of introduced zebra mussels to inland lakes in Michigan, USA based upon movement of trailered boats between a network of lakes adjacent to, and presumably initially invaded from, the Great Lakes. This effort was made more quantitative by surveying boaters and inspecting their equipment as it was trailered from Lake St. Clair to determine if larval or adult zebra mussels were being transported. These data were combined with estimates of survival of mussels outside water to determine the number of dispersal events

from the lake associated with seven different vectors. Application of different modeling tools may allow investigators to identify lakes that will serve as invasion hubs – from which other lakes are colonized – as well as vulnerability of regions or specific lakes to invasion. One of the most promising techniques that links invaded sources with non-invaded destination lakes is gravity modeling. Gravity models can be considered a form of ‘propagule pressure’ assessment since they seek to quantitatively link sources and destinations.

### VECTOR-BASED GRAVITY MODELS

Transportation or gravity models have been applied to many economic and social questions, and have been widely applied over the past decade to assess spatial patterns of aquatic NIS dispersal (Schneider *et al.* 1998, Bossenbroek *et al.* 2001, Drake and Bossenbroek 2004, Drake and Lodge 2004, Leung *et al.* 2004, 2006, MacIsaac *et al.* 2004, Muirhead and MacIsaac 2005). Gravity models of species spread estimate the frequency of dispersal events and are coupled with the explicit nature and spatial arrangement of potential colonization sites in contrast to diffusion models that assume a homogeneous landscape (e.g. Buchan and Padilla 1999). Gravity models provide information on the relative strength of vector movement (i.e. propagule pressure) from an invaded source to non-invaded (or invaded) destination lakes in a manner analogous to Newton’s Theory of Gravity for measuring the attractive force between two masses. Perhaps better than for any other type of ecosystem, gravity models hold the promise of accurately forecasting the dispersal of NIS amongst lakes.

Depending on the type of information available and objectives of the study, four classes of gravity models are available: total flow-constrained, production-constrained, attraction-constrained, and production-attraction or doubly-constrained (Haynes and Fotheringham 1984). In the total flow-constrained model, which requires the least knowledge of the system, information is available on only the total number of interactions and we are asked to forecast the interaction pattern among origins and destinations based on their distances. The model is constrained so that the total of the forecast interactions between sources and destinations is equal to the known total number of interactions. In production-constrained models, we have information only on outflows from each of the origins. The inflows into each destination are forecasted based upon the magnitude of outflows from each origin, the pairwise distances between origins and destinations, and an external measure of attractiveness to each destination such as lake area (Bossenbroek *et al.* 2001). During the calculation of predicted inflow, the sole constraint is that the predicted outflow of the balanced model is equal to the measured outflow. Likewise, for attraction-constrained gravity models, we have information on inflows to each of the destinations and are asked to forecast outflows from each of the origins under the constraint that predicted inflows for each destination is equal to

measured inflow. The doubly-constrained gravity model, in which information about both outflows and inflows is required, provides the best quality of interaction information and thus is the most spatially-explicit when forecasting dispersal to novel regions. In this model, the forecasted interactions between origins and destinations are constrained in such a manner that the predicted total outflow for each origin and total inflow for each destination are equal to measured outflows and inflows. Schneider *et al.* (1998) and MacIsaac *et al.* (2004) used doubly-constrained gravity models to forecast human-mediated spread of *D. polymorpha* and *B. longimanus*, respectively, in the Great Lakes region.

With the four types of gravity models, predictive ability scales with the amount of effort required to collect the data and the amount of measured information about flows in the system, especially with respect to forecasting the interaction flows between sources and destinations. The total-constrained model requires the least effort and offers the least predictive ability, since we have information only on the total number of interactions within the system (e.g. total number of boaters moving in the area). The summed outflows for each source, summed inflows for each destination, as well as the interaction flows between sources and destinations are unknown and must be solved.

