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Fecundity as a Basis for Risk Assessment of Nonindigenous Freshwater Molluscs

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Abstract: *The most efficient way to reduce future damages from nonindigenous species is to prevent the introduction of harmful species. Although ecologists have long sought to predict the identity of such species, recent methodological advances promise success where previous attempts failed. We applied recently developed risk assessment approaches to nonindigenous freshwater molluscs at two geographic scales: the Laurentian Great Lakes basin and the 48 contiguous states of the United States. We used data on natural history and biogeography to discriminate between established freshwater molluscs that are benign and those that constitute nuisances (i.e., cause environmental and/or economic damage). Two statistical techniques, logistic regression and categorical tree analysis, showed that nuisance status was positively associated with fecundity. Other aspects of natural history and biogeography did not significantly affect likelihood of becoming a nuisance. We then used the derived statistical models to predict the chance that 15 mollusc species not yet in natural ecosystems would cause damage if they become established. We also tested whether time since establishment is related to the likelihood that nonindigenous mollusc species in the Great Lakes and United States would cause negative impacts. No significant relationship was evident at the U.S. scale, but recently established molluscs within the Great Lakes were more likely to cause negative impacts. This may reflect changing environmental conditions, changing patterns of trade, or may be an indication of "invasional meltdown." Our quantitative analyses could be extended to other taxa and ecosystems and offer a number of improvements over the qualitative risk assessments currently used by U.S. (and other) government agencies.*

Keywords: biological invasion, ecological forecasting, ecological prediction, mollusk, risk analysis, risk assessment

La Fecundidad como Base para la Evaluación de Riesgo de Moluscos Dulceacuícolas No Nativos

Resumen: *La prevención de la introducción de especies perjudiciales es la manera más eficiente de reducir los daños futuros ocasionados por especies no nativas. Aunque los ecólogos han buscado predecir la identidad de tales especies durante mucho tiempo, avances metodológicos actuales prometen éxito en donde han fallado intentos anteriores. Aplicamos métodos de evaluación de riesgo, desarrollados recientemente, en moluscos dulceacuícolas en dos escalas regionales: la cuenca Laurentian de Grandes Lagos y los 48 estados contiguos de los Estados Unidos. Utilizamos datos de historia natural y biogeografía para discriminar moluscos dulceacuícolas establecidos que son benéficos de los que son perjudiciales (i.e., causan daño ambiental y/o económico). Dos técnicas estadísticas, regresión logística y análisis de árbol categórico, mostraron que el estatus perjudicial estaba asociado positivamente con la fecundidad. Otros aspectos de la historia natural y biogeografía no alteraron la probabilidad de convertirse en perjudicial. Posteriormente utilizamos los modelos estadísticos derivados para predecir la probabilidad de que 15 especies de moluscos que aun no están en ecosistemas naturales pudieran causar daños en caso de establecerse. También probamos si el tiempo transcurrido desde el establecimiento está relacionado con la probabilidad de que especies de moluscos no nativos en los Grandes Lagos y en Estados Unidos pudieran causar impactos negativos. No hubo relación significativa evidente en*

la escala de E. U. A., pero los moluscos recientemente establecidos en los Grandes Lagos tuvieron mayor probabilidad de provocar impactos negativos. Esto puede ser reflejo de condiciones ambientales cambiantes, de patrones de comercio cambiantes o puede ser un indicador de una "fundición invasiva." Nuestros análisis cuantitativos podrían ser extendidos a otros taxa y ecosistemas y ofrecen numerosas mejorías de las evaluaciones de riesgo cualitativas que actualmente son utilizadas por agencias gubernamentales de E.U.A (y otros países).

Palabras Clave: análisis de riesgo, evaluación de riesgo, invasión biológica, molusco, predicción ecológica, pronóstico ecológico

Introduction

Nonindigenous freshwater molluscs cause decreased agricultural (Lach & Cowie 1999) and utility production (Mackie 2000), increased health risks to humans, livestock, and wildlife (WHO 2002), and are an important threat to native biodiversity (Ricciardi et al. 1998). Worldwide, the economic and environmental costs of nonindigenous freshwater molluscs are increasing as growing numbers of species are transported beyond their native ranges (Mills et al. 1993; Cowie 1998; Levine & D'Antonio 2003). The principal pathways of this movement include ships' ballast water and the pet and live-food trades (Cowie & Robinson 2003). Although the majority of introduced species never establish reproducing populations and the majority of those that establish do not cause impacts (Williamson 1996), the rate of discovery of established species is increasing, presumably due to increasing pathway traffic (Cohen & Carlton 1998) or because of accumulating lags between introduction and discovery (Solow & Costello 2004).

Measures to prevent the spread of all freshwater molluscs—essentially ceasing trade—would bring enormous costs to society. An alternative, especially for intentional pathways such as the pet and live-food trades, is to predict which species are most likely to cause negative impacts and concentrate resources on preventing those from entering pathways. Particularly, quantitative methods based on information that can be easily identified in advance should be used to estimate the probability that introduced species will become a nuisance.

Nevertheless, a long history of work, including that by Baker (1974), suggests that lists of characteristics thought to confer negative impacts do not provide a sound basis for predictions. Although some generalizations exist that apply to a wide variety of taxa (Williamson 1996; Kolar & Lodge 2001), they are not sufficiently specific and robust to serve as a basis for predictions. Thus, some ecologists conclude that the invasion process is inherently too complicated for future nuisance species to be predicted with worthwhile accuracy (Williamson 1999).

In contrast recent approaches recognize that risk analyses must be more limited geographically and taxonomically and should be limited to specific "invasion steps" (Kolar & Lodge 2001). This approach explicitly acknowledges that to become a nuisance a species must pass through three steps: it must be transported; it must establish in a new range; and it must spread and cause harm. For example, on the basis of 24 characteristics of fishes introduced to the Great Lakes, Kolar and Lodge (2002) predicted with ∼90% accuracy the identity of introduced species that became established and the identity of established species that caused negative impacts. Similar success was achieved in predicting the identity of woody plant invaders in the United States (Reichard & Hamilton 1997), and strong correlations have been found between biological traits and likelihood of negative impacts for nonindigenous birds in New Zealand (Veltman et al. 1996), nonindigenous fishes in California (Marchetti et al. 2004), and nonindingenous conifers worldwide (Richardson & Rejmánek 2004).

We extended this approach in three ways. First, we applied the methods to molluscs, a taxonomic group for which relatively little natural history data are available. This allowed us to test whether these methods are robust when only small amounts of data are available to explain species impact. Second, we applied these methods to a smaller data set than has been done previously. Statistical methods work best with large sample sizes, and our analyses tested whether the risk analysis methods described are robust to low numbers of species. This is important because in many taxonomic groups only a small number of species have become established beyond their native range. If quantitative risk assessments are to be applied to these groups, then knowing the robustness of these methods to small sample sizes is essential. Finally, we compared the results from logistic regression and a categorical and regression tree (CART) approach.

We applied these statistical discrimination techniques to nonindigenous freshwater molluscs in the Laurentian Great Lakes basin and in the 48 contiguous states of the United States, of which the Great Lakes is a subset. We examined the final step in the invasion process—from established to nuisance—because this is the important economic and ecological step, and because data on the earlier steps are unavailable. We tested longstanding hypotheses about which characteristics are related to impact and show that risk assessment for nuisance mollusc species in the United States may require very little natural history data.

Methods

We classified all established nonindigenous freshwater mollusc species as either nuisance or benign. Nuisance species are those for which we could find credible evidence of environmental and/or economic harm. We accepted published scientific literature or unpublished scientific data made available by other scientists as credible evidence. We classified as benign all established species for which we could find no evidence of negative impacts. Thus, we have attempted to identify species that society might have made efforts to prevent from becoming established had their eventual impacts been known. Our definition of *nuisance* is similar to some definitions of *invasive* (e.g., Kolar & Lodge 2001), but to avoid ambiguity we do not use the term *invasive* (e.g., Richardson et al. 2000; Colautti & MacIsaac 2004). From a societal perspective, our distinction between nuisance and benign is the most relevant distinction for determining whether or not a species proposed for import should be permitted.

From a literature search we determined that 18 species of nonindigenous molluscs are established in the Great Lakes basin (Mills et al. 1993; Turgeon et al. 1998; Grigorovich et al. 2000). Four of these are native to other North American drainages (*Elimia virginica, Gillia altilis, Lasmigona subviridis, Viviparus georgianus,* Table 1) (Mills et al. 1993). For each nonindigenous species we conducted a literature search for natural history characteristics. Because the natural history literature on molluscs is poor for most species, we occasionally asked experts to provide unpublished data. Despite these efforts lack of information forced us to eliminate from our analysis several characteristics that we originally hoped to include (e.g., growth rate, tolerances for pH, temperature, oxygen, and all other metrics of environmental tolerance). Our analyses were thus based on eight natural history traits for which adequate data existed (Table 2). In addition, we collected data on the time since establishment for each established mollusc species (Table 2).

Two statistical discrimination techniques were used for data analysis. First, we tested for relationships between the natural history of a species and its impact with CART approach (Therneau & Atkinson 2005). Because our response data were binary (nuisance/benign), we created categorical trees. CART works by finding the split in one of the available predictor variables that maximizes the within-group homogeneity of the two groups produced (De'ath & Fabricius 2000). Any predictor variable could be used to make this split, and further splits within the resulting groups are made until the user-defined limit tree size is reached. CART is nonparametric, does not assume normality, is relatively robust to the distribution for predictor variables, and operates on both categorical and continuous data (De'ath & Fabricius 2000). CART's splitting points are placed at the midpoint between the two cases where the best split exists. Hence, if the split occurs between cases with values of, for example, 10 and 20, the split will be at 15. The true split could be anywhere between 10 and 20, however. More data in this range would be required for a better estimate.

All natural-history variables (eight variables, Table 2) were used as input data for the CART model. Each

Table 1. Established nonindigenous molluscs in the Laurentian Great Lakes and 48 contiguous states of the United States.

Family and species	Impacts	Fecundity[a]
Ampullariidae		
Marisa cornuarietis	environmental	1711
Pomacea bridgesi		
Pomacea canaliculata	economic	4355
Pomacea haustrum		
Bithyniidae		
Bithynia tentaculata[b]	economic	174
Corbiculidae		
Corbicula fluminea[b]	economic, environmental	68,678
Dreissenidae		
Dreissena bugensis[b]	economic, environmental	960,000
Dreissena polymorpha[b]	economic, environmental	960,000
Hydrobiidae		
Gillia altilis[b,c]		
Potamopyrgus antipodarum[b]	environmental	230
Lymnaeidae		
Radix auricularia[b]		1300
Physidae		
Stenophysa marmorata		
Stenophysa maugeriae		
Planorbidae		
Biomphalaria glabrata		356
Drepanotrema aeruginosus		
Drepanotrema cimex		
Drepanotrema kermatoides		
Pleuroceridae		
Elimia virginica[b,c]		
Sphaeriidae		
Pisidium amnicum[b]		10
Pisidium henslowanum[b]		5.8
Pisidium moitesserianum[b]		3.1
Pisidium supinum[b]		12
Sphaerium corneum[b]		62
Thiaridae		
Melanoides tuberculata	environmental	365
Melanoides turriculus		
Tarebia granifera		213
Unionidae		
Lasmigona subviridis[b,c]		
Valvatidae		
Valvata piscinalis[b]		150
Viviparidae		
Cipangopaludina chinensis[b]		65
Cipangopaludina japonica[b]		65
Viviparus georgianus[b,c]		39