The gain in predictive ability of the production- or attraction-constrained model over the total-flow constrained alternative is large relative to the effort required to collect additional information. For production-constrained models, information of outbound propagule pressure from invaded sources can easily be obtained by surveys of the number of boaters leaving a lake, or the number of owners of boat licenses at regional scales. Bossenbroek *et al.* (2001) modeled the propagule pressure of transporting zebra mussels by the number of boats that could potentially leave a county from five midwestern States and arrive at a particular lake, with lake area as a measure of attractiveness. Leung *et al.* (2004) use a similar production-constrained gravity model approach to model the risk of transporting zebra mussels via boater traffic from Michigan counties to lakes in the State, and again used the number of registered boaters per county as a measure of potential outbound traffic. In their assessment of the utility of using production-constrained gravity models to capture boater traffic within Michigan, Leung *et al.* (2006) used lake area as a proxy for lake attractiveness. The advantage in using these models is that data on the number of boat licenses, which can be used as a proxy for potential outbound traffic, is often available from government databanks. However, these gravity models are limited by the lack of data on the actual inbound vector traffic, which becomes important when forecasting relative risk by contrasting invaded vs. currently non-invaded destinations.

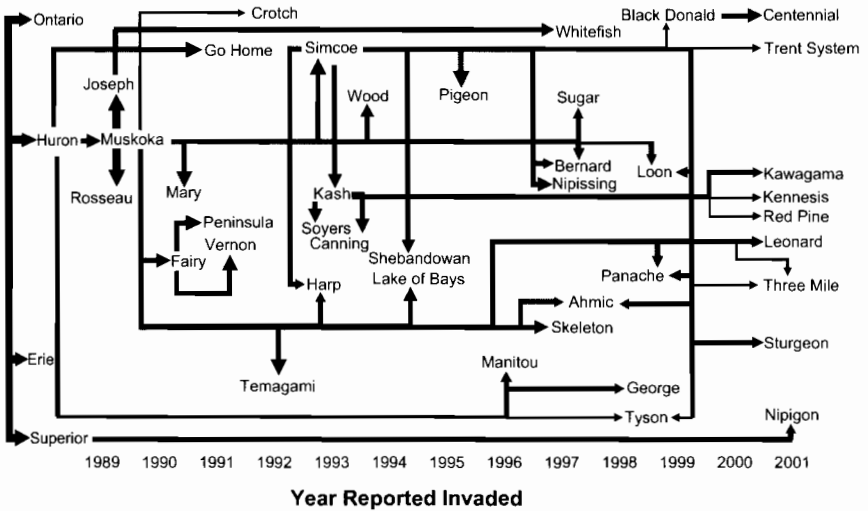
In attraction-constrained models, the converse is true. Explicit inbound vector data is required for each destination, and usually will require more intensive survey work, either through contacting officials responsible for monitoring recreational lake use or via mail-based or creel surveys, since the number of non-invaded or invaded destinations is usually greater than the number of invaded sources. This form of model is not normally used as a risk assessment



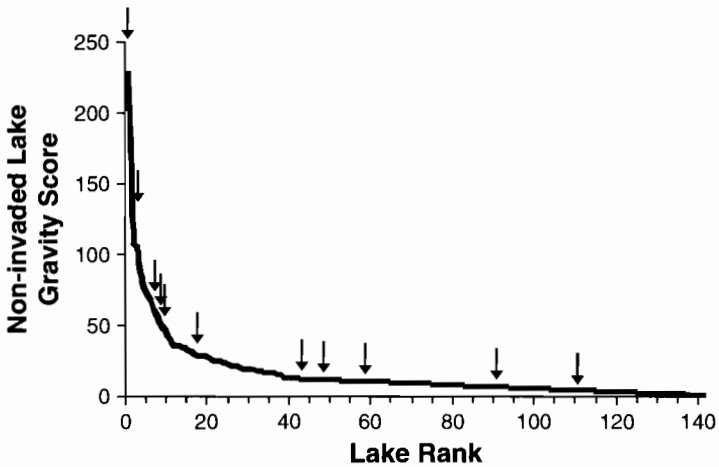
tool for invasions since it only forecasts putative sources for invasion if currently unknown. One advantage of this form of model is its greater confidence in the relative risk of a destination being invaded, but at the cost of lack of information pertaining to the source of the invading propagules. Since survey information for each destination is usually required, the same amount of effort can be used to collect data necessary for the construction of a doubly-constrained model.