[a]*Number of eggs or live offspring produced/female/year.*
[b]*Established in Laurentian Great Lakes.*
[c]*Native to the United States but not the Laurentian Great Lakes.*

Table 2. Variables, including mollusc natural-history traits and time since introduction, analyzed to determine whether differences exist between nuisance and benign, nonindigenous species in the Laurentian Great Lakes.[a]

Variable	Type	Levels (categorical) or units (continuous)
Type of reproduction	categorical	sexual, sequential hermaphrodite, simultaneous hermaphrodite, parthenogenetic
Egg brooding	categorical	yes/no
Maximum size	continuous	mm
Fecundity[b]	continuous	number of eggs or live offspring released/female/year
Longevity	continuous	years
Non-native elsewhere	categorical	yes/no
Latitude range	continuous	max. latitude minus min. latitude
Larval stage	categorical	yes/no
Time since introduction	continuous	year of first occurrence

[a]*Full data for all variables available on request from R.P.K.*
[b]*All individuals of parthenogenetic and simultaneous hermaphrodite species were considered females.*

resulting tree was assessed for accuracy on the basis of its misclassification rate (i.e., proportion of species that the derived models would have assigned the wrong nuisance status to) and splitting was based on recursive partitioning with the Gini index (De'ath & Fabricius 2000). Because of the small sample size, and to avoid overfitting, we set the minimum number of species allowed at any tree node to three. In addition, we used jack-knife analyses to test the derived CART models by removing one species from the full list and constructing a CART model with the remaining data. This was repeated for each species, and the jack-knife misclassification rate was the proportion of times the removed species would be incorrectly classified. The effect of time since establishment on species nuisance status was assessed with the same methods.

Second, we tested for a relationship between impact status and species natural history with logistic regression, which is used to find the probability of an event occurring (in our case, a species becoming nuisance) on the basis of the level of some predictor variable(s). Input variables can be either continuous or categorical, with continuous variables assumed to have a normal distribution. Advantages of logistic regression are that the relative risks posed for all levels of the predictor variable can be assessed, and confidence intervals can be calculated. As above, we used eight natural-history variables as input (Table 2). Fecundity was $\log_{10}$ transformed to meet regression assumptions. Predictive power was not improved by simultaneously including multiple explanatory variables in the model, so this approach was not pursued. Instead, we used likelihood ratio tests to assess the null hypothesis

that each natural-history character did not affect impact status (Quinn & Keough 2002).

For logistic regression we used an alpha level of 0.05, and for each significant result we calculated the receiver operating characteristic (ROC) curve to determine accuracy (Fielding & Bell 1997). An ROC output (area under the curve) of $c = 0.5$ indicates that the derived logistic curve is no more accurate than tossing a coin: $c = 1.0$ indicates perfect accuracy, and values above $c = 0.7$ indicate a good fit between model and data. Species for which data were not available were excluded from analysis. We also used logistic regression to test the null hypothesis that time since establishment is not related to nuisance status.

To broaden our approach we expanded our species list, based on Turgeon et al. (1998), to include all 27 nonindigenous freshwater molluscs in the 48 contiguous states (Table 1). We excluded *Physella acuta* on the basis of recent work suggesting that it is probably native to the United States (Dillon et al. 2002). Fourteen species from the Great Lakes data set described earlier (excluding species native to the United States but not the Great Lakes) formed a subset of this larger group (Table 1). We searched for estimates of annual fecundity and time since establishment (the only significant variables from our first analysis, see Results) for these 27 species, but were able to obtain fecundity data for only 19 species (Table 1). For time since establishment, we obtained data for 23 species. In categorizing species as nuisance or benign and in conducting logistic regression and CART, we used the same methods as for the Great Lakes analysis.

Unfortunately, our overall data set was too small to conduct phylogenetically independent contrasts (Rejmánek et al. 2005). Instead, we conducted sensitivity analyses to determine whether any one family was driving the significance of the logistic regression results by iteratively eliminating one family from the data set and recalculating the logistic relationship between natural history and impact status.

Using the logistic and CART models derived from the Great Lakes and U.S. analyses, we estimated the probability of becoming a nuisance for 15 species not yet present in the United States (Table 3). We selected these 15 species for predictive analysis because reliable fecundity data were available. Each species was assessed for likely impact status for both the Great Lakes and the 48 contiguous states.

Because the 48 contiguous states encompass a broad range of climates and habitats, we assumed that all 15 test species could become established somewhere in the United States. For each species tested we also used available information (especially the known geographical range) to predict whether it could survive in the Great Lakes (Table 3). Specifically, if a species' distribution was limited to tropical and/or subtropical conditions, it was considered incapable of establishing in the Great Lakes.

Table 3. Estimated probabilities of 15 mollusc species becoming invasive in the Laurentian Great Lakes and the 48 contiguous United States should they become established.[a]

Species	Great Lakes		United States	
	logistic	CART	logistic	CART
Ancylus fluviatilis	0.107	no	0.090	no
Indoplanorbis exustus[b]	0.859	yes	0.940	yes
Physa fontinalis	0.257	yes	0.280	yes
Lymnaea natalensis[b]	0.874	yes	0.950	yes
Lymnaea palustris	0.355	yes	0.414	yes
Lymnaea peregra	0.650	yes	0.772	yes
Planorbis contortus	0.085	no	0.067	no
Biomphalaria alexandrina[b]	0.744	yes	0.858	yes
Biomphalaria straminea[b]	0.687	yes	0.808	yes
Biomphalaria pfeifferi[b]	0.912	yes	0.970	yes
Bulinus abyssinicus[b]	0.800	yes	0.900	yes
Bulinus globosus[b]	0.688	yes	0.809	yes
Bulinus tropicus[b]	0.917	yes	0.971	yes
Bulinus truncatus[b]	0.657	yes	0.779	yes
Pisidium hibernicum	0.061	no	0.043	no

[a]*CART (categorical and regression tree) model gives yes/no prediction of whether a species will become invasive if established.*
[b]*Unlikely (on the basis of environmental constraints not included in the statistical analysis) to become established in the Great Lakes region.*

Results

Five nonindigenous molluscs were classified as nuisance in the Laurentian Great Lakes; three additional species were classified as nuisance at the level of the 48 contiguous states (Table 1). Of these eight nuisance species, three, two, and three species were categorized as nuisances, respectively, on the basis of their environmental and economic impacts, economic impacts only, and environmental harm only (Table 1). For the Great Lakes nuisance species were the bivalves *Dreissena polymorpha*, *Dreissena bugensis* (see Mackie 2000 for a review of *Dreissena* spp. impacts), and *Corbicula fluminea*, which has fouled power station water intakes (W.P. Kovalak, personal communication), and the gastropod *Bythinia tentaculata*, which previously fouled water-supply systems throughout the Great Lakes (Baker 1898). Although *C. fluminea* satisfies our definition of nuisance and is widely established in the southern Great Lakes basin, it is rarely recorded in the Great Lakes proper except at sites heated by thermal effluent. Hence, its ability to cause impact largely depends on industrial activities. *Potamopyrgus antipodarum* was included as a nuisance species based on its high densities ($\leq 5653/m^2$, Zaranko et al. 1997), rapid spread through the Great Lakes (Zaranko et al. 1997; Grigorovich et al. 2003), and history of negative impacts in other temperate habitats in North America (Hall et al. 2003).

Three additional species were added to the list of nuisance molluscs when the analysis was expanded to consider all 48 states. *Marisa cornuarietis* has caused large changes in the macrophyte communities of some Texas rivers (Horne et al. 1992); *Pomacea canaliculata* has become established at a number of sites in the southern United States, including Texas rice-growing areas, where farmers are adjusting their management practices to control populations (Howells & Smith 2002); and *Melanoides tuberculata* reduces native snail diversity in Utah streams (Rader et al. 2003).

Results from the CART analysis of natural-history characteristics for the Great Lakes were straightforward: species with fecundities >162 offspring/female/year were categorized as nuisances five out of six times, whereas species with lower fecundities were always categorized as benign (Fig. 1a). No characteristics other than fecundity were included in the tree. This tree has an estimated misclassification rate of 1 in 15 (7%). Jackknife analysis gave a misclassification rate of 20%, with the splitting point of fecundity ranging from a minimum of 119.5 (*Valvata piscinalis* removed) to a maximum of 190 (*B. tentaculata* removed). Although larger data sets are preferable for CART analysis, the simplicity of this result (i.e., using only one predictor variable) suggests that overfitting was not a problem. Logistic regression also showed that annual fecundity was the only natural-history
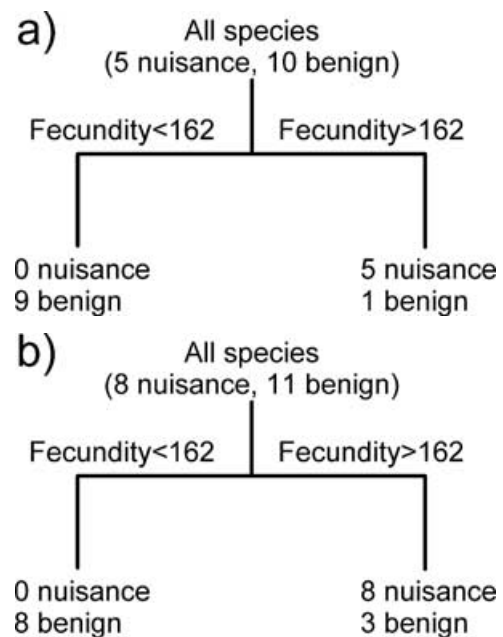

Figure 1. Decision trees for determining whether a freshwater mollusc species will be a nuisance (i.e., cause economic and/or environmental harm) or benign, produced with categorical and regression tree analysis, for (a) the Laurentian Great Lakes basin and (b) the 48 contiguous states of the United States. For the Great Lakes analysis fecundity was one of eight predictor variables (Table 2) but the only one chosen by the model. For the U.S. analysis fecundity was the only predictor used. Fecundity is the annual number of eggs or live offspring released per female.

characteristic significantly predictive of nuisance status for the Great Lakes ($p = 0.002$, $c = 0.960$; Fig. 2). As for CART, none of the other seven natural-history variables was significantly associated with nuisance status.

Time since establishment was significantly related to nuisance status in the Great Lakes based on logistic regression ($p = 0.022$, $c = 0.815$), but in a counterintuitive direction; species that recently established were more likely to cause impacts. This result is supported by CART, which split the data once at 35.5 years ago. All four species that became established more recently than this (i.e., after 1970) have become a nuisance, whereas only 1 out of 14 species established before 1970 was classified as nuisance, giving an estimated misclassification rate of 1 in 18 (6%). Under jack-knife analysis the split always occurred at 35.5, except when *C. fluminea* was removed and it became 31.5. The jack-knife misclassification rate was identical to that of the full model (6%).