In the doubly-constrained model, spatially-explicit knowledge of the vector outflow from invaded sources as well as inflow to currently invaded and non-invaded destinations requires the greatest commitment in terms of data collection. Information on specific trips is necessary to gauge the interaction between sources and destinations, and thus is usually collected in the form of surveys. This form of gravity model allows the best predictive ability since it forecasts interactions between sources and destinations based on distance and external measures of attraction, and is constrained so that summed outflows from sources and summed inflows to destinations are equal to measured outflows and inflows. In other words, the accuracy of the forecast interactions in the doubly-constrained model is likely closest to actual flow than that predicted by the other forms of gravity models. Similar to the production-constrained model, we are able to predict invasions by forecasting inflows to other destinations for each source lake. Likewise, for each destination, we can assess the relative inflow from each of the sources. Schneider *et al.* (1998) used a doubly-constrained gravity model to assess the risk of transporting zebra mussels to inland lakes in Illinois, USA. Based on both creel surveys and contacting officials responsible for boat-access sites, propagule pressure was estimated by the number of boats used per year. In their model, an assumption was made that attractiveness of a particular destination was correlated with boat use. MacIsaac *et al.* (2004) modeled the risk of transporting the spiny waterflea among inland lakes in Ontario using mail and on-site surveys. The doubly-constrained gravity model allows for the greatest confidence in predicting which currently non-invaded lakes are at risk of invasion. Both Schneider *et al.* (1998) and MacIsaac *et al.* (2004) developed prioritized lists of lakes likely to be invaded. Doubly-constrained models may be validated by backcasting the order in which lakes were invaded based on current relative inbound vector traffic if one assumes that human activity patterns have not changed over the time invasions occurred (Fig. 2a). Gravity models may also be validated by comparing forecasts with observed invasions. MacIsaac *et al.* (2004) found that lakes with high inbound traffic were likely to be invaded in subsequent years (Fig. 2b). In addition to providing watershed managers with an assessment of relative inbound traffic to currently non-invaded destinations, doubly-constrained models also can be used to provide an assessment of the relative outbound traffic from invaded sources. This data can be used to identify existing and future "hubs", thereby allowing management efforts to focus on these lakes (Fig. 3) (Muirhead and MacIsaac 2005). By contrast, Drake and Lodge's (2004) assessment of a global network of ship movements amongst ports suggested that

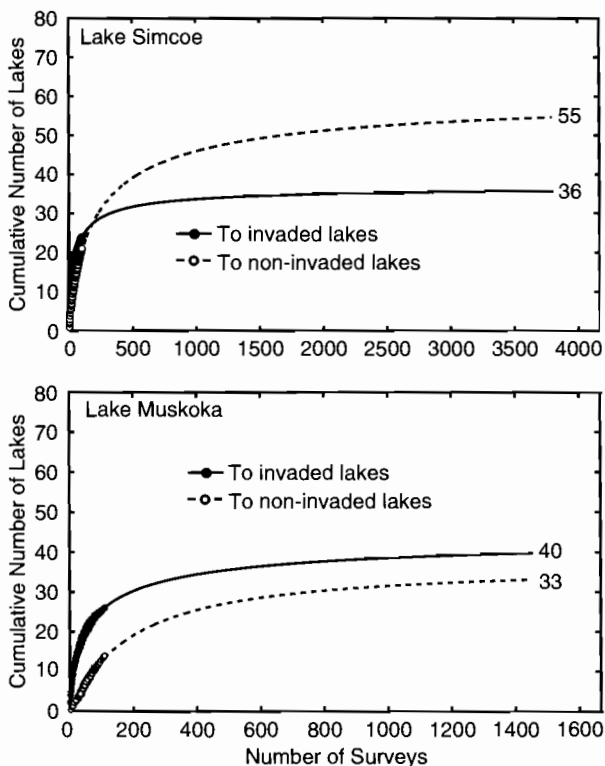
(a)



(b)



**Fig. 2** a) Sequence of introduction of the spiny waterflea *Bythotrephes longimanus* to inland lakes in Ontario from the Great Lakes (Lake Huron). Backcasting sequences are based upon reported order in which lakes were invaded and surveys of boater/angler movements from invaded source lakes to non-invaded destination lakes. Arrow thickness indicates strength of vector from donor lake (left side) to destination lake (right side). b) Forecast of invasion risk for non-invaded lakes in relation to gravity score (a measure of introduction effort). Lakes that switched from non-invaded to invaded status are indicated with an arrow, and had significantly higher vector inflows than lakes that remained non-invaded. (Modified from MacIsaac *et al.* 2004)



**Fig. 3** Cumulative number of lakes visited by boaters that arrived from invaded source lakes (Simcoe, Muskoka) in Ontario. Dotted line represents visitations to non-invaded lakes, solid lines visitations to invaded lakes. Asterisks represent the estimated number of boaters leaving each lake per year. A disproportionate number of boaters leaving Lake Simcoe arrive to lakes that have not yet been invaded (55 vs. 36), whereas most outflow from Lake Muskoka is to other lakes that have already been invaded (40 vs. 33). Lake Simcoe may develop into a future hub for dispersal of the species, whereas Lake Muskoka, which has already caused many invasions, is less likely to cause future invasions. Results are based upon surveys of boaters leaving the lakes and were modeled using Monte Carlo simulations and nonlinear regression. (Modified from Muirhead and MacIsaac 2005)

a reduced invasion rate could be better obtained through small reductions per ship-invasion risk through ballast control than by knocking out particular "hub" ports. While much remains to be learned about gravity models, these techniques offer insights into how lakes are connected as networks owing to human activities and they ought to be applied much more widely to studies of other aquatic NIS.

Survey methods have also been used to predict spread of other aquatic NIS. Many of these studies involve bait or food fishes that are imported and sold live,

following which the purchasers release some or all of their stock. As with their gravity model counterparts, either coarse or fine-scale spatial predictions may be made regarding vulnerability of lakes to NIS introduction depending on the nature of the survey questions. As an example, surveys by Litvak and Mandrak (1993) at bait-fish shops in Toronto, Ontario illustrated that 41% of anglers who purchased bait fishes released unused specimens at destinations up to hundreds of kilometers from their source. The same methodologies may be used to track introduction and potential spread of species in water garden and aquarium trades.

### Modeling environmental suitability

Ecologists have used a number of other techniques to model habitat suitability of aquatic NIS. One approach is to empirically determine limnological differences between lakes with and without a particular species. For example, Ramcharan *et al.* (1992) assessed differences in 278 European lakes with and without *D. polymorpha* using discriminant-function analysis (DFA). Their analysis revealed that lakes with *Dreissena* could be separated from those without the species using only two variables: pH and calcium content of lake water. This analysis was extended to demonstrate that lakes with high mussel densities differed from those with low densities based upon nutrient levels ( $\text{NO}_3$ ,  $\text{PO}_4$ ). MacIsaac *et al.* (2000) also used DFA to identify lakes in Europe with and without the waterflea *Bythotrephes*. In this case, lakes with the species tended to be larger, deeper, and have higher Secchi transparency than those without the species. Functions generated in both Ramcharan *et al.*'s (1992) and MacIsaac *et al.*'s (2000) models were then used to predict where these respective species would potentially occur in North America.