The effect of fecundity on nonindigenous mollusc nuisance status for the 48 contiguous states, estimated with CART, was identical to those for the Great Lakes and had a misclassification rate of 3 in 19 (16%) (Fig. 1b). All eight species with fecundities <162 were benign, whereas 8 of the 11 with higher fecundities were nuisance species. Jack-knife analysis gave a misclassification rate of 32%, with the splitting point ranging from a fecundity of 119.5 (*Valvata* piscinalis removed) to 1505.5 (*p. antipodarum* or *M. tuberculata* removed). According to logistic regres-
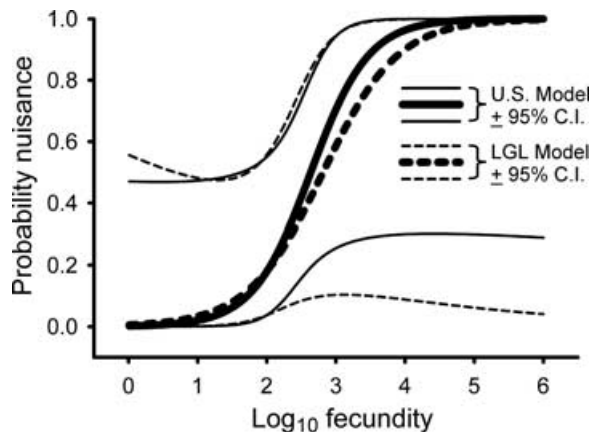
sion fecundity was significantly related to impact for the contiguous 48 states ($p < 0.001$, $c = 0.923$). The logistic relationships between probability of invasiveness and fecundity were similar for the Great Lakes and for the 48 contiguous states (Fig. 2). The close relationship between results for the two geographic regions is not surprising given that the Great Lakes data set is a subset (except for species native to the U.S. but not the Great Lakes, Table 1) of the U.S. data set. Hence, these should not be interpreted as independent analyses.

For the United States as a whole we failed to detect a significant effect of time since establishment on nuisance status (logistic regression, $p = 0.238$). This was consistent with results from CART in which species established for <47 or >78.5 years were classified as benign. Other species were classified as nuisance species and the tree had a high misclassification rate of 7 out of 23 (30%). We did not attempt further analysis of this result because it included multiple splits in a single continuous predictor variable, making any interpretation difficult, especially considering the small sample size ($n = 23$ observations). We therefore concluded that nuisance status was not significantly related to time since establishment at the scale of the 48 contiguous United States.

Sensitivity analyses based on logistic regression showed that no single family was driving the significance of the logistic relationship at either the Great Lakes or U.S. level. The greatest increase in p value for each geographic scale occurred when the family Dreissenidae was removed, but this did not affect significance at either the Great Lakes ($p = 0.025$, $c = 0.933$) or continental U. S. ($p = 0.002$, $c = 0.897$) scales.

According to the logistic model 14 of the 15 species not yet in the United States pose a substantial risk (>5% chance) of harm if they become established (Table 3). The CART model predicted that 12 of the 15 species would become nuisance species. Several species pose extremely high risks to the contiguous United States according to the logistic model, including *Bulinus globosus*, a gastropod species native to tropical Africa, *Physa fontinalis*, a gastropod native to Europe, and *Indoplanorbus exustus*, a gastropod native to the Asian subcontinent (Table 3). These species are also predicted to be nuisances by the CART model, but because CART produces simple nodes we could not determine the relative likelihood of a species becoming a nuisance compared with other species within its node. For the Great Lakes the largest risks were posed by *Physa fontinalis*, a snail species native to Eurasia, and *Planorbis contortus*, a snail species native to Europe.

Nine of the 15 tested species have geographic ranges that suggested they would not establish in the Great Lakes (Table 3). Examples of these species are *Biomphalaria straminea*, a species native to the Caribbean (Pointier et al. 1991), and *Indoplanorbus exustus,* a species native to South and Southeast Asia that laboratory studies show

Figure 2. Logistic curves ($\pm$95% CI) showing the relationship between fecundity and probability of becoming a nuisance (i.e., causing economic and/or environmental harm) for molluscs in the Laurentian Great Lakes (LGL) and 48 contiguous states of the United States. For the Great Lakes analysis eight predictor variables were used; fecundity was the only significant one. For the U.S. analysis, fecundity was the only variable used. Fecundity is the annual number of eggs or live offspring released per female.

has a lower temperature tolerance of 15° C (Parashar & Rao 1985).

Discussion

Our results show that information about one relatively simple piece of natural history—fecundity—is sufficient to explain the likelihood of economic and/or environmental consequences of freshwater molluscs should they become established. The risk posed by a freshwater mollusc species likely to be transported in any pathway can be assessed based on its fecundity, with the clear implication that high-risk species should be kept out of trade in pathways in which species are specifically marketed (e.g., aquarium trade, aquaculture trade, live-food trade). The implications for the management of risk in pathways that do not discriminate on the basis of species (e.g., ballast, snails hitch-hiking on watergarden plants) are less straightforward. For all pathways, however, the relative risks should guide the magnitude of investment in both prevention and any post-establishment management.

The importance of fecundity as a predictor of impact is not surprising (e.g., Baker 1974; Kolar & Lodge 2001; Marchetti et al. 2004). Furthermore, McMahon (2002) suggested that invasive freshwater species are likely to have higher fecundities and lower resistance to environmental extremes than native species. Although data are not available to statistically test the resistance hypothesis, our results are the first to provide quantitative support that mollusc fecundity is positively linked to impact. In contrast, a number of species traits often linked to undesirable impacts (e.g., history of establishment beyond the native range, latitudinal range; Kolar & Lodge 2001) were not predictive for molluscs in the Great Lakes.

Our results also showed that for the Great Lakes (but not for the 48 contiguous United States) recently established molluscs are more likely to cause harm than species that have been established for a long time. This is surprising because many nuisance species are known to have long lag times before population densities increase and they have impacts (Crooks & Soulé 1999). Nevertheless, we observe that recently introduced molluscs in the Great Lakes generally have high fecundities and vulnerable juvenile stages (e.g., *Dreissenid* veligers). It is possible that these species have been entering pathways for a long time but have only recently been able to survive passage because travel times, particularly of intercontinental ships, have been reduced. Such a pattern of increased harm from recently established species is also consistent with the "invasional meltdown" hypothesis (Simberloff & Von Holle 1999; Ricciardi 2001). Although time since establishment is significantly related to the likelihood that a species has undesirable impacts, this character is not useful for predicting the outcome of future introductions. Our result

does, however, indicate that there are increasing benefits to be gained from preventing new species of freshwater molluscs becoming established in the Great Lakes.