Allen and Ramcharan (2001) used logistic regression to differentiate river systems in the USA with and without *Dreissena*. They found that permanent populations tended to occur in systems with moderate ionic strength and some degree of impoundment. Again, based upon this classification, the authors were able to extend their analyses to predict whether *Dreissena* would occur in other, untested river systems.

In a very thorough study, Marchetti *et al.* (2004) used multivariate models to explore determinants of invasion success for all stages of fish invasions – from introduction to integration – in California catchments. They determined that propagule pressure and prior invasion history were significant predictors of fish-establishment success, as were biological features such as parental care and physiological tolerance. During secondary dispersal after establishment, distance from nearest native source and trophic status were important predictors. Maximum size, physiological tolerance, and distance from nearest native source were the best predictors of abundance for established populations. This study clearly highlighted the importance of different factors to success of fish species at different stages of an invasion. In an earlier assessment of assembly rules for

aquatic invasions, Moyle and Light (1996) observed that most invasions failed but that all systems are invulnerable. Among their findings, they noted that piscivores and detritivores/omnivores were most successful in relatively undisturbed systems, and that any species could invade so long as they possessed appropriate environmental tolerances.

Kolar and Lodge (2002) also used multivariate analyses to identify different factors important to different stages of fish introductions to the Great Lakes. Because data were available on failed as well as successful fish introductions, the authors were able to specifically distinguish between characteristics associated with each. Kolar and Lodge (2002) used DFA to determine that successful invaders at the establishment stage grew relatively fast, tolerated greater variation in temperature and salinity, and had more extensive histories of invasiveness than species that failed at this stage. Similar results were obtained when the authors used another methodology, categorical and regression tree analysis (CART). At the spread stage, DFA demonstrated successful species had slower relative growth rates and poor survival in high water temperatures, although they did exhibit a broader temperature range than slow-spreading species. At a final stage of analysis, the authors noted that 'nuisance' species had smaller eggs, wider salinity tolerance, and survive low water temperatures better than nonproblematic fishes.

At this stage we would like to highlight the importance of distinguishing between lakes that are unsuitable for an NIS (e.g. those that have experienced failed invasions) and lakes that possess suitable environmental conditions but which lack sufficient propagule pressure (i.e. they could be viewed as 'not yet colonized'). Both types of lakes have the same characteristic – lack of an established NIS population – yet they differ fundamentally with regard to invasibility. Studies on the invasion in Bellarussian lakes found that even after 200 years, some lakes with suitable environmental conditions are still not invaded by zebra mussels due to limited propagule pressure (Karatayev *et al.* 2003). Similarly, Johnson *et al.* (2006) found that only ~10% of lakes with suitable environmental conditions had been invaded by zebra mussels after 15 years in areas of North America that already support the species. Hence, the distinction between unsuitable lakes and suitable but not-yet-invaded lakes is crucial while studying the invasion process.

### **Ecological niche modeling**

Ecological niche modeling is a methodology that seeks to predict the potential range of NIS based upon matching of environmental characteristics in the native range with those in the introduced range (see Peterson 2003). A wide variety of approaches are available (Elith *et al.* 2006), including two – CLIMEX and Genetic Algorithm for Rule-set Prediction (GARP) – that have been utilized to predict ranges of NIS. CLIMEX seeks to identify the potential distribution and relative abundance of species in relation to climate models, while GARP uses

georeferenced environmental and biological information to predict suitable habitat in a species' introduced range. GARP is an iterative machine-learning tool that employs an array of methods including logistic regression, range rules, negated range rules, and atomic rules to identify heterogeneous rule-sets describing a species' environmental niche. Models are constructed using species presence in the native range together with geo-referenced environmental data. GARP models may also be developed using species presence and environmental data from one introduced range to determine where the species could spread in the future. As an example, GARP was used to predict range expansion and boundary limitations for zebra mussels dispersing into the western USA, based upon its distribution patterns in the eastern USA (Drake and Bossenbroek 2004). Resultant models identified environmental, geological, and biological correlates of its occurrence in the east, and forecasts of vulnerable areas in the west. Some areas, including the Columbia and Colorado rivers, were identified as highly vulnerable to establishment, should mussels be introduced, thereby providing managers with spatially-explicit insights into where exclusion programs would be most useful. Similarly, Herborg *et al.* (2007a) developed separate GARP models for Chinese mitten crabs (*Eriocheir sinensis* H. Milne Edwards) in native East Asia and in its introduced range in Europe to develop forecasts of where the species could be expected to establish in North America. GARP may be most useful if combined with measures of introduction effort, which collectively provide managers with information on where species are being introduced as well as the suitability of these habitats.