Implications for Risk Assessment and Risk Management

The fact that two different statistical techniques related mollusc fecundity to nuisance status increases our confidence that this relationship can reasonably be applied in risk assessment. Because the two models give different types of predictions and because this will inevitably lead to some species being classified in different ways depending on the model used, it is necessary to choose a preferred model, or some combination of models, to apply as a predictive scheme. If one selects the logistic models, a risk threshold must be set. Determining the acceptable level of risk is a policy decision that must be informed by many considerations in addition to those presented here. If an acceptable risk of harm (should a species become established) is set at 1 in 20, then in the United States all species with fecundities >25/year should be excluded (Fig. 2), implying prohibition of all 15 species we screened (Table 3). At the same acceptable risk of harm for the Great Lakes, the result is even more conservative: all species with fecundities >17/year should be excluded (Fig. 1). One in 20 is not a particularly conservative risk threshold compared with thresholds set for other environmental hazards. For example, California requires special labeling and handling of products that have a > 1:100,000 chance of causing human cancers over 70 years of exposure (OEHHA 2006). Finally, we reiterate that the 15 test species were chosen on the basis of availability of reliable fecundity data, and they may not be a representative sample of species likely to be introduced to the United States in the future.

Although the ROC results (i.e., c values) indicate a strong relationship between fecundity and impact, the confidence intervals for these predictions were large (Fig. 2). Many, however, did not include probabilities of <0.05, which, as we suggest above, would be a reasonable upper limit of acceptable risk. Hence, consideration of confidence limits on the estimated probabilities would still support unambiguous management recommendations. By contrast, application of the CART models at both spatial scales is straightforward: species with annual fecundities >162 should be excluded and others permitted. This corresponds to a threshold of acceptable risk based on the logistic model for the Great Lakes of 25% and for the United States of 27%.

Although fecundity data are often not readily available, future risk assessments based on our results will be possible. Once a threshold of acceptable risk is specified, surrogate data often will be sufficient to classify a species as acceptable or unacceptable. For instance, any broadcast spawners are likely to have a fecundity in the thousands

or greater and hence will always present a large risk. *Limnoperna fortunei* is an emerging invasive freshwater mollusc species in Asia and South America that is a broadcast spawner, so our model predicts that it poses a high risk to the United States. Likewise, *Anodonta woodiana* is a broadcast spawner and a recent invader of Europe. Although this latter species has a glochidial juvenile stage that develops by attaching to specific fish hosts, many of these hosts are present in the United States, so we consider that it also poses large risks. Similarly, apple snails (family Ampullariidae) in the genus *Pomacea* generally have minimum clutch sizes of 100 eggs. Given that they lay many clutches in a season, any species in this genus will pose a risk far >5% in the logistic model and will likely fall above the CART model threshold of 162. Hence, a broader taxonomic approach, or in some cases records of a single clutch from the species of interest, will often be sufficient to determine whether a species poses an unacceptable risk.

Ultimately, deciding on an appropriate model or combination of models for risk assessment depends on the priorities of the management agencies involved. Our models can be used singly or in combination, and we recognize that factors other than fecundity will need to be included in a working risk assessment. Although some of these additional factors will be subjective, the basis of the risk assessment would remain quantitative, making the entire process more defensible than many current risk assessments, which rely almost entirely on the judgment of the user (e.g., Orr 2003).

It is not clear how our models would perform if applied to molluscs in regions other then the United States, and such a test would require a data-gathering and modeling effort similar to ours. The results would, however, be enlightening, first, because they would determine the generality of the models presented here. Our models were developed and validated based on U.S. data, so such additional work would test whether fecundity is related to nuisance status in other regions. In addition, if fecundity were found to be associated with nuisance status in other regions, it would provide a strong validation of the models developed here. Until our models are tested for other regions it should not be assumed that they apply to molluscs outside the United States.

It would also be interesting to test our models on nuisance marine molluscs. Although we do not have sufficient data for a formal test, we have observed that many harmful marine species have very high fecundities (e.g., the gastropod *Littorina littorea*, an invader of the U.S. east coast that can produce up to 100,000 eggs/female/year [Jackson 2005]) and the bivalve *Perna viridis*, an invader of Australia, South America, and Florida that is a broadcast spawner and is therefore likely to have very high fecundity). We stress again, however, that a modeling study similar to ours would be required to quan-

titatively determine the relationship between life history and impacts for marine molluscs.

Reasons for Caution

Although our approach is consistent with many recent recommendations (Mack et al. 2000) and is a considerable advance over qualitative risk-assessment tools, there are nevertheless a number of reasons for caution. First, the number of species available to construct the models was too low to put aside a subset of species for use as an independent data set with which to test the model.

Second, because the limited number of species precluded phylogenetically independent contrasts, our results may have been driven by relationships at taxonomic levels above or below family. The fecundities of some families (e.g., Dreissenidae) indicate that higher-level relations may be influencing the results, but the fecundities of Thiaridae support our methods (see Table 1). Our sensitivity analyses, however, suggest that the significant relationships found with logistic regression are phylogenetically independent at the family level. Related to this caveat, it is possible that fecundity is correlated to another life-history variable for which data are not available. We consider this unlikely, however, given that fecundity has been related to impacts across a broad range of taxa, including plants (Richardson & Rejmánek 2004), fishes (Marchetti et al. 2004), and birds (Veltman et al. 1996).