Below we develop a simple combined model that incorporates a GARP model to identify where Chinese snakehead (*Channa asiatica* Linnaeus) fishes could survive in North America.

#### *An Example of the Chinese snakehead in North America*

The Chinese snakehead (*C. asiatica*) is a freshwater fish native to central and southern China (18°–35° N). Its ecology is poorly described, but it is reported to be predaceous and capable of short-distance overland migration. Various species of the genus *Channa* are available on Asian food markets in the USA and Canada, despite bans from import and interstate transport between all American States. Snakeheads are also sold as aquarium fish, but due to their rapid growth and high cost they are not widely used. Despite *C. asiatica*'s availability to aquarists in the USA since the early 1900s and occasional reports of the fish in Florida in the 1960s, no established populations have been reported, although other members of this genus have successfully established in the USA (Courtenay and Williams 2004).

We developed a GARP model for *C. asiatica* based on its native distribution (Courtenay and Williams 2004). Polygons representing the native range of the species were converted into 200 occurrence points in a GIS (ArcMap 9.1). The development of ecological niche predictions was consistent with previous

applications of GARP (see Herborg *et al.* 2007a). A GARP simulation using all possible combinations of the environmental coverage, allowed determining the effect of each environmental variable on model accuracy using multiple regression analysis. The global climatic and geographic coverages tested included: frost frequency, slope, compound topographic index, precipitation, river discharge, minimum annual air temperature, mean annual air temperature, maximum annual air temperature, and wet day index. Once suitable environmental coverages were determined, 100 models were generated following the best subset method (see for details Anderson *et al.* 2003) and converted into a map of percentage environmental match using ArcMap 9.1. Finally, hierarchical partitioning analysis was applied to test the effect of environmental coverages on predictive accuracy of the final models (Peterson and Cohoon 1999). Once the model was developed and tested, we applied it to identify suitable environments for *C. asiatica* in North America. We refined the analysis by identifying States that are most at risk from *C. asiatica* establishment by using a very crude measure of propagule pressure: the number of individuals of the genus *Channidae* (e.g. snakeheads) reported in the wild by the United States Geological Survey (<http://nas.er.usgs.gov/queries/default.asp>) (Table 1). We used reports from all species of snakeheads as the same two vectors – aquarium trade and/or

**Table 1** Summary of all reports of occurrences of the Asian snakehead genus *Channa* in the contiguous USA, as reported by the United States Geological Survey online database (<http://nas.er.usgs.gov/queries/default.asp>). Multiple reports from established populations are not included in the number of isolated reports, as they are most likely caused by reproduction rather than human introduction. Occurrence reports are used as a crude measure of potential propagule pressure in a State.

US State	Number of isolated reports	Number of established populations
California	2	
Florida	4	1
Illinois	1	
Massachusetts	3	
Maryland	2	1+1#
Maine	1	
North Carolina	1	
New York	1	
Pennsylvania	2	1
Rhode Island	2	
Tennessee	1	
Virginia	0	1
Wisconsin	1	

# Population has been successfully eradicated in 2002

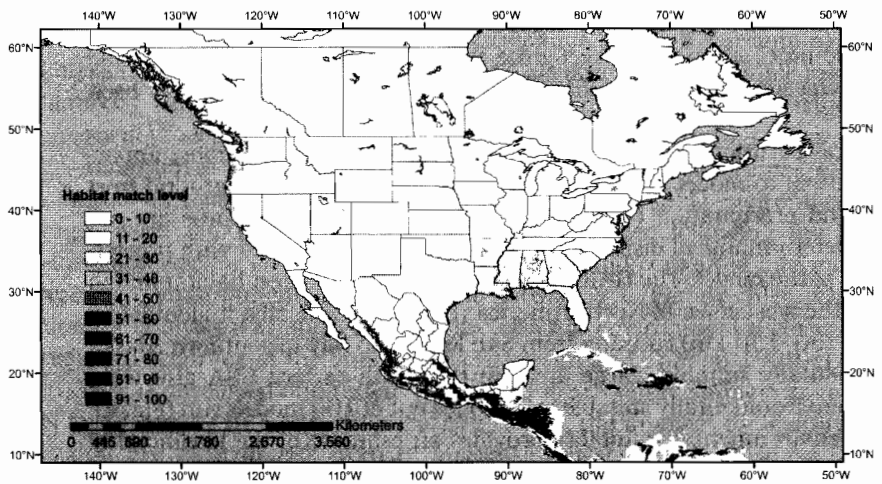
live fish markets – are responsible for introducing individuals of all congeneric species including *C. asiatica*. We recognize that additional sites may have had snakehead releases which either have failed or, if successful, have not been reported.

Hierarchical partitioning of the GARP model revealed that the most important contributors to model accuracy were mean air temperature, ground frost frequency, and precipitation (Table 2). It should be noted that these are not necessarily determinants of distribution, but rather are correlated with predictive accuracy of the model. The GARP model predicted the highest habitat match levels along the west coast of North America (Fig. 4). Specifically, it identified a narrow strip (50–150 km) running from San Francisco Bay to southern Alaska as environmentally suitable. Large areas in the south-eastern USA also were predicted as environmentally suitable in 20 to 30 out of 100 models run (Fig. 4). The level of environmental suitability provides an estimate of the likelihood of survival of the species, as it is based on the number of models out of 100 that predicted a particular area suitable. Nevertheless, there is no defined cutoff point for the level of environmental match below the species cannot survive. For all of these areas deemed suitable, establishment of the species could only occur if an introductory pathway exists. One albeit crude measurement of introduction effort is the number of snakehead introductions reported for each US State (Fig. 5). By combining these data with areas of suitable habitat, locations vulnerable to snakehead establishment can be identified. The combination of propagule supply and potentially suitable habitat places Florida at a high risk of establishment. North Carolina, and to a lesser extent, northern California also have suitable habitat and reports of snakehead occurrences, although they are fewer than in Florida (Table 1). Occurrence data are not available for British Columbia, although the species is sold there and habitat matching suggests that it can survive in that region.

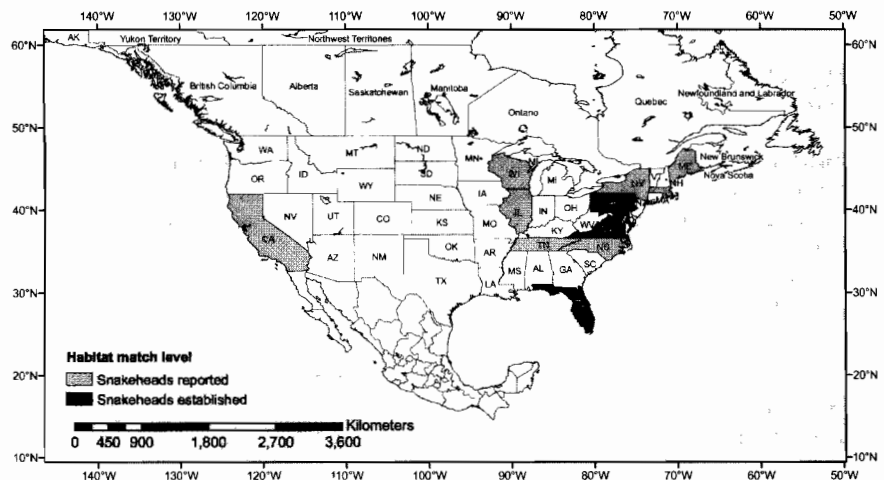
**Table 2** Hierarchical partitioning of environmental variables that contributed significantly to predictive models of *Channa asiatica* distribution in North America. The importance of each environmental variable is given as a relative percentage contribution to model accuracy.