Third, the water-quality characteristics of U.S. freshwater ecosystems have changed markedly since the first introduced molluscs became established. Changing species × ecosystem interactions make it possible that different natural history characteristics will be required in the future for species to become nuisances than for the species that have already passed through this step. Given the simplicity of our result, however, we are confident that it is robust to considerable environmental change.

Fourth, it is possible that some already established species will become nuisances in the future although they are not causing perceptible harm currently. Our models do not control for time since introduction, so species whose nuisance status has not yet become apparent would cause noise in our regression. Nevertheless, our data suggest that for the Great Lakes recent introductions are more likely to become invasive ($p = 0.022$), suggesting that our results are robust to concerns about lag times.

Finally, future nuisance molluscs could have impacts of a kind not yet seen and hence might not be identified by our model. If, for example, a disease vector becomes established, then the human-health impact would be different from all the previous invaders on which the model was built, and the predictors of that impact might also be different. *Bulinus globosus* and *Indoplanorbus exustus* are species from our test group (Table 3) that pose large

risks of economic and environmental impacts and are also intermediate hosts for schistosomiasis (Marti et al. 1985; Parashar & Rao 1985). Knowledge of such potential impacts should be cause for concern, even for species with low fecundities.

Preventing Future Invasions

Our predictions show that a number of freshwater molluscs not yet in the United States are likely to cause economic and environmental impacts should they become established. Given the enormous cost of nuisance molluscs and the fact that eradication is usually impossible, efforts to prevent the establishment of any species considered likely to become a nuisance will be the most cost-effective approach to minimizing damages such as the market (O'Neill 1997; Leung et al. 2002) and nonmarket costs (Ricciardi et al. 1998) of zebra mussel (*D. polymorpha*), quagga mussel (*D. bugensis*), and Asian clam (*C. fluminea*). Prevention requires that species be assessed before introduction, a difficult task given the variety of potential sources of freshwater molluscs. The problem of risk analysis is further complicated by changing patterns of world trade (Drake & Lodge 2004). New trading routes and products will inevitably lead to new suites of species that need to be assessed. Nevertheless, identification of possible nuisance species before introduction will usually provide a more logistically feasible and economical option than attempting to keep out all molluscs or eradicating those that become established.

The statistical approach to risk analysis of nuisance species that we have described is more rigorous and transparent than the methods currently used by U.S. agencies (e.g., Orr 2003). Risk assessment of species proposed for importation to the United States is rarely conducted, and the methods used are largely qualitative (Orr 2003). Although this allows more information to be considered, it is not transparent or repeatable, qualities that policy-determining risk assessments should have (Mack et al. 2000). We believe that statistical approaches should be used in combination with the more species-specific, qualitative, expert analysis typically used by United States, and state agencies.

When species are found to pose an unacceptable risk according to a statistical model (e.g., Reichard & Hamilton 1997; Kolar & Lodge 2002; our model), additional information and expert opinion should be assembled before a policy decision is made. This is the process we followed when predicting likelihood of Great Lakes invasion. The same applies to apparently low-risk species, especially with respect to an evaluation of potential impacts unlike those considered in model building. Finally, a policy decision must consider potential benefits as well as the potential harms that a species may impose on society (e.g., value to the pet industry). In practice, however, at least in the United States, these sorts of commercial ben-efits are already given priority, whereas the probability of harms identified by the model presented here are often ignored. Our hope is that quantitative risk assessment models like ours will make possible more balanced evaluations of costs and benefits of nonindigenous species and the pathways that deliver them.

Acknowledgments

Literature Cited

Baker, F. C. 1898. The mollusca of the Chicago area: the Pelecypoda. The Natural History Survey, Chicago.

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics **5:**1–24.

Cohen, A., and J. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science **279:**555–558.

Colautti, R. I., and H. J. MacIsaac. 2004. A neutral terminology to define 'invasive' species. Diversity and Distributions **10:**135–141.

Cowie, R. H. 1998. Patterns of introduction of nonindigenous nonmarine snails and slugs in the Hawaiian Islands. Biodiversity and Conservation **7:**349–368.

Cowie, R. H., and D. G. Robinson. 2003. Pathways of introduction of nonindigenous land and freshwater snails and slugs. Pages 93–122 in G. Ruiz and J. T. Carlton, editors. Invasive species: vectors and management strategies. Island Press, Washington, D.C.

Crooks, J. A., and M. E. Soulé. 1999. Lag times in population explosions of invasive species: causes and implications. Pages 103–125 in O. T. Sandlund, P. J. Schei, and A. Viken, editors. Invasive species and biodiversity management. Kluwer Academic Publishers, Dordrecht, The Netherlands.

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology **81:**3178–3192.

Dillon, R. T., A. R. Wethington, J. M. Rhett, and T. P. Smith. 2002. Populations of the European freshwater pulmonate *Physa acuta* are not reproductively isolated from American *Physa heterostropha* or *Physa integra*. Invertebrate Biology **12:**226–234.

Drake, J. M., and D. M. Lodge. 2004. Global hot spots of biological invasions: evaluating options for ballast-water management. Proceedings: Biological Sciences Series B (print) **271:**575–580.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24:**38–49.

Grigorovich, I. A., A. V. Korniushin, and H. J. MacIsaac. 2000. Moitessier's pea clam *Pisidium moitessierianum* (Bivalvia, Sphaeriidae): a cryptogenic mollusc in the Great Lakes. Hydrobiologia **435:**153–165.

Grigorovich, I. A., A. V. Korniushin, D. K. Gray, I. C. Duggan, R. I. Colautti, and H. J. MacIsaac. 2003. Lake Superior: an invasion coldspot. Hydrobiologia **199:**191–210.

Hall, R., J. Tank, and M. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Frontiers in Ecology and the Environment **1:**407–411.

Horne, F., T. Arsuffi, and R. Neck. 1992. Recent introduction and potential botanical impact of the giant rams-horn snail, *Marisa cornuarietis* (Pilidae), in the Comal springs ecosystem of central Texas. The Southwestern Naturalist **37:**194–214.

Howells, R. G., and J. W. Smith. 2002. Status of the applesnail *Pomacea canaliculata* in the United States. In T. Wada, Y. Yusa, R. C. Joshi, and A. I. S. Ghesquiere, editors. The seventh international congress on medical and applied malacology. Available from http://pestalert.applesnail.net (accessed July 2006).

Jackson, A. 2005. *Littorina littorea*. Common periwinkle. Marine life information network, biology and sensitivity key information sub-programme. The Marine Biological Association, Plymouth, Devon, United Kingdom. Available from http://www.marlin.ac.uk/species/Littorinalittorea.htm (accessed February 2006).

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution **16:**199–204.

Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science **298:**1233–1236.

Lach, L., and R. H. Cowie. 1999. The spread of the introduced freshwater apple snail *Pomacea canaliculata* (Lamarck)(Gastropoda: Ampullariidae) on O'ahu, Hawai'i. Bishop Museum Occasional Papers **58:**66–71.

Leung, B., D. M. Lodge, D. Finnoff, 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: Biological Sciences **269:**2407–2413.

Levine, J. M., and C. M. D'Antonio. 2003. Forecasting biological invasions with increasing international trade. Conservation Biology **17:**322–326.

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.

Mackie, G. L. 2000. Ballast water introductions of mollusca. Pages 219–254 in R. Claudi and J. H. Leach, editors. Nonindigenous freshwater organisms: vectors, biology and impacts. Lewis Publishers, Boca Raton, Florida.

Marchetti, M. P., P. B. Moyle, and R. Levine. 2004. Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. Freshwater Biology **49:**646–661.

Marti, H. P., M. Tanner, A. A. Degremont, and T. A. Freyvogel. 1985. Studies on the ecology of *Bulinus globosus*, the intermediate host of *Schistosoma haematobium* in the Ifakara area, Tanzania. Acta Tropica **42:**171–187.

McMahon, R. F. 2002. Evolutionary and physiological adaptations of aquatic invasive animals: *r* selection versus resistance. Canadian Journal of Fisheries and Aquatic Sciences **59:**1235–1244.

Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research **19:**1–54.

OEHHA (Office of Environmental Health Hazard Assessment). 2006. Proposition 65: process for developing safe harbor numbers. OEHHA, Sacramento, California. Available from www.oehha.ca.gov/ (accessed August 2006).

O'Neill, C. R. 1997. Economic impact of zebra mussels—results from the 1995 national zebra mussel information clearinghouse study. Great Lakes Research Review **3**(1):35–42.

Orr, R. 2003. Generic nonindigenous aquatic organisms risk analysis review process. Pages 415–438 in G. M. Ruiz and J. T. Carlton, editors. Invasive species: vectors and management strategies. Island Press, Washington, D.C.

Parashar, B. D., and K. M. Rao. 1985. Effect of temperature on growth, reproduction and survival of freshwater snail, *Indoplanorbis exustus* (Gastropoda: Pulmonata), vector of schistosomiasis. Archiv fur Hydrobiologie **102:**379–386.

Pointier, J., J. Torraft, and M. Lefevre. 1991. Life tables of freshwater snails of the genus *Biomphalaria* (*B. glabrata, B. alecandrina, B. straminea*) and of one of its competitors *Melanoides tuberculata* under laboratory conditions. Malacologia **33:**43–54.

Quinn, G. P., and M. J. Keough 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, United Kingdom.

Rader, R., M. Belk, and M. Keleher. 2003. The introduction of an invasive snail (*Melanoides tuberculata*) to spring ecosystems of the Bonneville Basin, Utah. Journal of Freshwater Ecology **18:**647–657.

Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Conservation Biology **11:**193–203.

Rejmánek, M., D. M. Richardson, S. I. Higgins, M. J. Pitcairn, and E. Grotkopp. 2005. Ecology of invasive plants: state of the art. Pages 104–161 in H. A. Mooney, R. N. Mack, J. A. McNeely, L. E. Neville, P. J. Schei, and J. K. Waage, editors. Invasive alien species: a new synthesis. Island Press, Washington, D.C.

Ricciardi, A. 2001. Facilitative interaction among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Canadian Journal of Fisheries and Aquatic Sciences **58:**2513–2525.

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.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions **6:**93–107.

Richardson, D. M., and M. Rejmánek. 2004. Conifers as invasive aliens: a global survey and predictive framework. Diversity and Distributions **10:**321–331.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions **1:**21–32.

Solow, A. R., and C. J. Costello. 2004. Estimating the rate of species introductions from the discovery record. Ecology **85:**1822–1825.

Therneau, T. M., and B. Atkinson. 2005. Rpart: recursive partitioning. R package. Version 3.1–22. Mayo Foundation for Medical Education and Research, Rochester, Minnesota. Available from http://cran.r-project.org/src/contrib/Descriptions/rpart.html (accessed November 2005).

Turgeon, D. D., et al. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: molluscs. American Fisheries Society, Bethesda, Maryland.

Veltman, C. J., S. Nee, and M. J. Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. The American Naturalist **147:**542–557.

WHO (World Health Organization). 2002. Schistosomiasis: strategic direction for research. WHO, Geneva.

Williamson, M. H. 1996. Biological invasions. Chapman & Hall, London.

Williamson, M. H. 1999. Invasions. Ecography **22:**5–12.

Zaranko, D., D. Farara, and F. Thompson. 1997. Another exotic mollusc in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). Canadian Journal of Fisheries and Aquatic Sciences **54:**809–814.