Factor	Contribution to Model Accuracy (%)
Ground-frost frequency (number of days)	19
Topographic index (wetness index based on flow accumulation and slope)	1
Precipitation ( $\text{mm day}^{-1}$ )	17
River Discharge ( $\text{km}^3 \text{ yr}^{-1}$ )	2
Mean temperature ( $^{\circ}\text{C}$ )	53
Wet day index (number of days of precipitation)	8





**Fig. 4** Predicted occurrence of the Chinese snakehead *Channa asiatica* in North America based on Genetic Algorithm for Rule-set Prediction, an ecological-niche modeling technique, developed using environmental data for its native range in Asia. Areas of greatest habitat suitability include regions of Central America, Jamaica, Puerto Rico, and Hispanola.



**Fig. 5** States in which individual snakeheads (gray stippling) or established populations (dark stippling) were reported, based on the invasive species database of the United States Geological Survey. It is not known whether reports of individual fish-finds reflect established populations.

One of the benefits of environmental niche models is that risk models can be formulated even for those species, like Chinese snakeheads, for which little ecological information exists. While gravity models can provide detailed predictions on vector transport, they do not address the principal question of whether the NIS could survive in the introduced environment. The combination of ecological-niche modeling and basic vector-traffic predictions presented here has the ability to answer and identify locations where a species can survive and a transport vector exists. Clearly a vector-traffic model of higher predictive power (e.g. gravity model) would provide more detailed results, but is outside the scope of this study. However, our prediction identified the highest invasion risk for Florida, followed by North Carolina and California, information that could help policy makers to focus management efforts. One limitation of GARP is that validation tests are rarely conducted for introduced ranges, but two recent studies (Iguchie *et al.* 2004, Herborg *et al.* 2007b) found high predictive accuracy for GARP models in identifying introduced ranges based upon native distribution data. Another issue for prediction of suitable environments of aquatic species is the lack of hydrological datasets (i.e. water temperature, water chemistry, flow speed, etc.) with a wider coverage. The basic output of the GARP also provides no information on the operational procedures by which models are constructed and weightings of environmental criteria are 'black-box' and beyond simple assessment by the investigator. Nevertheless, through additional analysis described in this study (see Herborg *et al.* 2007a for more detail) as well as other recently published methods (Elith *et al.* 2005), relevant environmental parameters and their suitable ranges can be identified, thereby facilitating a deeper understanding of the model.

## CONCLUSIONS

Collectively, these studies demonstrate that a broad array of modeling and statistical techniques can be brought to bear on the question of what determines invasion success. It is clear that answers can be far more complex than earlier models of invasion success, as different environmental factors or biological characteristics may be important at different stages of invasion. At the first stage of the invasion sequence, models of natural and human-mediated dispersal have been shown to forecast vulnerability of lakes to invasion. Environmental niche modeling can predict if a potential invaders can pass through the second stage of the invasion process (i.e. physiological filters). Predicting the ability of potential invader to survive the third and final stage – the biological filter – is more complex, and is only possible if biological interactions between the invader and native species are understood, which is typically not the case. Future models that incorporate all three stages of the invasion process will produce spatially-explicit predictions of where an NIS can establish. Lake systems are ideal models for developing and testing invasion theory because

they are clearly defined habitats, because natural and human-mediated dispersal can often be quantified, and because they vary in physical–chemical constitution and biological composition. Hence, results of NIS studies conducted on lake ecosystems can be applied to a wider array of habitats in future to predict determinants of invasion success.

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